Prairie pioneers : ecology, history and culture : proceedings of the Eleventh North American Prairie Conference held 7-11 August 1988, Lincoln, Nebraska. 1989

Lincoln, Nebraska: University of Nebraska printing, 1989

https://digital.library.wisc.edu/1711.dl/MMFVKHYDJRJ328Z

PROCEEDINGS OF THE ELEVENTH NORTH AMERICAN PRAIRIE CONFERENCE

PRAIRIE PIONEERS: ECOLOGY, HISTORY, AND CULTURE

Thomas B. Bragg and James Stubbendieck, Editors

NORTH AMERICAN PRAIRIE CONFERENCES

The Eleventh North American Prairie Conference was the most recent of a series of biennial meetings begun in 1968. Through the Fifth Conference, these meetings were referred to as Midwest Prairie Conferences. Reflecting the broadening interest in native grassland and savanna, later meetings have been termed North American Prairie Conferences.

The previous Conference Chairs constitute the only "organization" for the Prairie Conferences. This group, or as many of the group as possible, meets at some time during each Conference to determine the host for the next North American Prairie Conference. Other than this, there is neither a central organization nor a budget. Coordination between the present and previous Conference Chairs has proven adequate to organize each meeting; local financial assistance has been used to meet required expenses.

Listed below are the chairs of the prairie conferences to date. In addition, a listing of all previous conferences is given in the suggested citation format, except for additional information which is included in brackets.

PREVIOUS CONFERENCE CHAIRS:

1st. Peter Schramm
2nd. James H. Zimmerman
3rd. Lloyd C. Hulbert
4th. Mohan K. Wali
5th. David C. Glenn-Lewin and Roger Q. Landers.
6th. Ralph E. Ramey
7th. Clair L. Kucera
8th. Richard Brewer
9th. Richard H. Pemble
10th. Arnold Davis, Geoffrey Stanford, and Madge Lindsay
11th. Thomas B. Bragg and James Stubbendieck

NORTH AMERICAN PRAIRIE CONFERENCES:

FIRST: Schramm, Peter, Editor. 1970. *Proceedings of a Symposium on Prairie and Prairie Restoration*. Knox College Biological Field Station Special Publication No. 3. 14-15 September 1968, 66 pages. [For proceedings, contact Peter Schramm, Knox College, Galesburg, Illinois 61401. $5.50 (US) payable to "Peter Schramm".]

SECOND: Zimmerman, James H., Editor. 1972. *Proceedings of the Second Midwest Prairie Conference*. 18-20 September 1970, 242 pages. [Published by the editor. For proceedings, contact James H. Zimmerman, 2114 Van Hise Ave., Madison, Wisconsin 53705. $8.50 (US) payable to "James H. Zimmerman".]

THIRD: Hulbert, Lloyd C., Editor. 1973. *Third Midwest Prairie Conference Proceedings*. Division of Biology, Kansas State University, Manhattan, Kansas 66506. 22-23 September 1972, 91 pages. [For proceedings, make check for $6.00 (US) payable to "Division of Biology".]

FOURTH: Wali, Mohan K., Editor. 1975. *Prairie: A Multiple View*. The University of North Dakota Press, Grand Forks, North Dakota 58202. 19-21 August 1974, 433 pages.

Pemble, Richard.H., Ronald L. Stuckey, and Lynn E. Elfner. 1975. *Native Grassland Ecosystems East of the Rocky Mountains in North America: A Preliminary Bibliography*. University of North Dakota Press, Grand Forks, North Dakota 58202. 466 pages. [A supplement to the proceedings.]

[Make check for proceedings (Prairie: A Multiple View) for $10.00 plus postage and, for supplement, $7.00 (US) + postage, to "University of North Dakota Press".]

FIFTH: Glenn-Lewin, D.C. and Roger Q. Landers Jr., Editors. 1978. *Proceedings of the Fifth Midwest Prairie Conference*. Extension Courses & Conferences, Iowa State University, Ames, Iowa 50011. 22-24 August 1976, 230 pages. [For copies, contact D.C. Glenn-Lewin, Department of Botany; $3.50 (US) postpaid with checks payable to "Botany Department Educational Fund".]

SIXTH: Stuckey, Ronald L. and Karen J. Reese, Editors. 1981. *The Prairie Peninsula — In the "Shadow" of Transeau: Proceedings of the Sixth North American Prairie Conference*. Ohio Biological Survey Biological Notes No. 15. 12-17 August 1978, 278 pages. For proceedings, make checks for $12.50 (US) + postage to "Ohio Biological Survey", 484 W. 12th Ave., Columbus, Ohio 43210.

SEVENTH: Kucera, Clair L., Editor. 1983. *Proceedings of the Seventh North American Prairie Conference*. Southwest Missouri State University, Springfield, Missouri 65804. 4-6 August 1980, 321 pages. [For proceedings, contact Wallace R. Weber, Department of Biology, with checks for $10.00 (US) postpaid payable to "Southwest Missouri State University".]

EIGHTH: Brewer, Richard, Editor. 1983. *Proceedings of the Eighth North American Prairie Conference*. Department of Biology, Western Michigan University, Kalamazoo, Michigan 49008. 1-4 August 1982, 176 pages. [For proceedings, contact Department of Biology with check for $22.00 (US) payable to "Western Michigan University".]

NINTH: Clambey, Gary K. and Richard H. Pemble, Editors. 1986. *The Prairie - Past, Present and Future: Proceedings of the Ninth North American Prairie Conference*. Tri-College University Center for Environmental Studies. 29 July - 1 August 1984, Moorhead, Minnesota. 264 pages. [For proceedings, contact Richard H. Pemble; make check for $20.00 (US) postpaid payable to "Tri-College University", 306 Ceres Hall, North Dakota State University, Fargo, North Dakota 68105.]

TENTH: Davis, Arnold and Geoffrey Stanford, Editors. 1988. *The Prairie - Roots of Our Culture; Foundation of our Economy: Proceedings of the Tenth North American Prairie Conference*. Native Prairie Association of Texas. 22-26 June 1986, Texas Woman's University, Denton, Texas. 334 pages. [For proceedings make check for $35.50 (US) postpaid to "Native Prairies Association of Texas", 7575 Wheatland Road, Dallas, Texas 75249.]

ELEVENTH: Bragg, Thomas B. and James Stubbendieck, Editors. 1989. *Proceedings of the Eleventh North American Prairie Conference*. University of Nebraska, 7-11 August 1988. [For proceedings, make check for $20.00 (US) postpaid payable to 11th North American Prairie Conference and mail to 11th North American Prairie Conference, ATTN: Tom Bragg, Department of Biology, University of Nebraska at Omaha, Omaha, Nebraska 68182-0040.

PROCEEDINGS OF THE ELEVENTH NORTH AMERICAN PRAIRIE CONFERENCE

Prairie Pioneers: Ecology, History and Culture

Held 7-11 August 1988, Lincoln, Nebraska.

Edited by
THOMAS B. BRAGG
Department of Biology, University of Nebraska at Omaha, Omaha, NE 68182
and
JAMES STUBBENDIECK
Department of Agronomy, University of Nebraska–Lincoln, Lincoln, NE 68583

1989

University of Nebraska Printing, Lincoln, Nebraska

Proceedings of the Eleventh North American Prairie Conference. Prairie Pioneers: Ecology, History, and Culture. ISBN 0-939870-00-3

Printed by University of Nebraska Printing, Lincoln, Nebraska

CONTENTS

REVIEWERS

Roger C. Anderson, Illinois State University
Royce E. Ballinger, University of Nebraska-Lincoln
Robert F. Betz, Northeastern Illinois University
Ardell J. Bjugstad, USDA/Forest Service, South Dakota
Chuck H. Butterfield, University of Nebraska-Lincoln
Leslie D. Burger, University of Missouri
Paul A. Christiansen, Cornell College, Iowa
Calvin L. Cink, Baker University
Gary K. Clambey, North Dakota State University
Mary Clausen, Nebraska Natural Heritage Program
Paul J. Currier, Platte River Whooping Crane Habitat Maintenance Trust
Arnold G. Davis, Prairie Restoration, Texas
C. L. Dewald, USDA/ARS, Oklahoma
Bohdan Dziadyk, Augustana College, Illinois
Thomas A. Eddy, Emporia State University, Kansas
John Faaborg, University of Missouri
Herbert G. Fisser, University of Wyoming
Theresa Flessner, University of Nebraska-Lincoln
Michael I. Fritz, Nebraska Natural Heritage Program
F. Robert Gartner, South Dakota State University
Richard W. Gray, Jr., Nebraska Department of Roads
John A. Harrington, University of Wisconsin - Madison
Evelyn A. Howell, University of Wisconsin-Madison
James R. Holler, University of Wisconsin-Platteville
Peter W. Jacoby, Texas A&M Univ. Agricultural Res. and Ext.
Anne Joyce, Manitoba Naturalists Society
Anthony Joern, University of Nebraska-Lincoln
Donald W. Kaufman, Kansas State University
Robert B. Kaul, University of Nebraska-Lincoln
Keith Lawrence, University of Nebraska-Lincoln
Mark K. Leach, University of Wisconsin-Madison
James H. Locklear, Nebraska Statewide Arboretum
Mark J. Loeschke, Iowa Department of Natural Resources
Kim A. Lutz, Pennsylvania Heritage Program
Robert A. Masters, University of Nebraska-Lincoln
Lowell E. Moser, University of Nebraska - Lincoln
J. Jeff Mullahey, University of Nebraska-Lincoln
Harold G. Nagel, Kearney State College
Arthur Ode, University of Nebraska-Lincoln
John A. Pearson, Iowa Department of Natural Resources
Steven J. Rothenberger, Midland Lutheran College
Jana J. Smith, University of Nebraska-Lincoln
Allen A. Steuter, The Nature Conservancy
David M. Sutherland, University of Nebraska at Omaha
Richard K. Sutton, University of Nebraska-Lincoln
Charles A. Taylor, Jr., Texas Agricultural Experiment Station, Sonora
Gary C. Trottier, Canadian Wildlife Service
Kenneth P. Vogel, University of Nebraska-Lincoln
Steven S. Waller, University of Nebraska-Lincoln
Gayle Weinstein, Denver Botanic Gardens
Gary D. Willson, U.S. National Park Service

PREFACE

"The scenery of the prairie is striking and never fails to cause an exclamation of surprise. The extent of the prospect is exhilarating. The outline of the landscape is beautiful; the absence of shade, and consequent appearance of profusion of light, produce a gaiety which animates the beholder."

Quote by Judge James Hall (ca 1839)
John Madson's "Where the Sky Began — Land of the Tallgrass Prairie".

The original prairies, consisting of a variety of types of communities, stretched east and west across the middle portion of North America and from southern Canada southward into Texas. In addition to the diverse plant communities, this ecosystem included immense herds of bison and elk accompanied by grizzly bear, wolves, and a host of other animals. As the natural ecosystem became increasingly modified with the arrival of european settlers, the size and number of extant prairie decreased until today, many of the original prairies exist only as patches in a matrix of agricultural land. Preserving and managing these patches, as well as some larger systems, such as the Kansas Flint Hills or the Nebraska Sandhills, has become the focus of considerable efforts across the prairie region. The North American Prairie Conferences, of which these Proceedings represent the eleventh meeting, are designed to provide a time and place for discussions on all aspects of prairie.

From 7 to 11 August 1988, 405 prairie enthusiasts, from 25 states and 3 Canadian provinces, met on the campus of the University of Nebraska - Lincoln to join in the exchange of experiences and knowledge about North American prairies. The selection of the University of Nebraska is especially appropriate since the study of grassland ecology in North America has its roots there in the work of such eminent researchers as Charles E. Bessey, Frederic E. Clements, and John E. Weaver. Bessey and Clements were, themselves, "prairie pioneers" as they laid the foundation for the study of grassland ecosystems from which arose many basic ecological concepts. Weaver followed in their footsteps, earning a reputation as one of the foremost grassland ecologists of North America. The tradition of prairie ecology continues in Nebraska today with many individuals, professional and amateur, working on a variety of aspects of basic ecology, management, and preservation of tallgrass, mixed, shortgrass, and sandhills prairie ecosystems.

The four-day, conference included 103 papers with a diverse range of subjects from categories including basic ecology, restoration, management, landscaping, and prairie culture. As with previous conferences, it included pre- and post conference field trips to a variety of grassland habitats. Keynote addresses by Gerald Tomanek, Frances Kaye, Roger Welsch, and Dick Whetsell provided additional diversity and expertise to the conference as did a Photography and a Landscape Design competition. Abstracts of all the contributed papers were published in an abstract booklet which was available to all conference registrants. A few Abstract booklets are still available at a cost of $3.00 postpaid (make check to 11th North American Prairie Conference and mail to Tom Bragg, Department of Biology, University of Nebraska at Omaha, Omaha, NE 68182-0040).

This volume, the *Proceedings of the Eleventh North American Prairie Conference,* contains, in manuscript form, 55 papers. Each of the manuscripts has been reviewed by one or more persons outside the editorial staff. Reviewers are listed on page vi. We appreciate their careful reviews, constructive criticism, and prompt response. We also thank the authors who provided prompt, responsive revisions, even when such revisions required substantial modifications of the original manuscript. A special acknowledgement is given to Sue Peterson for her extraordinary efforts in retyping manuscripts and preparing them in the final computer disk form.

The North American Prairie Conferences provide opportunities not only for the exchange of ideas but also for establishing or renewing friendships. This is an important aspect of the conference and the loss of a frequent participant is noticed. Such a loss occurred with the death of Dr. Lloyd C. Hulbert on 23 May 1986. He was both a source of many ideas and a friend to many of us. His contributions to prairie ecology have yet to be fully realized. In recognition of his work, the planning committee unanimously agreed that these proceedings should be dedicated to him. A special section, starting on page ix, is intended both to recognize his many contributions and to serve as a reminder of what can be accomplished by those who are dedicated, enthusiastic, and proficient.

Thomas B. Bragg
James Stubbendieck
6 October 1989

Lloyd C. Hulbert
1918-1986

PROCEEDINGS DEDICATION

Because we have and will yet all benefit from his vision, leadership, and unselfish efforts, it is fitting that these Proceedings be dedicated to Lloyd C. Hulbert, Professor of Biology, Plant Ecologist for the Kansas Agricultural Experiment Station, and Director of the Konza Prairie Research Natural Area.

Born 27 June 1918 in Lapser, Michigan, Lloyd Hulbert received his Bachelor's degree (Wildlife Conservation) from Michigan State University in 1940 and his Ph.D. (Botany, Plant Ecology) from Washington State University in 1953 where he worked under Dr. R. F. Daubenmire. In the mid-1940's, he worked variously for the U.S. Forest Service in range reseeding research in Montana and as an active ''smoke jumper''. His experiences as a smoke jumper fueled a subsequent interest in the role of fire in natural ecosystems which became a major focus of his research in later years. During the 1940's, he also held a variety of academic assignments as an Instructor in Botany and Mathematics at Montana State University and at the University of Minnesota.

In 1955, Lloyd joined the Kansas State faculty as an Assistant Professor of Botany earning subsequent promotions to Associate and Full Professor. During his tenure at Kansas State University, Lloyd held teaching and research assignments with the Division of Biology and with the Kansas Agricultural Experiment Station and he was a member of a variety of professional societies including the Ecological Society of America, Sigma Xi, Phi Kappa Phi, Botanical Society of America, American Society of Agronomy, and the Society for Range Management. His many activities included positions as Editorial Board member for the journal *Ecology,* President of the Kansas Academy of Science and Chairman of the Conservation Committee of the Academy, state representative for The Nature Conservancy, and a member of Kansas' Committee on Scientific and Natural Areas. He also organized and chaired the Third Midwest Prairie Conference in 1972.

Dr. Hulbert was internationally known for his ecological research on tallgrass prairie and prairie-forest interactions. His work, which included various studies on the effects of fire and soil in the tallgrass community, has been widely published as indicated below. Lloyd's publication list, however, does not adequately indicate his contribution to grassland ecology. Upon his arrival at Kansas State University, Lloyd began his studies on the impact of fire on the dynamics of the tallgrass prairie. However, as early as 1958 he realized that the most meaningful research would require decades rather than years of study and, therefore, a special site was needed. Such a research site, with adequate size and environmental variability, was needed so that long-term investigations could be conducted with reasonable expectation that the site would remain intact in perpetuity. This, Lloyd decided, would be his best contribution. In the 1960's, Lloyd continued his studies on the ecology of the tallgrass prairie but much of his time and energy became devoted to identifying a prairie preserve where such long term investigations could be initiated.

During the course of his search for a long-term research site, Lloyd's efforts evolved into a broader vision - a vision of a system of natural areas in Kansas that could serve as scientific controls for many types of field studies in all parts of the State. The Conservation Committee of the Kansas Academy of Science, under Lloyd's leadership, expressed this vision in "A Plan for Natural Areas in Kansas" published in the *Transactions of the Kansas Academy of Science* in 1966 (Vol. 69). Later Lloyd chaired a state *ad hoc* committee that explored the need for a system of natural areas. This committee drafted legislation to provide for the establishment of a system of natural and scientific preserves. The Kansas Legislature passed this legislation in 1974 as the Natural and Scientific Areas Preservation Act. Lloyd's efforts were crucial in the success of these efforts. His colleagues appreciated the leadership of Lloyd on committees as well as his meticulous attention to detail and his insistence on a solid basis of information to support decisions.

For more than 25 years, Lloyd contributed his biological expertise and administrative assistance towards the identification and establishment of natural areas across Kansas. His ability to judge the quality of potential sites and his assistance in expressing the rationale for natural area preservation have helped many projects, such as those directed toward the establishment of the Sand Prairie Natural History Reservation in Kansas, achieve success. The culmination of Lloyd's quest for a long-term research site, however was the acquisition and establishment of Konza Prairie Research Natural Area, 3487 ha of tallgrass prairie situated 10 km south of Manhattan, Kansas. This site, purchased with the support of The Nature Conservancy from 1971-1977, was acquired largely because of Lloyd's perseverance, dedication, and hard work. Konza Prairie was established for research purposes including the kind of long-term ecological research that Lloyd realized was so important.

With the establishment of Konza Prairie, Lloyd formulated an initial management plan and then invited fellow ecologists to participate in research at the site. Thus, he established both the general goals for Konza Prairie and the tradition of welcoming researchers with diverse interests. His foresight and planning allowed the Konza Prairie Research Natural Area to establish research programs and efforts including the Long Term Ecological Research program of the National Science Foundation and the NASA-FIFE program. In addition, Konza Prairie is a National Aeronautics and Space Administration research site, one of the sites in the National Benchmark Hydrologic Network of the U.S. Geological Survey, and it is recognized by UNESCO as a Biosphere Reserve. Konza Prairie has become the premier research site for the study of the tallgrass prairie ecosystem.

Lloyd's volunteer efforts in conservation were recognized with receipt of The Nature Conservancy's Oak Leaf Award in 1977 and their President's Stewardship Award in 1978. He was also thumously awarded the 1986 Sol Feinstone Environmental Award, a national award presented annually to only five individuals whose voluntary efforts contribute to environmental improvements.

Lloyd Hulbert was a dedicated biologist and family man. He had a special love for wildlife and conveyed that in his work with Konza Prairie. He also aimed his efforts toward benefiting humankind in its understanding of the prairie ecosystem believing that natural areas can help scientists prevent human misery through understanding land use problems and gaining insight into land management. Lloyd will be remembered by many. Those who knew him professionally will remember him, not only for his work with Konza Prairie, but also as an excellent scholar and as a teacher highly regarded by his students and his peers.

PUBLICATIONS OF L.C. HULBERT

Gibson, D.J., C.C. Freeman, and L.C. Hulbert. Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie (in preparation).

Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69(1):46-58.

Gibson, D.J. and L.C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72:175-185.

Abrams, M.D. and L.C. Hulbert. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. American Midland Naturalist 117(2):442-445.

Abrams, M.D., A.K. Knapp, and L.C. Hulbert. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: Effects of fire and topographic position. American Journal of Botany 73(10):1509-1515.

Hulbert, L.C. 1986. Fire effects on tallgrass prairie. Pages 138-142 in Proceedings of the Ninth North American Prairie Conference (G.K. Clambey and R.H. Pemble, editors). Tri-College University Center for Environmental Studies, North Dakota State University; 1984. Fargo, North Dakota.

Knapp, A.K. and L.C. Hulbert. 1986. Production, density and height of flower stalks of three grasses in annually burned and unburned eastern Kansas tallgrass prairie: A four year record. The Southwestern Naturalist 31(2):235-241.

Freeman, C.C. and L.C. Hulbert. 1985. An annotated list of the vascular flora of Konza Prairie Research Natural Area, Kansas. Transactions of the Kansas Academy of Science 88(3-4):84-115.

Knapp, A.K., M.D. Abrams, and L.C. Hulbert. 1985. An evaluation of beta attenuation for estimating aboveground biomass in a tallgrass prairie. Journal of Range Management 38(6):556-558.

Hulbert, L.C. 1985. History and use of Konza Prairie Research Natural Area. The Prairie Scout 5:63-95.

Hulbert, L.C. and J.K. Wilson. 1983. Fire interval effects on flowering of grasses in Kansas bluestem prairie. Pages 255-257 in Proceedings of the Seventh North American Prairie Conference (C.L. Kucera, editor). Southwest Missouri State University; 1980. Springfield, Missouri.

Brehm, R.W. and L.C. Hulbert. 1980. Decomposition of litter in Kansas bluestem prairie. Transactions of the Kansas Academy of Science 83(1):33-35.

Hulbert. L.C. 1978. Natural area needs for range research. Pages 263-265 in First International Rangeland Congress Proceedings (D.N. Hyder, editor). 1978. Denver, Colorado.

Hulbert, L.C. 1978. Controlling experimental bluestem prairie fires. Pages 169-171 in Fifth Midwest Prairie Conference Proceedings (D.C. Glenn-Lewin and R.Q. Landers, Jr., editors). Extension Courses and Conferences, Iowa State University; 1976. Ames, Iowa.

Dokken, D.A. and L.C. Hulbert. 1978. Effect of standing dead on stem density in bluestem prairie. Pages 78-81 in Fifth Midwest Prairie Conference Proceedings (D.C. Glenn-Lewin and R.Q. Landers, Jr., editors). Extension Courses and Conferences, Iowa State University; 1976. Ames, Iowa.

Bragg, T.B. and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29(1):19-24.

Bellah, R.G. and L.C. Hulbert. 1974. Forest succession on the Republican River floodplain in Clay County, Kansas. The Southwestern Naturalist 19(2):155-166.

Hulbert, L.C. 1973. Management of Konza Prairie to approximate pre-whiteman fire influences. Pages 14-17 in Third Midwest Prairie Conference Proceedings (L.C. Hulbert, editor). Kansas State University; 1972. Manhattan, Kansas.

Hulbert, L.C. (editor). 1973. Third Midwest Prairie Conference Proceedings. Kansas State University; 1972. Manhattan, Kansas.

Alizai, H.U. and L.C. Hulbert. 1970. Effects of soil texture on evaporative loss and available water in semi-arid climates. Soil Science 110(5):328-332.

Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. Ecology 50(5):874-877.

Robel, R.J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23(4):295-297.

Oehme, R.W., W.E. Bailie, and L.C. Hulbert. 1968. *Astragalus mollissimus* (locoweed) toxicosis of horses in western Kansas. Journal of the American Veterinary Medical Association 152(3):271-278.

Conservation Committee, Kansas Academy of Science, L.C. Hulbert (chair). 1966. A Plan for Natural Areas in Kansas. Kansas Academy of Science Transactions 69(1):1-10.

Hulbert, L.C. and F.W. Oehme. 1960. Plants poisonous to livestock. Selected plants of the United States and Canada of importance to veterinarians, lst Edition (1960; 54 pp.), 2nd Edition (1963; 102 pp), 3rd Edition (1968; 138 pp.). Kansas State University Press, Manhattan, Kansas.

Hulbert, L.C. 1963. Gates' phenological records of 132 plants at Manhattan, Kansas, 1926-1955. Transactions of the Kansas Academy of Science 66(1):82-106.

Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual bromegrasses. Ecological Monographs 25(2):181-313.

TALLGRASS PRAIRIE REMNANTS OF EASTERN NEBRASKA

Judith F. Boettcher and Thomas B. Bragg
Department of Biology, University of Nebraska at Omaha,
Omaha, Nebraska 68182-0040

Abstract. Ten eastern Nebraska tallgrass prairie remnants were evaluated up to four times during the 1979 growing season to assess vegetative composition and the effects of mowing, topographic and size differences, and season of evaluation. Frequent mowing resulted in a reduced canopy cover of some species, such as big bluestem (*Andropogon gerardii* Vitman) (21% lower with frequent mowing), but increased cover of others, particularly the introduced species smooth brome (*Bromus inermis* Leyss. subsp. *inermis*) (35% higher cover with frequent mowing). In addition, frequent mowing resulted in a higher proportion of disturbance species. Comparing the time of mowing, canopy cover of warm-season species averaged 54% higher and cool-season species 26% lower with early summer mowing. Individual species' cover also varied by topoedaphic setting; total plant cover, grass cover, and forb cover were lowest on hilltops and south-facing slopes. Additionally, canopy cover of individual species varied throughout the growing season with total plant cover and the total number of species highest in the August evaluation. A significant, positive correlation ($P = 0.05$, $r = 0.44$) was found between remnant prairie size and the number of species.

Key Words. prairie, tallgrass, management, mowing, Nebraska

INTRODUCTION

Weaver (1965) described the floristic composition of several eastern Nebraska tallgrass prairie remnants and identified nearly 250 species in lowlands and 200 species in uplands. Dominant grasses included big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Andropogon scoparius* Michx.), indiangrass [*Sorghastrum nutans* (L.) Nash], switchgrass (*Panicum virgatum* L.), reed canary grass (*Phalaris arundinacea* L.), prairie cordgrass (*Spartina pectinata* Link), and porcupine-grass (*Stipa spartea* Trin.). Kentucky bluegrass (*Poa pratensis* L.), a non-native grass species (Cronquist *et al.* 1977), occurred in upland and lowland prairies (5% frequency). Invasion of this species was attributed to its introduction by European settlers and the suppression of naturally occurring prairie fires. Flowering spurge (*Euphorbia corollata* L.), prairie phlox (*Phlox pilosa* L.), wholeleaf rosin-weed (*Silphium integrifolium* Michx.), and white prairieclover (*Dalea candida* Michx. *ex* Willd.) were some of the common forbs in these native prairies.

Prairies in eastern Nebraska once were subject both to grazing by large herbivores, such as elk (*Cervus canadensis*) and bison (*Bison bison*) (Bradbury 1819), and to burning (Long 1823, Higgins 1986). Burning continues to be used to maintain many native prairies for cattle grazing, however, many remnants in eastern Nebraska are neither grazed nor burned but rather are managed for hay production. Prairie remnants are most commonly mowed in late summer or early fall. The season and frequency with which mowing occurs, however, affects species composition and productivity. With respect to season of mowing, Hover and Bragg (1980) and Holderman and Goetz (1981) reported increases in porcupine-grass in Nebraska and needle-and-thread (*Stipa comata* Trin. & Rupr.) in western North Dakota with mid-growing season mowing. Forbs, such as soft goldenrod (*Solidago mollis* Bartl.), also increased with annual late summer mowing (Launchbaugh and Owensby 1978). On the other hand, spring mowing favored warm-season species like big bluestem and also increased total net tallgrass prairie production (Launchbaugh and Owensby 1978, Hover and Bragg 1980, Gillen and McNew 1987). With respect to effects of frequent mowing (i.e. mowing more than once during the growing season), Biswell and Weaver (1933), Weaver and Rowland (1952) and Hulbert (1969) suggested that this type of management reduced net primary production.

Topographic and edaphic heterogeneity are additional factors that are reflected in prairie remnants (Diamond and Smeins 1985). Variability in these parameters is expected to be greater in large than in small prairies thus influencing vegetative composition such that larger prairies are likely to include a greater number of species (Crockett 1964, Van der Maarel 1971). In addition, a large prairie remnant is more likely to support a greater number of dispersed populations of any one species than is a smaller remnant (Thompson 1975) so that the chance elimination of one population does not preclude the reestablishment of the species from another nearby population. In a small prairie remnant, however, with some species occurring as only a single population, a particular type of management may result in the inadvertent destruction of a population with no nearby seed source for reestablishment. Should this occur, species diversity is more likely to decrease in small prairie remnants than in large ones. Nepstad and Hoffhines (1980), for example, suggested a direct relationship between prairie size and species diversity. Similar relationships between the size of an area and species diversity have been reported for many other ecosystems including islands (Case and Cody 1987) and terrestrial landscape patches (Forman and Godron 1981), such as isolated prairie remnants surrounded by cropland.

An additional factor reflected in data obtained from prairie remnants may, in fact, be an artifact of sampling procedures. Most studies on native prairies appear to have been conducted only once during a growing season. The phenology of grassland species, however, is known to vary (Anderson and Schelfhout 1980), thus, the season of evaluation may affect the results obtained, particularly with respect to species richness.

This study was designed to provide quantitative information on the floristic composition of ten, extant native prairie remnants in eastern Nebraska and also to consider the effects of season and frequency of mowing, topoedaphic variability, prairie remnant size, and season of evaluation. The principal limitation of the study was the absence of a suitable number of replicates of each treatment due to the limited number of extant prairie remnants.

METHODS

Study Sites

In 1979, 10 native prairie remnants in Douglas and Sarpy counties in eastern Nebraska were selected for study. The specific location of each study site is available in Boettcher (1981). The bases for selection were domination by native vegetation; no evidence of cultivation, herbicide use, or interseeding; ease of access; and topoedaphic similarity. Recent management history of each prairie remnant (Table 1) was determined by contacting present landowners. Soils on all sites were deep, nearly level to steeply sloping, silty loams or silty clay loams formed in loess (Table 1). Six topoedaphic settings were separately evaluated; north-, south-, east-, and west-facing slopes, hilltops (narrow ridge tops of uplands), and broad uplands. Evaluations were conducted midslope or centered on hilltops or uplands.

Table 1. Study sites. Mowed frequently = mowed 6 or more times during a growing season. Soil Type Symbols (from Bartlett 1975): Ma = Marshall silty clay loam, Mf = Marshall silty clay loams and Ponca silt loams, Ms = Monona and Ida silt loams, C = 3-7% slopes, D = 7-11% slopes, E = 11-17% slopes, F = 17=30% slopes. Topoedaphic Settings: N = north-facing slope, S = south-facing slope, E = east-facing slope, W = west-facing slope, H = hilltop or narrow ridgetops, U = broad upland.

Site number	*Size (ha)*	*Management*	*Topoedaphic setting*	*Soil type*
1	8.5	Mowed annually in July	N,S,E	MaD
2	1.2	Mowed annually in August/September	N	MoE
3	6.9	Mowed annually in August/September	N,S	MoE
			H	MoC
4	2.0	Mowed annually in August	N,S	MoD
			H	MsE
5	2.0	Mowed frequently	N,S	MoD
6	4.9	Mowed annually in June	S	MsF
			H	MoC
7	2.0	Mowed annually in July	S	MsF
8	2.0	Mowed frequently	U	MaB
9	4.9	Mowed annually in August	W	MoD
10	18.2	Mowed annually in late August	N,E,W	MfE
			H	MaC

Vegetative Analysis

A total of 21 transects (10 m long) were evaluated. These transects included seven topoedaphic settings (Table 1), although all settings were not present at any one site. Each topoedaphic setting within a site was evaluated by dividing the area into thirds and then establishing three replicate plots centered within each third. Ten circular microplots (1 m^2) were systematically located 1 m apart on alternate sides of each 10-m transect. Vegetation within each microplot was evaluated three times during 1979: 30 May-6 June, 20-27 June, and 30 July-13 August. Some sites were also evaluated from 22-30 September depending on the time of mowing or the ability to obtain permission from landowners to establish exclosures from mowing.

Within each microplot, percent canopy cover was estimated for each species as well as for total vegetative, grass, forb, woody plant, and moss cover. Coverage categories used were: 0-5%, 5-25%, 25-50%, 50-75%, 75-95%, and >95% (Daubenmire 1959). Data were analyzed by using mid-point values of each coverage category. Floristic composition was described using two parameters, average canopy cover and frequency. Dominant species are defined as those with the highest average canopy cover value for a topoedaphic setting that also have a frequency of at least 50% within that area. Additional species were considered dominants, regardless of frequency, if their average canopy cover for a topoedaphic setting was within 10% of the species initially designated as dominant. In addition to quantitative data within each microplot, species present at a site, but not found within study plots, were recorded throughout the season. Plant identifications were verified at the University of Nebraska at Omaha Herbarium

Table 2. Maximum canopy (% ± S.E.) from the 1st, 2nd, or 3rd evaluation for north-facing slopes. Only dominants and selected species are included. tr = < 0.5% cover. Underlined values indicate the dominant species for each topoedaphic study area. A complete listing of species is available in Boettcher (1981). For scientific names, see text or Great Plains Flora Association (1986).

Floristics	*Study sites of the north-slope topoedaphic setting*					
	1	*2*	*3*	*4*	*5*	*10*
	% ± S.E.					
Total Cover	91±1.5	97±0.6	98±0.0	98±0.0	74±2.5	98±0.0
Grass Cover	83±1.6	92±1.8	89±1.1	88±1.4	73±2.5	97±0.6
Forb Cover	47±3.7	43±3.8	26±3.8	49±4.5	3±0.8	59±4.6
Woody Cover	15±4.1	2±1.2	7±1.1	71±3.3	1±0.7	8±2.4
Moss Cover	22±2.4	2±0.2	10±1.1	12±1.0	2±0.2	18±1.7
Grass and Sedges:						
big bluestem	61±2.6	57±2.9	76±3.1	48±4.2	27±2.1	0±2.1
little bluestem	6±2.2	1±0.2	0	1±tr	3±0.8	50±3.7
smooth brome	1±0.1	0	0	17±3.5	52±2.9	tr
Japanese brome	33±4.0	0	0	48±3.2	2±0.2	0
Mead's sedge	3±0.6	tr	2±0.2	tr	1±0.5	6±1.2
Kentucky bluegrass	26±2.2	43±2.9	58±1.7	29±2.1	40±3.0	34±1.6
yellow foxtail	0	0	0	0	3±0.9	0
porcupine-grass	10±2.3	12±2.9	51±7.3	27±3.9	0	18±5.4
Forbs:						
silky aster	tr	0	1±0.	0	0	1±0.5
white aster	1±0.2	10±1.8	1±0.2	3±1.4	tr	1±0.2
daisy fleabane	6±1.0	tr	tr	0	0	1±1.5
horseweed	tr	0	0	0	0	0
false sunflower	0	tr	2±0.8	33±4.9	0	0
red clover	27±3.5	6±1.0	0	0	1±0.5	25±2.2
Woody Plants:						
leadplant	4±1.4	1±1.3	7±1.5	12±2.0	1±0.7	6±1.5
New Jersey tea	11±4.1	0	0	61±4.2	0	2±2.1
Equisetum spp.:	tr	14±2.6	23±3.1	0	0	0

Table 3. Maximum canopy (% ± S.E.) from the 1st, 2nd, or 3rd evaluation for south-facing slopes. Only dominants and selected species are included. tr = < 0.5% cover. Underlined values indicate the dominant species for each topoedaphic study area. A complete listing of species is available in Boettcher (1981). For scientific names, see text or Great Plains Flora Association (1986).

Floristics	*Study sites of the south-slope topoedaphic setting*					
	1	*3*	*4*	*5*	*6*	*7*
	% ± S.E.					
Total Cover	96±0.8	91±1.2	97±0.4	76±2.6	91±1.5	94±1.4
Grass Cover	91±1.5	84±1.4	86±1.1	76±2.6	71±2.9	85±1.8
Grass Cover	91±1.5	84±1.4	86±1.1	76±2.6	71±2.9	85±1.8
Forb Cover	58±4.9	13±1.8	37±4.5	3±0.7	65±2.9	28±3.7
Woody Cover	21±4.1	17±3.6	64±6.0	1±0.7	50±3.2	18±3.9
Moss Cover	4±0.7	7±1.4	5±1.0	7±1.5	tr	1±0.2
Grasses and Sedges:						
big bluestem	54±4.6	43±3.6	44±4.9	35±4.6	34±4.5	62±3.7
little bluestem	3±0.9	4±1.8	2±0.8	3±0.8	28±3.9	18±4.4
smooth brome	21±5.6	3±0.1	40±5.8	59±1.9	tr	10±1.9
Japanese brome	29±5.0	0	41±3.3	2±0.2	0	10±2.8
Mead's sedge	2±0.5	tr	0	0	3±0.9	tr
Kentucky bluegrass	20±2.3	35±1.4	32±2.3	37±1.8	21±2.7	13±2.1
yellow foxtail	0	0	0	2±0.7	0	0
porcupine-grass	47±5.8	39±3.9	6±2.5	0	2±1.2	1±0.7
Forbs:						
white aster	tr	tr	7±2.5	tr	1±0.2	6±1.6
daisy fleabane	10±2.5	1±0.5	1±0.2	0	tr	0
horseweed	1±0.5	0	tr	tr	0	0
false sunflower	0	tr	tr	0	56±3.6	tr
red clover	40±3.9	0	0	tr	0	0
Woody Plants:						
leadplant	21±4.1	16±3.6	7±1.9	1±0.7	25±4.3	15±3.2
New Jersey tea	1±0.5	0	58±6.7	0	22±4.7	3±2.8
Equisetum spp.:	0	3±0.2	0	0	0	0

(OMA). Common and scientific nomenclature follows that in the Great Plains Flora Association (1986).

Vegetative diversity within each topoedaphic setting was calculated using the Shannon-Wiener diversity index (H'); higher values indicate higher diversity (Krebs 1978). Species richness, the total number of species present, was also calculated for each topoedaphic setting and for each site. Pearson's correlation was used to determine relationships between prairie remnant size, species richness, and species diversity (Ott 1977).

RESULTS

Floristic Composition

During the study, 153 species were recorded for all sites combined, of which 99 occurred within evaluated microplots (Boettcher 1981). Average vegetative cover for all sites varied between 60-98% with substantial seasonal variations in cover for grasses (30-98%), forbs (1-68%), woody plants (0-64%), and mosses (0-33%). Using canopy cover data from the first three evaluation periods, seven species were found to dominate (Tables 2, 3, 4, and 5). Big bluestem was the single most prevalent species occurring in all 21 of the transects evaluated, dominating in 13, and averaging a higher canopy cover in all topoedaphic settings than any other species. Kentucky bluegrass also occurred in all study areas although it dominated in only two. Porcupine-grass, a native cool-season grass, dominated in five areas and was present in all sites except one which was predominantly smooth brome. Other dominants included little bluestem, false sunflower [*Heliopsis helianthoides* (L.) Sweet var. *scabra* (Dun.) Fern.], and New Jersey tea (*Ceanothus americanus* L. var. *pitcheri* T.& G.). Leadplant (*Amorpha canescens* Pursh) and white aster (*Aster ericoides* L.) were common in all study areas although they were not dominants as defined in this study.

Mowing Management

Frequency of mowing.

Effects of mowing frequency were compared on north-facing slopes of two adjacent sites (Sites 4 and 5). These sites were similar in size and topography and thus are most likely to differ only in management. Site 5 had been mowed frequently throughout the growing season while Site 4 had been mowed only once each year in August. Total vegetative cover, grass cover, woody plant cover (primarily New Jersey tea), and forb cover averaged, respectively, 24%, 15%, 70%, and 46% lower with frequent mowing than with a single annual mowing (Tables 2 and 3). Mowing frequency also affected individual species. For example, the more frequently mowed site averaged 35% higher cover for smooth brome and 11% higher for Kentucky bluegrass, but 21% lower for big bluestem. Porcupine-grass was absent from the frequently mowed area but averaged 27% cover on the annually mowed site. In addition, disturbance species such as horseweed [*Conyza canadensis* (L.) Cronq.] and yellow foxtail [*Setaria glauca* (L.) Beauv.] were present in greater numbers on the frequently mowed areas (14 species) than on the area mowed once annually (7 species) (Boettcher 1981). Despite this increase in disturbance species, species diversity (H') was 25% lower and species richness 28% lower with frequent mowing than with annual mowing (Boettcher 1981). Similar effects on species diversity and species richness were seen both on south slopes of the same sites and on other non-adjacent sites.

Table 4. Maximum canopy (% ± S.E.) from the 1st, 2nd, or 3rd evaluation for east- and west-facing slopes. Only dominants and selected species are included. tr = < 0.5% cover. Underlined values indicate the dominant species for each topoedaphic study area. A complete listing of species is available in Boettcher (1981). For scientific names, see text or Great Plains Flora Association (1986).

Floristics	*Topoedaphic setting and study site*			
	East slope		*West slope*	
	1	*10*	*9*	*10*
	% ± S.E.			
Total Cover	93 ± 1.1	98 ± 0.0	96 ± 1.3	95 ± 0.9
Grass Cover	81 ± 1.9	98 ± 0.0	91 ± 3.1	92 ± 1.8
Forb Cover	51 ± 2.8	68 ± 4.4	39 ± 4.5	54 ± 4.3
Woody Cover	3 ± 2.6	12 ± 3.3	3 ± 0.8	7 ± 2.7
Moss Cover	5 ± 0.9	20 ± 1.7	7 ± 1.2	33 ± 3.6
Grasses and Sedges:				
big bluestem	37 ± 3.7	46 ± 5.3	69 ± 6.3	61 ± 2.9
little bluestem	4 ± 1.5	22 ± 5.2	11 ± 4.1	15 ± 2.7
smooth brome	0	0	5 ± 1.8	0
Japanese brome	9 ± 2.6	0	tr	0
Mead's sedge	3 ± 0.6	2 ± 0.5	0	3 ± 0.7
Kentucky bluegrass	13 ± 1.6	40 ± 2.6	36 ± 1.8	41 ± 1.6
porcupine-grass	41 ± 4.0	42 ± 4.9	9 ± 2.9	22 ± 3.7
Forbs:				
white aster	1 ± 0.2	5 ± 1.5	12 ± 3.8	8 ± 2.6
daisy fleabane	4 ± 0.9	4 ± 0.9	1 ± 0.5	10 ± 1.1
horseweed	1 ± 0.2	0	0	0
false sunflower	0	tr	tr	tr
red clover	20 ± 2.9	1 ± 0.5	0	0
Woody Plants:				
leadplant	13 ± 2.6	12 ± 3.3	3 ± 0.8	5 ± 1.9
Equisetum spp.:	0	3 ± 1.4	tr	0

Season of mowing.

The effects of mowing during different seasons are apparent when comparing the hilltops and south-facing slopes of Site 4, mowed in August, and Site 6, mowed in June. While general vegetative characteristics did not indicate specific trends, such trends were consistently shown by individual species for both topoedaphic settings. June mowing resulted in higher cover for little bluestem (+19%) and leadplant (+12%). Whereas, August mowing resulted in higher cover values for New Jersey tea (+44%) and porcupine-grass (+18%) (Tables 3 and 5). The design of this study was such that it is not clear whether these different treatments actually favor the species that increase or if they only indicate different degrees to which the species are adversely affected by late-season mowing. The higher amount of Japanese brome (*Bromus japonicus* Thunb. *ex* Murr.) (+24%), does, however, suggest that late-season mowing provides conditions suitable for such annual, disturbance species. Also, the high cover for the introduced grass, smooth brome (40% for August mowing; trace for June mowing), suggests that late-season mowing results in conditions that encourage the expansion of this species into native prairie.

Topography

Using average values combined for each transect for each topoedaphic setting, total vegetative cover, grass cover, and forb cover averaged respectively 92%, 83% and 30% lower on hilltops and south-facing slopes than on other topoedaphic settings (Tables 3 and 5). Of the dominant species, big bluestem averaged highest (65%) on west-facing slopes and, in addition, averaged higher than any other species on all topoedaphic settings except the one upland site evaluated (Tables 2, 3, 4, and 5). Canopy cover of smooth brome, false sunflower, and New Jersey tea averaged highest on south slopes (22%, 19%, and 14% respectively), while little bluestem and Kentucky bluegrass cover averaged highest on uplands (33% and 67% respectively). Porcupine-grass averaged highest on east-facing (42% cover) and south-facing (43% cover) slopes. Such topographic preferences of species were also noted for individual study sites and for species other than dominants.

The complexity of the response of species to management was indicated by considering different effects of management on different topoedaphic settings. While not conclusive due to the absence of replicates, one such comparison involved the contrast in species composition of the north-facing and south-facing slopes between Site 5 (mowed frequently throughout the growing season) and Site 4 (mowed annually in August). This comparison suggested that frequent mowing favored smooth brome to the extent that it dominated both topoedaphic settings (52% and 59% cover for north-facing and south-facing slopes respectively). A single annual mowing, however, resulted in 23% higher cover for smooth brome on north-facing slopes (40% cover) than on south-facing slopes (17% cover). Frequent mowing, however, did not result in similar coverage on all topoedaphic settings for all species. Porcupine-grass and false sunflower, for example, averaged 21% and 33%, respectively, higher on north-facing than on south-facing slopes in the frequently mowed area.

Species diversity (H') and species richness were more commonly highest on east-facing slopes, hilltops, and uplands (H' = 3.79, 3.14, and 3.67, respectively) (Boettcher 1981). Such effects, however, are not reflected in data for all sites or for all seasons of the year.

Table 5. Maximum canopy (% ± S.E.) from the 1st, 2nd, or 3rd evaluation for hilltop and upland topoedaphic settings. Only dominants and selected species are included. tr = < 0.5% cover. Underlined values indicate the dominant species for each topoedaphic study area. A complete listing of species is available in Boettcher (1981). For scientific names, see text or Great Plains Flora Association (1986).

Floristics	*Topoedaphic setting and study site*				
	Hilltop			*Upland*	
	3	*4*	*6*	*10*	*8*
	% ± S.E.				
Total Cover	87 ± 2.1	92 ± 1.8	94 ± 1.0	95 ± 1.0	97 ± 0.4
Grass Cover	79 ± 2.0	81 ± 2.2	85 ± 1.9	92 ± 1.5	97 ± 1.6
Forb Cover	15 ± 2.9	25 ± 2.8	19 ± 2.5	47 ± 3.9	57 ± 4.3
Woody Cover	17 ± 4.4	47 ± 5.3	18 ± 5.3	10 ± 3.2	17 ± 4.1
Moss Cover	10 ± 2.0	5 ± 1.1	3 ± 0.6	29 ± 2.3	3 ± 0.6
Grasses and Sedges:					
big bluestem	59 ± 3.2	20 ± 4.0	74 ± 2.7	45 ± 6.4	32 ± 4.4
little bluestem	0	tr	11 ± 2.4	25 ± 4.9	33 ± 4.6
smooth brome	2 ± 1.4	40 ± 5.3	0	0	1 ± 0.6
Japanese brome	0	6 ± 1.9	0	0	0
Mead's sedge	tr	tr	tr	2 ± 0.5	3 ± 0.1
yellow foxtail	0	tr	0	0	0
porcupine-grass	15 ± 4.0	30 ± 5.7	4 ± 1.4	19 ± 3.6	3 ± 1.5
Forbs:					
white aster	1 ± 0.2	1 ± 0.7	4 ± 0.7	9 ± 2.7	1 ± 0.2
daisy fleabane	1 ± 0.2	tr	1 ± 0.2	9 ± 1.5	1 ± 0.2
horseweed	0	0	tr	0	tr
false sunflower	tr	4 ± 0.9	5 ± 1.5	tr	0
red clover	0	0	0	tr	38 ± 5.0
Woody Plants:					
leadplant	7 ± 2.1	12 ± 2.5	18 ± 3.7	20 ± 3.2	14 ± 4.1
New Jersey tea	11 ± 4.5	31 ± 5.1	0	0	0
Equisetum spp.:	0	0	0	0	tr

Seasonal Variations

Combining all sites, the general category "Total Vegetative Cover" averaged lowest in the first and highest in the fourth evaluation although forb cover averaged 11-16% higher in the third evaluation than for all others (Boettcher 1981). Differences in evaluation time also were reflected in individual species data. For example, Kentucky bluegrass, a cool-season species, averaged 3-17% higher during the first than during subsequent evaluations. On the other hand, big and little bluestem, warm-season species, averaged 11-20% and 10-15% higher, respectively, during the third than during the fourth evaluation.

Seasonal variations in species diversity were detected with the maximum diversity occurring during the first evaluation for 10 of the 21 transects (Boettcher 1981). Only the frequently mowed site (Site 5) consistently had higher diversity during the third and fourth evaluations for all topoedaphic settings. Of the 99 species present in study plots, only 65 were found in all four evaluations. Four species, hoary puccoon [*Lithospermum canescens* (Michx.) Lehm.], false dandelion [*Microseris cuspidata* (Pursh) Sch.-Bip.], prairie ragwort (*Senecio plattensis* Nutt.), and American germander (*Teucrium canadense* L.), were found only in the first evaluation. Thirteen species were present in the first, second, and third evaluations but not in the fourth: bluntleaf milkweed (*Asclepias amplexicaulis* Sm.), common milkweed (*Asclepias syriaca* L.), Mead's sedge (*Carex meadii* Dew.), purple coneflower (*Echinacea angustifolia* DC.), annual fleabane [*Erigeron annuus* (L.) Pers.], daisy fleabane (*Erigeron strigosus* Muhl. *ex* Willd.), rough false pennyroyal (*Hedeoma hispidum* Pursh), clammy ground cherry (*Physalis heterophylla* Nees), breadroot scurf-pea (*Psoralea esculenta* Pursh), white-eyed grass (*Sisyrinchium campestre* Bickn.), goatsbeard (*Tragopogon dubius* Scop.), western ironweed (*Vernonia baldwinii* Torr.), and golden alexanders [*Zizia aurea* (L.) Koch.] (Boettcher 1981). Of all the seasons available for sampling, however, mid-summer sampling was found to be the best time to locate all but a few early spring plants.

Prairie Remnant Size

The preliminary survey of remnant prairies in the Omaha area revealed that the size of extant remnants ranged from < 1 ha (not used in this study) to 18 ha with the second largest only 8 ha in size. A significant correlation ($P < 0.05$, $r = 0.44$) was found between species richness and prairie remnant size when considering both species density within study plots and the total number of species listed for the entire remnant prairie, both inside and outside of study plots (Fig. 1). No significant correlation was found between Species Diversity (H') and the size of remnant prairies.

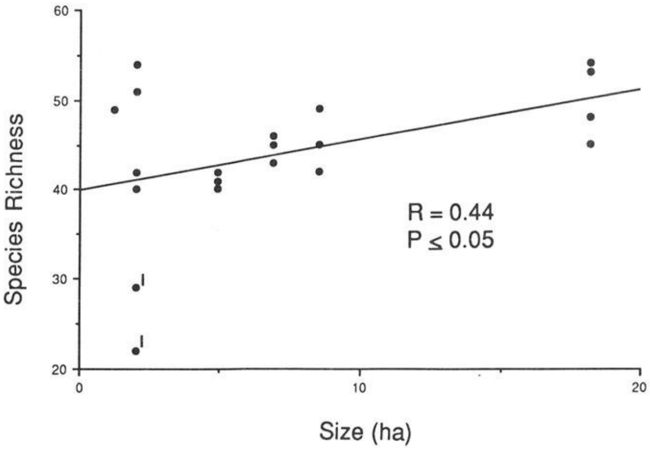


FIG 1. Species Richness and prairie size relationships for all transects (ˡareas mowed more frequently than once annually).

DISCUSSION

A comparison between the present study and an earlier study conducted approximately 80 km to the east (Weaver and Fitzpatrick 1934) suggests that species composition of prairie remnants has changed during the last 40-50 years. Big bluestem and porcupinegrass, which were both dominants circa 1934, still dominate but introduced species, such as Kentucky bluegrass, smooth brome, Japanese brome, and red clover (*Trifolium pratense* L.), are all more common than previously recorded. There also appears to have been a decline in the total number of native upland species as suggested by the difference between a total of 200 species mentioned by Weaver (1965) and the 153 identified by Boettcher (1981).

While the difference in the number of native species between 1965 and 1981 may be attributable to original site differences, this study suggests that the fewer species noted in 1981 is a consequence of different mowing management being applied during the intervening years. Frequent mowing reduced species diversity, decreased total vegetative cover, and altered composition by encouraging disturbance species or aggressive, introduced species. In addition, the season of mowing effected species composition, a conclusion also reached by Hover and Bragg (1980). Such effects clearly could explain the differences in species composition between 1965 and 1980.

Individual prairie locations were unlikely to have been identical even prior to European settlement. This study, however, suggests that differences in prairies today are more likely to reflect different types of management over the past decades than original site differences. The significance of this observation is twofold: first, extant prairie remnants are unlikely to duplicate the composition and diversity of the presettlement ecosystem, and second, future management may continue to cause prairies to degenerate as, for example, introduced species increase in number and possibly outcompete and replace native species. Natural evolutionary and environmental changes cause compositional changes over long periods of time but, for the short term, careful and continued monitoring of on-going management is essential to assess the effects of any management plan. Additionally, in those locations where it is possible to do so, consideration should be given to reestablishing the natural factors, such as the fire and large-herbivore grazing and their related frequency and intensity of occurrence, that affected ecosystem "management" prior to European settlement.

ACKNOWLEDGEMENTS

The authors express their appreciation to J.E. Bate, The Bauermeister family, H.A. Brooker, L. Enselman, A. F. Hover, M. Jensen, F. King,, B. Long, J. M. Melota, W. Stolley, E. Whitson, and the Omaha and Millard Public School Districts all of whom gave access to study sites. In addition, we also express our appreciation to Larry Boettcher and Jim Kurtz, who assisted in portions of data collection, and to Dr. David M. Sutherland, who assisted with species identification. This study fulfilled part of the requirements of the Master of Arts Degree in Biology (Plant Ecology) by the first author.

LITERATURE CITED

Anderson, R.C., and S. Schelfhout. 1980. Phenological patterns among tallgrass prairie plants and their implications for pollinator competition. American Midland Naturalist 104:255-263.

Bartlett, P.A. 1975. Soil Survey of Douglas and Sarpy Counties,Nebraska. Soil Conservation Service, U.S. Department of Agriculture, Washington, D.C.

Biswell, H.H., and J.E. Weaver. 1933. Effect of frequent clipping on the development of roots and tops of grasses in prairie sod. Ecology 14:368-390.

Boettcher, J.F. 1981. Native tallgrass prairie remnants of eastern Nebraska: Floristics and effects of management, topography, size, and season of evaluation. Master of Arts Thesis, University of Nebraska at Omaha, Omaha.

Bradbury, J. 1819. Travels in the interior of America 1809-1811. *In* R.C. Thwaits (ed.). 1905. Early western travels 1748-1846, Volume V. Arthur Clark Company, Cleveland.

Case, T.J., and M.L. Cody. 1987. Testing theories of island biogeography. American Scientist 75:402-411.

Crockett, J.J. 1964. Influence of soils and parent materials on grasslands of the Wichita Mountains Wildlife Refuge, Oklahoma. Ecology 45:326-335.

Cronquist, A., A.H. Holmgren, N.H. Holmgren, J.L. Reveal, and P.K. Holmgren. 1977. Intermountain flora: Vascular plants of the intermountain western U.S.A., Volume 6. Columbia University Press, New York.

Daubenmire, R. 1959. A canopy coverage method of vegetational analysis. Northwest Science 33:43-64.

Diamond, D.D., and F.E. Smeins. 1985. Composition, classification and species response patterns of remnant tallgrass prairies in Texas. American Midland Naturalist 113:294-308.

Forman, R.T.T., and M. Godron. 1981. Patches and structural components for a landscape ecology. BioScience 31:733-740.

Gillen, R.L., and R.W. McNew. 1987. Seasonal growth rates of tallgrass prairie after clipping. Journal of Range Management 40:342-345.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Higgins, K.F. 1986. Interpretation and compendium of historical fire accounts in the Northern Great Plains. Fish and Wildlife Service, U.S. Department of the Interior Resource Publication 161.

Holderman, C.A., and H. Goetz. 1981. Response of western North Dakota mixed prairie to intensive clipping and five stages of development. Journal of Range Management 34:188-193.

Hover, E.I., and T.B. Bragg. 1980. Effects of season of burning and mowing on an eastern Nebraska *Stipa-Andropogon* prairie. American Midland Naturalist 105:13-18.

Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. Ecology 59:874-877.

Krebs, C.J. 1978. Ecology: The experimental analysis of distribution and abundance, 2nd Edition. Harper and Row, New York.

Launchbaugh, J.L., and C.E. Owensby. 1978. Kansas rangelands: Their management based on a half century of research. Kansas Agricultural Experiment Station Bulletin 622.

Long, S.H. 1823. Expedition from Pittsburgh to the Rocky Mountains 1819-1820. *In* R.C. Thwaits (ed.). 1905. Early western travels 1748-1846, Volume XV. Arthur Clark Company, Cleveland.

Nepstad, D.C., and M. Hoffhines. 1980. An island biogeographical analysis of the flora of Southwestern Michigan fens. Page 9. *In* Abstracts of Contributed Papers, Seventh North American Prairie Conference, Southwest Missouri State University, Springfield.

Ott, L. 1977. An introduction to statistical methods and data analysis. Wadsworth Publishing Company, Belmont, California.

Thompson, P. 1975. The floristic composition of prairie stands in southern Michigan prairie. Pages 317-331. *In* M.K. Wali (ed.). Prairie: A multiple view. The University of North Dakota Press, Grand Forks.

Van der Maarel, E. 1971. Plant species diversity in relation to management. Pages 45-62. *In* E. Duffey and A.S. Watt (eds.). The scientific management of animal and plant communities. Blackwell Scientific Publications, Oxford, London.

Weaver, J.E. 1965. Native vegetation of Nebraska. University of Nebraska Press, Lincoln.

Weaver, J.E., and T.J. Fitzpatrick. 1934. The prairie. Ecological Monographs 4:109-295.

Weaver, J.E., and N.W. Rowland. 1952. Effects of excessive mulch on development, yield, and structure of native grassland. Botanical Gazette 114:1-19.

VEGETATION DYNAMICS OF THREE TALLGRASS PRAIRIE SITES

Jon K. Piper and Mark C. Gernes
The Land Institute, 2440 East Water Well Road, Salina, Kansas 67401

Abstract. As part of research to develop a sustainable agriculture that incorporates many aspects of the North American Prairie, 1) the seasonal phytomass levels supportable by native prairie and 2) how plant taxa shift in temporal importance within the community were examined. This report summarizes the first two years of a study documenting community patterns on three tallgrass prairie sites in Saline County, Kansas that differ in soil type and annual productivity. Average August phytomass at the three sites ranged from 284 to 682 g/m^2 in 1986 and from 377 to 1077 g/m^2 in 1987. Diversity declined with standing crop biomass and from spring to summer at all sites. Although big bluestem (*Andropogon gerardii* Vitman) dominated all sites, legumes represented as much as 26% of total phytomass on the poorest site. Some composite species were ubiquitous, but never constituted more than 5% of vegetation. Spring forbs and cool-season grasses were of greatest importance in April and May. The results, in concert with other ongoing research, have implications for the design of perennial seed crop mixtures suited for the Great Plains.

Key Words. diversity, legumes, production, tallgrass prairie, soil type, sustainable agriculture, Kansas

INTRODUCTION

Presently, agriculture on the North American Great Plains is characterized by extensive monocultures of annual grain crops which are subsidized largely by petroleum, synthetic fertilizers, and pesticides. The environmental and social consequences of such large-scale industrialized farming include high levels of soil loss, pesticide and fertilizer contamination of soil and groundwater, complete dependence upon finite fossil fuel resources, loss of cultural knowledge, and the depopulation of rural communities.

During settlement native species were commonly replaced with wheat [*Triticum aestivum* (L.) L.], soybean [*Glycine max* (L.) Merr.], and sorghum (*Sorghum* spp. Moench) introduced from other continents. Agroecosystems in North America were then modified to accommodate the biological requirements of these new crops.

These agroecosystems differ ecologically from the climax grasslands they replaced in many ways. The most apparent difference between the two is in degree of diversity in both space and time. Within the prairie, species use different portions of the soil volume, have different ecological roles, and the demand on both biotic and abiotic resources, is spread out over the growing season (Weaver and Fitzpatrick 1934, Parrish and Bazzaz 1976, Rabinowitz *et al.* 1981). Monocultures of annual grain crops, on the other hand, use the soil volume less efficiently, and plants' demands on environmental resources occur simultaneously. Secondly, the prairie displays tight nutrient cycles, as most nutrients are tied up in living biomass and soil organic matter (Woodmansee 1979, Knapp and Seastedt 1986). But most nutrients in monocultures are supplied externally, and are rapidly removed from the system via harvest, leaching, and erosion. Thirdly, the prairie has the sun as its primary energy source, in contrast to most temperate zone agricultural systems which rely heavily also upon human-applied fossil fuels. Lastly, because the climax prairie represents a later, rather than an earlier, successional stage, its biotic components are likely more integrated (Odum 1969, Risser *et al.* 1981).

The objectives of this research were to determine 1) relative phytomass contributions by grasses, legumes, and composites; 2) seasonal and site related variation in productivity, richness, diversity, and evenness; and 3) phenological differences among major taxonomic groups.

METHODS

Productivity and Species Composition

Research was conducted on prairie sites, Wauhob, Corner, and Hill, located in Saline County, Kansas (S5 T15S R2W, Hutchinson Quadrangle), within the western edge of the tallgrass prairie region [transition between Bluestem Prairie and Bluestem-Grama Prairie (Küchler 1974)]. The Wauhob site is on a west-facing 6-12% grade with thin Kipson shaly silt loam soil. The soil of the Corner site is a Geary silt loam and the Hill site is on a deep Longford silt loam. The Wauhob site lies approximately 640 m southwest of the Corner site; the hilltop site is located 110 m north of the Corner. The sites were grazed seasonally prior to this study. The Wauhob site was burned in April 1984 and in March 1987. The Corner and Hill sites were burned during April in 1982, 1984, and 1985 and in March 1987. Growing season (March through August) precipitation at the Salina reporting station (approximately 7 km NW of the field sites) was 54.9 cm in 1986 and 61.0 cm in 1987 (National Oceanic and Atmospheric Administration 1986 and 1987).

Aboveground live phytomass was sampled within 12 quadrats (50 x 50 cm) at each site in April, May, June, and August, 1986; and May, June, and August in 1987. The spring sampling dates coincided with the time that ephemeral forbs flower and set seed while most grasses were just emerging. August sampling corresponded to the flowering period of the dominant tall grasses and probably represents peak live phytomass on the prairie (Risser *et al.* 1981). Vegetation within each sample frame was clipped and separated by taxon, then dried at 60 C to constant mass and weighed to the nearest 0.01 g. In 1986, vegetation was divided into grasses (Gramineae), composites (Compositae), legumes (Leguminosae), and the rest (e.g. Liliaceae, Cyperaceae, Labiatae, Umbelliferae, etc.) was combined. In 1987, plants were separated by species in the field prior to drying. Species determinations followed Great Plains Flora Association (1986).

Biomass was compared between years by Student's t test, and among sites by ANOVA followed by Duncan's Multiple Range Test. In all analyses, the 0.05 significance level was used. Means in text and tables are given with ± one standard error.

From the 1987 data, richness, diversity, and evenness were calculated for each site. Richness is the cumulative number of species sampled over the season. Alpha diversity [exp(H')], a function of richness and evenness, was calculated using the Shannon-Weiner Index (H'):

$$H' = -\Sigma\, p_i \ln p_i,$$

Evenness, a measure of biomass equitability among species, is expressed:

$$E = \exp(H') - 1/(1/\Sigma\, p_i^2) - 1$$

where pi is the relative biomass of each species i (Collins 1987).

Phenology

To examine temporal differences in resource use among plant families, the sampling area and surrounding prairie was sampled biweekly from 5 April to 22 October 1987, noting during each census whether a species had emerged, flowered, or was setting seed. Plants were recorded as emerged on the first date that the species was recognizable. Thus, unfamiliar taxa may have been up for some time before their emergence was recorded.

RESULTS

Productivity and Species Composition

Total aboveground phytomass varied seasonally, among sites, and between years (Figure 1). Because of the favorable combination of spring burning and high precipitation in 1987, all sites had higher production that year. Production was highest on the Hill site in both years. Aboveground phytomass on the Wauhob site was similar in both years, except that production in June was lower in 1987 ($t = -2.70$, $p < 0.05$). In 1987, phytomass on the Hill site was greater during both May ($t = 5.52$, $p < 0.001$) and August ($t = 3.24$, $p < 0.01$) sampling periods compared with 1986. This increased production may have been due in part to the 1987 spring burning, although there were no corresponding increases at the Corner site which was also dominated by C_4 grasses.

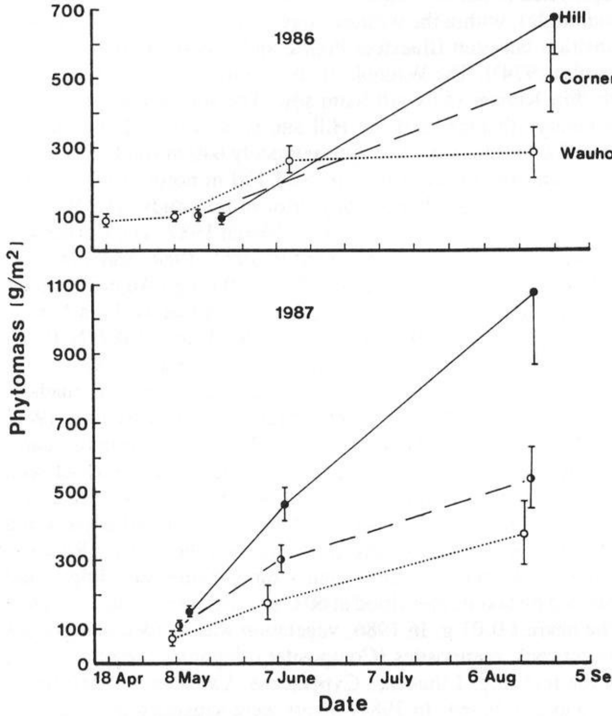


FIG. 1. Mean annual aboveground production (g/m 2) for three prairie sites in 1986 and 1987. Vertical bars denote standard errors.

Table 1. Seasonal aboveground phytomass (mean grams/m² ± S.E.) within 12 quadrats (0.25 m²) at three sites in 1986.

Site	*April*	*May*	*June*	*August*
	grams/m²			
Wauhob				
Leguminosae	8.2 ± 3.0	13.8 ± 2.2	45.0 ± 18.2	50.0 ± 24.8
Compositae	5.4 ± 2.0	4.2 ± 1.3	12.4 ± 3.0	5.5 ± 5.0
Gramineae[1]	21.6 ± 1.8	57.9 ± 5.3	152.7 ± 15.5	180.6 ± 23.4
Other	52.2 ± 4.5	21.9 ± 8.0	51.5 ± 13.3	48.0 ± 16.1
Corner				
Leguminosae	---[2]	0.0 ± 0.0	---[2]	0.0 ± 0.0
Compositae	---	11.2 ± 2.9	---	31.1 ± 9.2
Gramineae[1]	---	87.2 ± 8.1	---	460.5 ± 51.1
Other	---	5.2 ± 5.6	---	9.9 ± 7.4
Hill				
Leguminosae	---	0.0 ± 0.0	---	0.3 ± 0.3
Compositae	---	11.5 ± 3.4	---	16.7 ± 5.2
Gramineae[1]	---	74.0 ± 8.5	---	640.7 ± 52.2
Other	---	7.8 ± 3.2	---	24.3 ± 10.6

[1]Phytomass in June and August was significantly greater than in April and May ($p < 0.05$, Duncan's Multiple Range Test).

[2]Corner and Hill sites not evaluated in April and June.

In 1986, grass phytomass increased significantly from spring to summer at all sites (Table 1). The Wauhob site supported a relatively large complement of other species in April, but these declined by the May sampling date.

Richness, diversity, and evenness of species also varied among dates and sites in 1987 (Table 2). Diversity was inversely related to standing crop phytomass, reflecting relative dominance by big bluestem (*Andropogon gerardii* Vitman). This relationship held whether production was due to soil quality, burning, or season. Evenness varied less among sites.

Table 2. Richness, diversity, and evenness for three tallgrass prairie sites in 1987. Values are based on mean aboveground mass of species within 12 quadrats per site per sampling period.

Site	*Richness*	*Diversity*			*Evenness*		
		May	*June*	*August*	*May*	*June*	*August*
Wauhob	37	9.6	11.7	5.7	1.62	1.61	2.58
Corner	32	6.3	5.9	4.8	1.78	1.95	2.14
Hill	35	4.4	2.8	2.3	1.97	2.46	3.02

Although several species each contributed more than 5% of the phytomass per site per sampling period, big bluestem was the prominent species at all three sites throughout the 1987 season (Tables 3, 4, and 5). For example, its percentage phytomass varied from 33% in June on the Wauhob to 81% in August on the Hill site. The high diversity at the Wauhob site was indicated by the high proportions of many plant families: 12-26% legumes, 6-12% composites, 4-9% mints (Labiatae), and 5% lilies (Liliaceae). Several legume species contributed moderate phytomass to the Wauhob site in June, from a mean of 0.2% by wild alfalfa (*Psoralea tenuiflora* Pursh) to a mean of 8.3% by blue wildindigo [*Baptisia australis* (L.) R. Br.]. Purple prairie clover (*Dalea purpurea* Vent.) and catclaw sensitivebriar [*Schrankia nuttallii* (DC.) Standl.] contributed more than 5% of the phytomass on the Wauhob site in two successive sampling times (Table 3).

Sedges (*Carex* spp.) represented from 1-7% of phytomass on the Corner site, 2-11% on the Hill, but were virtually absent on the Wauhob. Together the C_4 grasses, big bluestem and little bluestem (*Andropogon scoparius* Michx.), constituted most of the Corner site phytomass and occurred together in every quadrat. Two sedges, *Carex gravida* Bailey and *Carex muhlenbergii* Willd., were present, but were combined due to our difficulty in separating them in their vegetative stages. Two other C_3 plants, Kentucky bluegrass (*Poa pratensis* L.) and annual bluegrass (*Poa annua* L.), did not represent more than 5% of the Corner phytomass, but singularly or together occurred in 11 of the 12 quadrats in June and all of the quadrats in August. These two bluegrasses are combined in Tables 4 and 5. Prairie goldenrod (*Solidago missouriensis* Nutt.) was the only composite that contributed more than 5% of the phytomass during any sample period.

The major contributors to the Hill site were also grasses and sedges. Here, grasses constituted 94% of vegetation in August of both years, up from 79% in May 1986 and 84% in May of 1987. In May, the C_3 bluegrasses and sedges together produced nearly half as much phytomass as did the C_4 big bluestem; in June, these C_3 taxa together produced only about 20% as much phytomass as did big bluestem (Table 5). Although species within the grass, composite, mint, spurge (Euphorbiaceae), and mallow (Malvaceae) families were sampled in all three sites during at least one of the sampling times (Tables 3, 4, and 5), the grass and composite families were the only ones represented on all sites during each sampling period.

Table 3. Seasonal aboveground phytomass (mean grams/m² ± S.E.) and frequency (%) for species sampled within 12 quadrats (0.25 m²) at the Wauhob site in 1987. Values less than 0.5 g are indicated by "tr".

Species	Phytomass			Frequency		
	May	June	August	May	June	August
	grams/m²			%		
Polygonaceae						
Polygonum aviculare	0.0±0.0	tr	tr	0.0	8.3	8.3
Malvacae						
Callirhoe alcaeoides	2.4±1.8	1.1± 0.7	0.0± 0.0	33.3	25.0	0.0
Leguminosae						
Amorpha canescens	0.0±0.0	4.2± 4.2	0.0± 0.0	0.0	8.3	0.0
Baptisia australis	5.7±5.7	21.1±15.2	1.8± 1.2	8.3	33.3	16.7
Dalea aureus	1.6±1.1	4.4± 3.7	tr	16.7	16.7	8.3
Dalea candida	0.0±0.0	0.0± 0.0	3.0± 2.2	0.0	0.0	16.7
Dalea purpurea	3.1±1.1	13.8± 5.4	11.7± 4.1	58.3	58.3	66.7
Psoralea argophylla	0.0±0.0	1.3± 1.0	0.0± 0.0	0.0	16.7	0.0
Psoralea esculenta	4.7±2.6	0.7± 0.4	0.0± 0.0	33.3	33.3	0.0
Psoralea tenuiflora	tr	tr	0.0± 0.0	25.0	16.7	0.0
Schrankia nuttallii	2.3±1.5	12.6± 4.7	16.1± 8.3	33.3	50.0	41.7
Onagraceae						
Gaura coccinia	0.0±0.0	0.0± 0.0	10.0± 9.8	0.0	0.0	16.7
Euphorbiaceae						
Euphorbia marginata	tr	tr	0.0± 0.0	16.7	16.7	0.0
Rhamnaceae						
Ceanothus herbaceous	1.2±1.2	10.2±10.2	18.8±18.8	8.3	8.3	16.7
Umbelliferae						
Lomatium foeniculaceum	tr	tr	0.0± 0.0	8.3	33.3	0.0
Labiatae						
Salvia azurea	8.2±3.8	15.1± 6.8	13.4± 4.1	58.3	66.7	83.3
Rubiaceae						
Hedyotis nigricans	0.0±0.0	0.0± 0.0	tr	0.0	0.0	16.7
Compositae						
Ambrosia psilostachya	0.6±0.2	2.0± 1.2	3.4± 1.1	66.7	66.7	75.0
Aster oblongifolius	1.5±0.5	3.4± 1.8	6.3± 2.6	66.7	50.0	58.3
Cirsium undulatum	0.0±0.0	tr	0.0± 0.0	0.0	8.3	0.0
Echinacea angustifolia	tr	1.1± 0.9	2.1± 2.0	25.0	16.7	41.7
Helianthus rigidus	3.9±2.1	4.3± 2.2	9.8± 7.2	33.3	50.0	16.7
Kuhnia eupatorioides	0.0±0.0	4.0± 4.0	0.6± 0.6	0.0	8.3	8.3
Lactuca scariola	0.0±0.0	tr	0.0± 0.0	0.0	8.3	0.0
Liatris punctata	tr	tr	0.0± 0.0	8.3	8.3	8.3
Microseris cuspidata	1.1±0.7	0.0± 0.0	0.0± 0.0	33.3	0.0	0.0
Gramineae						
Andropogon gerardii	25.8±3.2	60.1±14.6	215.9±44.7	100.0	91.7	100.0
Andropogon saccharoides	1.2±0.8	0.5± 0.4	7.0± 6.8	16.7	16.7	16.7
Bouteloua curtipendula	0.7±0.5	14.5± 3.6	23.4± 4.5	16.7	75.0	91.7
Buchloe dactyloides	tr	0.5± 0.5	2.9± 2.2	8.3	8.3	16.7
Panicum virgatum	3.2±3.2	15.3±15.3	1.6± 1.6	16.7	8.3	8.3
Liliaceae						
Allium drummondii	tr	0.0± 0.0	0.0± 0.0	75.0	0.0	0.0
Androstephium caeruleum	tr	tr	0.0± 0.0	16.7	16.7	0.0
Yucca glauca	4.7±3.9	12.0±12.0	22.5±21.1	41.7	8.3	33.3
Unknown						
Species 1	0.0±0.0	tr	0.0± 0.0	0.0	8.3	0.0
Species 2	0.0±0.0	tr	0.0± 0.0	0.0	8.3	0.0
Species 3	0.0±0.0	0.0± 0.0	0.6± 0.6	0.0	0.0	8.3

Table 4. Seasonal aboveground phytomass (mean ± S.E.) and frequency (%) for species sampled within 12 quadrats (0.25 m²) at the Corner site in 1987. Values less than 0.5 g are indicated by "tr".

Species	Phytomass			Frequency		
	May	June	August	May	June	August
	grams/m²			%		
Malvaceae						
Callirhoe alcaeoides	tr	tr	0.0 ± 0.0	33.3	41.7	0.0
Leguminosae						
Melilotus officinale	0.0 ± 0.0	tr	0.0 ± 0.0	0.0	8.3	0.0
Psoralea esculenta	0.0 ± 0.0	0.0 ± 0.0	tr	0.0	0.0	8.3
Euphorbiaceae						
Euphorbia maculata	tr	tr	tr	16.7	41.7	8.3
Oxalidaceae						
Oxalis stricta	tr	tr	tr	16.7	8.3	25.0
Oxalis violacea	0.0 ± 0.0	tr	0.0 ± 0.0	0.0	8.3	0.0
Asclepiadaceae						
Asclepias viridis	0.0 ± 0.0	tr	0.0 ± 0.0	0.0	8.3	0.0
Labiatae						
Teucrium canadense	0.0 ± 0.0	0.0 ± 0.0	tr	0.0	0.0	8.3
Compositae						
Achillea millefolium	0.0 ± 0.0	tr	0.0 ± 0.0	0.0	16.7	0.0
Ambrosia psilostachya	1.8 ± 0.7	3.6 ± 1.1	8.3 ± 4.9	100.0	83.3	83.3
Artemesia ludoviciana	tr	3.7 ± 1.4	9.8 ± 4.8	8.3	50.0	41.7
Aster ericoides	0.0 ± 0.0	3.8 ± 1.4	7.3 ± 2.6	0.0	66.7	66.7
Aster oblongifolius	2.0 ± 0.7	2.4 ± 2.2	0.0 ± 0.0	83.3	25.0	0.0
Cirsium altissimum	2.0 ± 0.9	10.4 ± 4.2	20.4 ± 13.5	75.0	75.0	33.3
Cirsium undulatum	1.6 ± 0.8	1.0 ± 1.0	0.0 ± 0.0	33.3	8.3	0.0
Liatris punctata	tr	0.0 ± 0.0	0.0 ± 0.0	8.3	0.0	0.0
Solidago missouriensis	7.0 ± 2.2	16.1 ± 4.8	4.8 ± 2.3	83.3	75.0	41.7
Taraxacum officinale	tr	0.0 ± 0.0	0.0 ± 0.0	16.7	0.0	0.0
Cyperaceae						
Carex sp.	7.0 ± 1.4	15.6 ± 2.2	6.4 ± 2.0	91.7	100.0	83.3
Cyperus esculentus	0.0 ± 0.0	tr	0.0 ± 0.0	0.0	25.0	0.0
Gramineae						
Agropyron smithii	tr	1.5 ± 0.8	0.0 ± 0.0	8.3	25.0	0.0
Andropogon gerardii	48.4 ± 7.2	145.2 ± 24.1	302.5 ± 52.6	100.0	91.7	100.0
Andropogon scoparius	20.5 ± 4.5	60.1 ± 11.4	102.6 ± 19.2	91.7	91.7	100.0
Bouteloua curtipendula	0.0 ± 0.0	0.0 ± 0.0	14.5 ± 11.7	0.0	0.0	58.3
Dichanthelium oligosanthes	8.2 ± 3.9	10.2 ± 3.0	11.3 ± 5.4	58.3	83.3	58.3
Leptoloma cognatum	0.0 ± 0.0	0.0 ± 0.0	2.1 ± 1.6	0.0	0.0	33.3
Panicum virgatum	tr	1.6 ± 0.7	8.3 ± 6.5	8.3	41.7	41.7
Poa sp.	4.5 ± 1.8	12.0 ± 2.5	20.4 ± 4.2	41.7	91.7	100.0
Sporobolus asper	4.7 ± 3.9	13.2 ± 8.0	14.9 ± 9.6	33.3	16.7	50.0
Unknown						
Species 1	0.0 ± 0.0	tr	0.0 ± 0.0	0.0	8.3	0.0
Species 2	tr	0.0 ± 0.0	0.0 ± 0.0	8.3	0.0	0.0
Species 3	0.0 ± 0.0	tr	0.0 ± 0.0	0.0	8.3	0.0

Phenology

Phenological patterns differed somewhat among predominant families. Flowering of such spring ephemerals as wild parsley [*Lomatium foeniculaceum* (Nutt.) Coult. & Rose], blue funnel lily [*Androstephium caeruleum* (Scheele) Torr.], and waveyleaf agroseris [*Microseris cuspidata* (Pursh) Sch.-Bip.] began the first week of April. By the first week of September all species had flowered or were flowering. Cumulative number of species flowering across the growing season was similar for grasses, legumes, and composites, except for an acceleration in number of composite species flowering during late summer (Figure 2). The patterns were also similar for seed set in the three families. Most grass species fruited from mid- to late summer, whereas composites showed a pulse from late summer to early autumn.

DISCUSSION

Three factors, soil type, annual precipitation, and spring burning, affect plant production on the prairie. Where soil was deep, average aboveground growth exceeded 1000 g/m² in 1987. Spring burning typically enhanced growth of prairie by removing litter and thereby increasing light and temperature at the soil surface. Spring burning in 1987 significantly increased aboveground phytomass on the Hill, but enhancement of growth was somewhat less pronounced on the other sites. Plant growth on the Wauhob site is probably limited by factors other than thickness of leaf litter.

Thirty-two to 37 species were collected within quadrats on the three sample sites in 1987. Overall, this prairie contains over 200 vascular plant species (Bender, unpublished; Piper and Gernes, unpublished) arrayed across habitats that differ in soil depth, mois-

Table 5. Seasonal aboveground phytomass (mean ± s.e.) and frequency (%) for species sampled within 12 quadrats (0.25 m²) at the Hill site in 1987. Values less than 0.5 g are indicated by "tr".

Species	Phytomass			Frequency		
	May	*June*	*August*	*May*	*June*	*August*
	grams/m²			%		
Chenopodiaceae						
Chenopodium alba	0.0±0.0	tr	0.0± 0.0	0.0	8.3	0.0
Polygonaceae						
Polygonum aviculare	0.0±0.0	0.0± 0.0	tr	0.0	0.0	8.3
Malvaceae						
Callirhoe alcaeoides	tr	0.0± 0.0	0.0± 0.0	8.3	0.0	0.0
Onagraceae						
Gaura coccinia	tr	0.0± 0.0	0.0± 0.0	8.3	0.0	0.0
Euphorbiaceae						
Euphorbia marginata	tr	0.0± 0.0	0.0± 0.0	33.3	0.0	0.0
Linaceae						
Linum sulcatum	0.0±0.0	tr	0.0± 0.0	0.0	33.3	0.0
Oxalidaceae						
Oxalis stricta	tr	tr	tr	66.7	66.7	33.3
Oxalis violaceae	tr	tr	0.0± 0.0	8.3	16.7	0.0
Asclepiadaceae						
Asclepias viridis	tr	tr	tr	8.3	8.3	8.3
Labiatae						
Teucrium canadense	0.0±0.0	tr	1.2± 1.2	0.0	16.7	8.3
Plantaginaceae						
Plantago patagonica	0.0±0.0	tr	0.0± 0.0	0.0	33.3	0.0
Compositae						
Ambrosia psilostachya	2.0±0.4	4.2± 1.5	4.2± 1.6	100.0	100.0	75.0
Artemesia ludoviciana	2.6±2.6	tr	2.9± 2.1	0.0	8.3	16.7
Aster ericoides	0.0±0.0	0.0± 0.0	tr	0.0	0.0	33.3
Aster oblongifolius	1.8±1.1	tr	0.0± 0.0	25.0	8.3	0.0
Cirsium altissimum	1.3±1.3	tr	0.0± 0.0	16.7	8.3	0.0
Cirsium undulatum	tr	0.0± 0.0	0.0± 0.0	8.3	0.0	0.0
Hieracium longiplum	0.0±0.0	tr	0.0± 0.0	0.0	8.3	0.0
Kuhnia eupatorioides	0.0±0.0	1.4± 1.1	tr	0.0	25.0	8.3
Solidago missouriensis	1.8±1.1	3.3± 1.3	11.5± 3.6	25.0	50.0	91.7
Taraxacum officinale	tr	tr	0.0± 0.0	8.3	8.3	0.0
Veronia baldwinii	tr	0.0± 0.0	12.7±12.4	8.3	0.0	16.7
Cyperaceae						
Carex sp.	16.6±4.9	45.3±11.6	24.3± 7.9	100.0	100.0	91.7
Cyperus esculentus	0.0±0.0	1.6± 1.5	0.0± 0.0	0.0	25.0	0.0
Gramineae						
Andropogon gerardii	87.4±6.0	347.0±26.5	898.5±117.5	100.0	100.0	100.0
Andropogon scoparius	1.9±0.9	3.5± 1.4	17.2± 5.6	58.3	58.3	66.7
Bouteloua curtipendula	0.0±0.0	1.6± 1.2	5.7± 2.8	0.0	25.0	41.7
Dichanthelium oligosanthes	13.1±4.0	12.7± 6.5	32.2±12.3	91.7	83.3	91.7
Koeleria pyramidata	0.0±0.0	0.0± 0.0	3.8± 3.8	0.0	0.0	8.3
Leptoloma cognatum	0.0±0.0	1.3± 1.0	7.4± 3.4	0.0	50.0	66.7
Poa sp.	19.8±3.4	25.2± 6.7	25.6± 5.3	100.0	100.0	100.0
Sporobolus asper	3.2±1.5	12.0± 4.8	29.7±10.2	58.3	66.7	75.0
Unknown						
Species 1	0.0±0.0	tr	0.0± 0.0	0.0	8.3	0.0
Species 2	0.0±0.0	0.0± 0.0	tr	0.0	0.0	8.3
Species 3	tr	0.0± 0.0	0.0± 0.0	8.3	0.0	0.0

ture, chemistry, and disturbance history. Species diversity varied both among sites and across the growing season, with a general inverse relationship between diversity and aboveground production. The Wauhob slope supported the least growth, but had the greatest diversity. Conversely, the Hill site produced more than did the Wauhob site, but the diversity was considerably lower, with only a few warm-season grasses predominating. Across the season, diversity on each site was greatest in spring (May) when standing phytomass was lowest, then declined toward peak production (August).

Grass species consistently predominated. Richness and diversity of these sites were similar to that of prairie sites studied in eastern Oklahoma (Collins 1987), although evenness here was higher. The higher diversity on the Wauhob was due principally to its poor, shallow soil which affords many forbs freedom from competition with tall grasses. Collins (1987) also found that species diversity

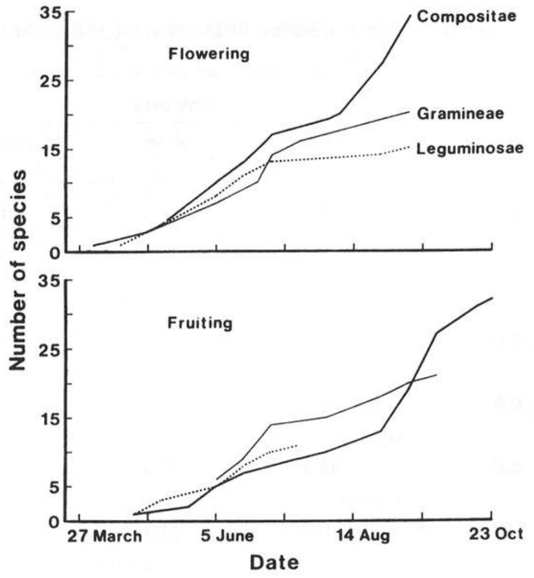


FIG. 2. Cumulative number of composite, grass, and legume species flowering and fruiting in Land Institute native prairie during 1987.

on his sites was inversely related to percentage cover by big bluestem. Although composites are widely distributed throughout the prairie, only prairie goldenrod was moderately represented in any instance.

Nitrogen-fixing legumes are integral to the nutrient dynamics of most terrestrial ecosystems. On native prairie, legumes are most common on marginal sites where soil is exposed and grasses have not formed dense stands. Although warm-season grasses dominated these three sampling areas, several legumes combined contributed as much as 26% of the phytomass on the Wauhob site. Though it may not be causally related, there was an inverse relationship between richness of legume species and dominance by grasses, especially big bluestem.

Although this study represents only two years of monitoring grassland dynamics, some consistent patterns are apparent. For example, an inverse relationship occurs between productivity of a site and plant species diversity. This means that the richest soils tend to be dominated by one or a few species, whereas poor sites appear to provide more available niches and can support a wider variety of plant species. Secondly, it was noted that the highest proportion of legumes occurs on the least fertile site. Legumes appear to be favored where soil is poor and tall grasses cannot dominate.

Relevance for Sustainable Agriculture

The dynamic stability of the prairie ecosystem arises from a complex series of adaptations and species interactions. By studying the vegetative structure and dynamics of native prairie, and using some imagination, the relevance of prairie patterns for the design and management of perennial polyculture agriculture can be explored. Such potential crops as wild rye [*Leymus racemosus* (Lam.) Tsvelev] (Barkworth and Dewey 1985), eastern gamagrass [*Tripsacum dactyloides* (L.) L.], and Illinois bundleflower [*Desmanthus illinoensis* (Michx.) MacM.] will be ecological analogs of prairie cool-season grasses, warm-season grasses, and legumes, respectively. Patterns that involve these categories of plants are particularly interesting. Plant-soil interactions, roles of soil microbes, and plant-mycorrhizal associations need to be investigated to understand better nutrient cycling across soil types and among plant communities at different successional stages.

Native prairie on marginal soils, without synthetic inputs, supported phytomass equal to or exceeding that produced by most major grain crops (Piper 1986), although harvest index is higher in annual grains. This productivity derives from the ability of warm-season perennial grasses to adapt to their environment, the tight nutrient budget with which prairie plants function (Knapp and Seastedt 1986), and the differential distribution of species' demands for resources over the growing season (Risser 1985). In many situations, C_3 and C_4 grasses co-occur with deeply-rooted forbs. Within these communities both seasonal and spatial partitionings of nutrients are feasible. Kendall (1987) has investigated whether these types of partitionings are possible in agronomic mixes involving perennial crop candidates.

Important aesthetic arguments aside, perhaps one of the most pragmatic reasons for preserving and studying native prairie is that it must serve as the only standard by which to judge the sustainability of agricultural practices in the future. Thus, long-term prairie research may turn out to be as important to agricultural science as it is to ecology. Biological patterns inherent in prairie ecosystems will appear ever more valuable as the principles of sustainable agriculture are discovered for this region.

LITERATURE CITED

Barkworth, M.E., and D.R.D. Dewey. 1985. Genomically based genera in the perennial Triticeae of North America: Identification and membership. American Journal of Botany 72: 767-776.

Collins, S.L. 1987. Interaction of disturbances in tallgrass prairie: A field experiment. Ecology 68:1243-1250.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Kendall, B. 1987. Growth and seed yield within a polyculture of *Leymus racemosus, Tripsacum dactyloides,* and *Desmanthus illinoensis*. The Land Institute Research Report 4:36-40.

Knapp, A.K., and T.R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. Bioscience 36: 662-668.

Küchler, A.W. 1974. A new vegetation map of Kansas. Ecology 55:586-604.

National Oceanic and Atmospheric Administration. 1986. Climatological data: Kansas. Volume 100.

National Oceanic and Atmospheric Administration. 1987. Climatological data: Kansas. Volume 101.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164:262-270.

Parrish, J.A.D., and F.A. Bazzaz. 1976. Niche separation in roots of successional plants. Ecology 57:1281-1288.

Piper, J.K. 1986. The prairie as a model for sustainable agriculture: a preliminary study. The Land Report Research Supplement 3:1-4.

Rabinowitz, D., J. Rapp, V. Sork, B. Rathcke, G. Reese, and J. Weaver. 1981. Phenological properties of wind and insect-pollinated prairie plants. Ecology 62:49-56.

Risser, P.G. 1985. Grasslands. Pages 232-256. *In* B.F. Chabot and H.A. Mooney (eds.). Physiological ecology of North American plant communities. Chapman and Hall, New York.

Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton, and J.A Wiens. 1981. The true prairie ecosystem. United States/International Biological Program Synthesis Series. Volume 16. Hutchinson Ross Publishing Company, Stroudsburg, Pennsylvania.

Weaver, J.E., and T.J. Fitzpatrick. 1934. The prairie. Ecological Monographs 4:109-295.

Woodmansee, R.G. 1979. Factors influencing input and output of nitrogen in grasslands. Pages 117-134. *In* N.R. French (ed.). Perspectives in grassland ecology. Springer-Verlag, New York, New York. 204 pages.

EXTENT OF WOODY VEGETATION ON THE PRAIRIE IN EASTERN NEBRASKA, 1855-1857

Steven J. Rothenberger
Department of Biology, Midland Lutheran College, Fremont, Nebraska 68025

Abstract. Early surveyors' notes from five counties bordering the Platte River in eastern Nebraska were utilized to measure the extent of original woody vegetation in this region. These data were compared to field studies from the same area made from 1979-1983, were used to determine areas of prairie-forest transition, and were used to tabulate the extent of woody vegetation in the lower Platte River Valley at the time of European settlement (1855-1857). Using a modified importance value based on relative density and relative dominance of witness trees, the highest ranking presettlement tree species were cottonwood [*Populus eltoides* Marsh. spp. *monilifera* (Ait.) Eckenw.], bur oak (*Quercus macrocarpa* Michx.), elms (*Ulmus* spp.), willows (*Salix* spp.), and black oak (*Quercus velutina* Lam.). The original survey indicated the presence of single trees and tree clusters within the original prairie vegetation of eastern Nebraska. Trees are presently more widespread, and their composition differs from the original woody vegetation. Presently, cottonwood, bur oak, American linden (*Tilia americana* L.), and rough-leaved dogwood (*Cornus drummondii* Meyer) are more common than they were 130 years ago.

Key Words. presettlement vegetation, woody vegetation, prairie-forest transition, tallgrass prairie, succession, Nebraska

INTRODUCTION

The eastern one-third of Nebraska originally consisted of tallgrass prairie. It has generally been accepted that the small amount of woody vegetation present prior to 1855 existed only along or near rivers and streams. This would have provided a rather distinct prairie-forest ecotone restricted primarily to river floodplains, terraces, or other uplands bordering rivers and streams. However, evidence does suggest the existence of savanna-like stands of trees, some of which were located in areas formerly thought to be exclusively tallgrass prairie (Rozmajzl 1988).

Invasion of woody vegetation into grassland has often been attributed to decreased fire intensity and frequency (Buell and Facey 1960, Vogl 1974, Towne and Owensby 1984, Abrams 1986, Hulbert 1986). Weaver (1960) described the ecotone between grassland and bur oak forest occurring on the upper slope of the bluffs bordering the Platte River as a "chaparral or scrub community containing wolfberry, dogwood, and prickly ash". More recent studies indicate that dense thickets of eastern red cedar (*Juniperus virginiana* L.), wild plum (*Prunus americana* Marsh.), choke cherry (*Prunus virginiana* L.), smooth sumac (*Rhus glabra* L.), and hazelnut [*Corylus americana* (L.) Walt.] were quite common along the margins of bur oak/bitternut hickory associations (Stephens 1973, Rothenberger 1985). These shrub communities are a direct result of post settlement fire exclusion, and they sometimes encroach upon the few grassy openings that still exist in this heavily cultivated region. This study was designed to compare present woody vegetation of the area with the presettlement woody vegetation as indicated by the General Land Office (GLO) records.

METHODS

Study Site

The study site included Dodge, Saunders, Douglas, Sarpy, and Cass counties in eastern Nebraska, which border the lower 96 km of the Lower Platte River above its confluence with the Missouri River (Figure 1). This part of the river valley presents an extension of oak-hickory upland forest (Braun 1950) and cottonwood-willow-elm riparian forest into the prairie. During presettlement times, these woodlands were bordered exclusively by tallgrass or true prairie. The study area was located within the Drift Hills Region of the Central Lowland Province (Figure 1) and was within the western portion of the tallgrass prairie formation (Küchler 1964). Nebraska is a transitional plains state in which the drift hills in the east give way to loess hills, sandhills, and ultimately tablelands or high plains of the Great Plains Province in the western part of the state. The study area included elevations ranging from 290 to 427 m and precipitation ranging from 74 to 80 cm per year.

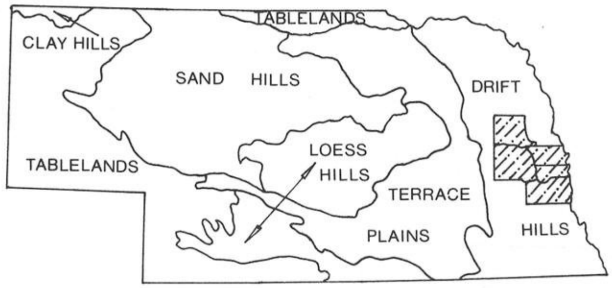


FIG 1. The physiography of Nebraska showing the five-county study site located in the Drift Hills region.

A wide variety of tills and post glacial deposits were present. Much of the five-county area was mantled with loess which is largely Medial Wisconsin in age, but Late Wisconsin loess mantled Late Wisconsin terrace deposits along many of the valley sites of the principal stream courses (Burchett and Reed 1967). The Platte River terraces and most of the adjacent uplands were capped by Peoria loess of Medial Wisconsin origin (Wayne 1985). Even though the underlying sediments and tills varied throughout the area, the overlying loess mantle formed the basis for the development of the original tallgrass prairie and adjacent woodlands along major streams and their tributaries.

Data Collection

Early GLO survey records were studied and compared to field data collected from 1979-1983 to determine the extent of original woody vegetation in a five-county study area of eastern Nebraska. The study area included Dodge, Saunders, Douglas, Sarpy, and Cass counties (Figure 1) and was selected because this area was originally composed of tallgrass prairie dissected by the Platte River (Küchler 1964). The Platte and its tributaries provided habitat conducive to the growth of woody plants in this area.

The original GLO survey occurred from 1855-1857 when significant settlement of Europeans first began in this area. Records were obtained at the county offices in Fremont, Papillion, Plattsmouth, Omaha, and Wahoo, Nebraska, and from the state surveyor's office in Lincoln. These records were in the form of original written descriptions, microfilm, and maps.

Some difficulties were encountered in interpreting certain writer's penmanship. Also, some inaccuracies due to species sampling errors and misuse of common names were probable. "Elm," "willow," and "hickory" were reported without designation as to species. "Spanish oak" (referring to *Quercus palustris* Muench.) and "white oak" (*Quercus alba* L.) were reported in the GLO survey but were not found to occur in the area of the study of 1979-1983 (Rothenberger 1985). "Hickory" was inferred to mean bitternut hickory [*Carya cordinformis* (Wang.) K. Koch.], the most common hickory in the area, and "Lynn" referred to American linden (*Tilia americana* L.). Despite these problems, the use of witness tree data and written descriptions of vegetation provided a reasonably reliable source of information for this study. The witness tree data from the survey included the number of trees and their sizes (diameter) and was used to calculate importance value, a modified value equal to the sum of the relative density and the relative dominance for each species. Importance values were calculated for each of the five separate county surveys. Botanical nomenclature follows the Great Plains Flora Association (1986).

RESULTS AND DISCUSSION

The concentration of witness trees recorded in the study area in 1855-1857 were much higher within the Platte Valley and along the uplands bordering the river than on the open grassland (Figure 2). However, some groupings of witness trees occurred on both upland and lowland sites away from the river. These small tree groves and single isolated witness trees located away from major streams and their tributaries were of special interest, because they gave evidence to the existence of some woody vegetation within the tallgrass prairie. Similar results were reported in Douglas and Washington counties, Nebraska, in which presettlement savanna relics were identified on uplands (Rozmajzl 1988). The incidence of these trees and tree "patches" was probably dependent on fire, climate, substrate, and topography (Bell and Hulbert 1974).

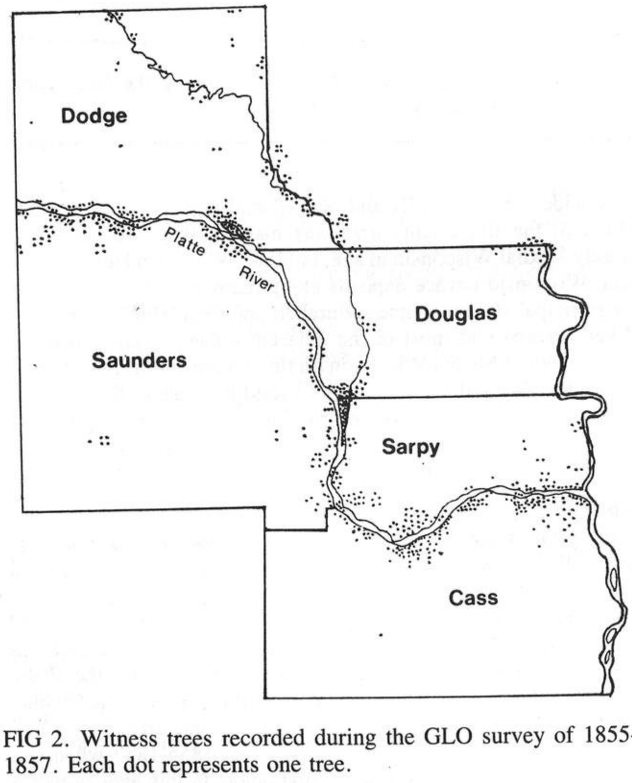


FIG 2. Witness trees recorded during the GLO survey of 1855-1857. Each dot represents one tree.

In the eastern Nebraska survey, bur oak savanna integraded sharply into tallgrass prairie on the uplands and gradually gave way to more established riparian forest types containing cottonwood [*Populus deltoides* Marsh. subsp. *monilifera* (Ait.) Eckenw.], green ash [*Fraxinus pennsylvanica* Marsh. var. *subintegerrima* (Vahl.) Fern.], willows (*Salix* spp.), and elms (*Ulmus* spp.) as the surveyors approached the Platte River. Fire-susceptible species, such as eastern red cedar, were seldom encountered. Solitary trees, most notably cottonwood, green ash, and elms are more difficult to explain but must have occurred along creeks, near wetlands, or on similar sites where they were afforded some measure of fire protection. At several locations, few witness trees were reported even though the survey notes indicated the presence of significant amounts of woody vegetation. Perhaps the survey team felt that these trees were too small to sample. Whatever the reason, the surveyors' notes did not always accurately reflect the presence of woody vegetation.

The exclusion of fire in the study area has resulted in successional changes in species composition and increases in the total amount of woody vegetation. Higher elevations on upland sites in eastern Nebraska were more open than they are now, with park-like bur oak stands interrupted by grassy areas (Lawson *et al.* 1980). In the Kansas Flint Hills, Bragg and Hulbert (1976) found prairies remaining unburned for 20 years or longer were replaced by forest on over one-half or more of their area.

During the 130-year period since the original survey, fluctuations in biotic and abiotic factors have caused inevitable changes in species composition. Table 1 compares the relative importance values of woody plants from the 1855-1857 GLO survey with those of the 1979-1983 study. Cottonwood and bur oak accounted for 73% of all witness trees reported. The high importance value for cottonwood also reflects the exceedingly large total basal area calculated for this species. Even though the GLO survey was not intended to be an ecological study, some interesting changes are noteworthy. These include:

1. Increases in fire-sensitive eastern red cedar probably because of fire suppression.
2. Increases in more mesic tree species, such as American linden, red mulberry (*Morus rubra* L.), green ash, hackberry (*Celtis occidentalis* L.), and red oak [*Quercus borealis* Michx. var. *maxima* (Marsh.) Ashe.].
3. A high incidence of rough-leaved dogwood (*Cornus drummondii* Meyer). It should be noted that rough-leaved dogwood is present in large numbers although it was only occasionally mentioned by the GLO surveyors.
4. A decrease in American elm (*Ulmus americana* L.), presumably because of Dutch elm disease (*Ceratocystis ulmi*).

A combination of factors have changed the species composition of woody vegetation in eastern Nebraska. This study indicates that, initially, trees were mostly limited to river valleys or to scattered trees or groves. Subsequent vegetative changes, resulting from fire exclusion, disease, grazing, human activities, and variable precipitation have combined to form a somewhat different woody vegetation type along the rivers and streams in the study area. These changes are likely to continue and may result in a woody plant composition even more different from that dominating the presettlement landscape.

Table 1. Total numbers and relative importance values for trees recorded during the original GLO survey compared to relative importance values of trees sampled in the study area from 1979-1983.

Species	1855-1857 Survey		1979-1983 Field Study
	Total trees	Relative importance value	Relative importance value
	--- no. ---	%	
Cottonwood [*Populus deltoides* Marsh subsp. *monilifera* (Ait.) Eckenw.]	345	55.6	12.9
Bur oak (*Quercus macrocarpa* Michx.)	177	21.3	12.0
Elm (*Ulmus americana* L.)	54	7.7	0.5
Willow (*Salix* spp.)	34	2.9	0
Black oak (*Quercus velutina* Lam.)	19	2.5	2.4
White oak (*Quercus alba* L.)	16	2.1	0
Green ash [*Fraxinus pennsylvanica* Marsh. var. *subintegerrima* (Vahl.) Fern.]	19	1.9	6.1
Pin oak (*Quercus palustris* Muench.)	4	1.0	0
American linden (*Tilia americana* L.)	4	1.0	9.9
Bitternut hickory [*Carya cordiformis* (Wang.) K. Koch]	10	0.9	2.6
Red oak [*Quercus borealis* Michx. var. *maxima* (March.) Ashe.]	6	0.7	5.0
Eastern red cedar (*Juniperus virginiana* L.)	6	0.6	5.4
Box elder (*Acer negundo* L.)	7	0.6	1.3
Silver maple (*Acer saccharinum* L.)	3	0.4	2.3
Hop hornbean [*Ostrya virginiana* (P. Mill.) K. Koch]	4	0.4	3.8
Red elm (*Ulmus rubra* Muhl.)	3	0.3	7.6
Hackberry (*Celtis occidentalis* L.)	1	0.1	5.2
Species not reported in the GLO Survey:			
Rough-leaved dogwood (*Cornus drummondii* Meyer)	0	0	9.0
Red mulberry (*Morus rubra* L.)	0	0	8.3
Black walnut (*Juglans nigra* L.)	0	0	1.4
Northern catalpa (*Catalpa speciosa* Warder)	0	0	0.8
Honey locust (*Gleditsia triacanthos* L.)	0	0	0.7
Common buckthorn (*Rhamnus cathartica* L.)	0	0	0.6
Peach-leaved willow (*Salix amygdaloides* Anderss.)	0	0	0.6
Kentucky coffee tree [*Gymnocladus dioica* (L.) K. Koch]	0	0	0.4
Black willow (*Salix nigra* Marsh.)	0	0	0.4
White mulberry (*Morus alba* L.)	0	0	0.3
Smooth sumac (*Rhus glabra* L.)	0	0	0.2
Juneberry (*Amelanchier arborea* (Michx. f.) Fern.]	0	0	0.1
Downy hawthorn [*Crataegus mollis* (T. & G.) Sheele]	0	0	0.1
Red osier dogwood (*Cornus stolonifera* Michx.)	0	0	0.1

ACKNOWLEDGMENTS

I would especially like to thank the staff and officials of Dodge, Douglas, Cass, Sarpy, and Saunders counties and the state surveyor's office in Lincoln for graciously allowing me access to records of the U.S. Land Survey. Their help was essential to this project.

LITERATURE CITED

Abrams, M.D. 1986. Historical development of gallery forests in northeast Kansas. Vegetatio 65:29-37.

Bell, E.L., and L.C. Hulbert. 1974. Effect of soil on occurrence of cross timbers and prairie in southern Kansas. Kansas Academy of Sciences Transactions 77:203-209.

Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19-24.

Braun, E.L. 1950. Deciduous forests of eastern North America. Hafner Press, New York.

Buell, M.F., and V. Facey. 1960. Forest-prairie transition west of Itasca Park, Minnesota. Bulletin of the Torrey Botanical Club 87:46-58.

Burchett, R.R., and E.C. Reed. 1967. Centennial guidebook to the geology of southeastern Nebraska. The University of Nebraska Conservation and Survey Division, Lincoln.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Hulbert, L.C. 1986. Fire effects on tallgrass prairie. Pages 138-142. *In* G.K. Clambey and R.H. Pemble (eds.). Proceedings of the Ninth North American Prairie Conference, Tri-College University, Moorhead, Minnesota.

Küchler, A.W. 1964. Potential natural vegetation of the conterminous United States. American Geographical Society, Special Publication Number 36.

Lawson, M.P., R. Heim Jr., J.A. Mangimeli, and G. Moles. 1980. Dendroclimatic analysis of bur oak in eastern Nebraska. Tree Ring Bulletin 40:1-16.

Rothenberger, S.J. 1985. Community analysis of the forest vegetation in the lower Plant River Valley, eastern Nebraska. Prairie Naturalist 17:1-14.

Rozmajzl, M.K. 1988. Presettlement oak savanna in eastern Nebraska. Master of Arts Thesis, University of Nebraska, Omaha.

Stephens, H.A. 1973. Woody plants of the North Central Plains. University Press of Kansas, Lawrence.

Towne, G., and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. Journal of Range Management 37:392-397.

Vogl, R.J. 1974. Effects of fire on grasslands. Pages 139-194. *In* T.T. Kozlowski and C.E. Ahlgren (eds.). Fire and Ecosystems. Academic Press, New York.

Wayne, W.J. 1985. Drainage patterns and glaciations in eastern Nebraska. Pages 111-117. *In* W. Dort, Jr. (ed.). TER-QUA Symposium, V. 1, Nebraska Academy of Sciences, Lincoln.

Weaver, J.E. 1960. Flood plain vegetation of the central Missouri Valley and contacts of woodland with prairie. Ecological Monographs 30:37-64.

PLANT SPECIES COMPOSITION AND GROUNDWATER LEVELS IN A PLATTE RIVER WET MEADOW

Paul J. Currier
Platte River Whooping Crane Maintenance Trust Inc., 2550 N. Diers Ave.,
Suite H, Grand Island, Nebraska 68803

Abstract. Species composition was monitored in seven permanent exclosures at Mormon Island Crane Meadows, near Grand Island, Nebraska from 1982 to 1987. Crane meadows is a 1,050 ha (2,600 acre) native lowland prairie complex with a corrugated topography of wetland swales and dry sand ridges. Variable precipitation, periodic over-bank flooding, and river stage fluctuations complicate the system's hydrology. In general, springs are wet, but, by late summer, the meadows are usually dry, closely paralleling river flows and precipitation patterns. A sustained high water period in 1983 and 1984 was responsible for major changes in species abundance. Plant responses were consistent with species distributions along the topographic moisture gradient. Species at the lower end of the gradient were subjected to the greatest fluctuation in moisture and responded the most. In wetland swales sedge (*Carex aquatilis* Wahl.), +37%; spikerush [*Eleocharis obtusa* (Willd.) J.A. Schult.], +36%; and American bulrush (*Scirpus americanus* Pers.), +14%; increased significantly during the high water period. At moderate elevations indiangrass [*Sorghastrum nutans* (L.) Nash], +22%; and switchgrass (*Panicum virgatum* L.), +24%; increased, but big bluestem (*Andropogon gerardii* Vitman), -28%; showed a significant decline. All species except switchgrass returned to their former cover when water levels declined. Groundwater levels (mean and maximum) were the most important environmental parameters associated with changes in species cover. Switchgrass, however, did not respond directly to groundwater levels. High water conditions probably promoted the expansion of this species but it was able to sustain itself under much lower subsequent moisture conditions. Big bluestem and switchgrass also increased significantly with prescribed burning.

Key Words. groundwater, plant composition, wetland, prairie, Platte River, Nebraska

INTRODUCTION AND STUDY SITE

This study was conducted at Mormon Island Crane Meadows (MICM) near Grand Island, Nebraska. Mormon Island is a 1,050 ha wet meadow complex, situated between the channels of the Platte River that is owned and managed by the Platte River Whooping Crane Critical Habitat Maintenance Trust. The Trust is a non-profit conservation organization that protects and maintains habitat for migratory birds in the 128 km reach of the Platte between Lexington and Grand Island, Nebraska. Crane Meadows is the largest contiguous grassland tract remaining on the Platte in this river reach. A few areas on the island have been plowed but the majority is virgin tallgrass prairie dominated by big bluestem (*Andropogon gerardii* Vitman), switchgrass (*Panicum virgatum* L.), and indiangrass [*Sorghastrum nutans* (L.) Nash] (Currier 1982, Nagel and Kolstad 1987). Nomenclature follows the Great Plains Flora Association (1986). Common forbs include Maximillian sunflower (*Helianthus maximillianii* Schrad.), many-flowered aster (*Aster ericoides* L.), ironweed (*Vernonia fasciculata* Michx.), and Canada goldenrod (*Solidago canadensis* L.). Prairie gentian [*Eustoma grandiflorum* (Raf.) Shinners], tall gayfeather (*Liatris pycnostachya* Michx.), sneezeweed (*Helenium autumnale* L.), and blue cardinal flower (*Lobelia siphilitica* L.) are characteristic forbs of the wet meadows. Prairie fringed orchid [*Habenaria leucophaea* (Nutt.) A. Gray], an endangered species candidate, is also present.

The meadows have a corrugated topography of ridges and swales oriented parallel to the river channel. At one time, probably several hundred years ago, the island was part of the active riverbed with the swales representing the former braided river channels and the ridges representing islands of moving sand on the alluvial bed (O'Brien and Currier 1987). Ridgetops are dominated by short-grass prairie species including little bluestem (*Andropogon scoparius* Michx.), hairy grama (*Bouteloua hirsuta* Lag.), and prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.] (Currier 1982, Nagel and Kolstad 1987). Lowland sites are dominated by sedge meadow species including sedges (*Carex spp.*), American bulrush (*Scirpus americana* Pers.), spikerush [*Eleocharis obtusa* (Willd.) J.A. Schult.], smartweeds (*Polygonum spp.*), and prairie cordgrass (*Spartina pectinata* Link). The dominant grasses, big bluestem, switchgrass, and indiangrass, occur on the intermediate slopes.

Nearly 150 species of migratory birds, about one-half of those found in the Platte River valley, use the wet meadows for nesting, feeding, and other activities (Currier *et al.* 1985). These include the endangered whooping crane, bald eagle, and least tern, the threatened piping plover, one-half million sandhill cranes, 7 to 9 million ducks and geese, and many grassland nesting species including the upland sandpiper and bobolink.

This study was initiated to provide baseline data on the interrelationships between hydrology and plants in wet meadows. The surface and ground water hydrology of the meadows is complex and not well understood. In general, major fluctuations in river discharge are reflected in groundwater levels beneath the meadows (Hurr 1983). In the spring and early summer, snow melt in the Rocky Mountains feeds the river, providing high discharge and a corresponding rise in groundwater. River flows and groundwater levels are usually low by July, and surface water has usually drained or evaporated from the meadows. Local precipitation, snow melt, and surface freezing and thawing also contribute to changes in meadow hydrology. In the spring, when surface soils are usually wet and groundwater levels high, precipitation often pools in sloughs and swales on the meadows. By summer, surface water has usually drained or evaporated, except immediately after major rainfall events.

Prescribed burning, rotation grazing, and haying are used in the management of the wet meadows at MICM to promote warm-season native prairie species and to reduce encroachment by tree and shrub species. The affects of burning inside exclosures were also examined in the study.

METHODS

Long-term vegetation composition and cover changes were monitored in this study in relation to wet meadow hydrology and grassland management. Data were sampled in six permanent, 1 m 2 plots located inside seven permanently fenced grassland areas in which cattle and haying were excluded. Each exclosure was oriented perpendicular to the ridge and swale topography. Sample plots were selected to represent a number of elevations including at least one ridge and one swale.

In late July to early August of 1982 through 1987, species composition and percent cover of each species were recorded by cover class (less than 1%, 1-5%, 6-15%, 26-50%, 51-75%, 76-100%) in the permanent plots. River discharge was monitored using records from the United States Geological Survey gauging station located near the Highway 34 bridge over the Platte River, about 13 km downstream of the study site. Groundwater levels were monitored monthly in several wells at the site by lowering a weighted tape from the top of the well casing to the water level. More frequent groundwater measurements were taken during some periods. From 1982 to 1984, Trust staff measured groundwater levels. In 1985, 1986, and 1987, well measurements were conducted by the Bureau of Reclamation. Groundwater levels were recorded at absolute elevations above sea level but for ease of analysis were converted to centimeters above elevation 578.0 m. Total monthly precipitation and average monthly temperature data were obtained from the National Weather Service for the Grand Island Station. Prescribed burns were conducted throughout the study. The percentage of permanent sample plots burned was monitored each year.

Mean cover values for each species were calculated by year (1982-1987), as were May-August values of a number of environmental parameters. The May-August period was chosen since it represented the major portion of the growing season when moisture conditions had the greatest direct influence on wet meadow plants. The environmental parameters included river discharge (total, maximum, and minimum), groundwater elevation (maximum, mean, and minimum), precipitation (total and deviation from normal), temperature (mean and deviation from normal), and whether or not an area had been recently burned. Species cover values were analyzed according to four moisture classes (wet, medium-wet, medium-dry, dry) based on elevation. The total elevational gradient of 1.8 m from swale to ridge top was divided into four equal classes representing 0.45 m. Mean cover values were compared statistically ($P < 0.05$) by year with oneway analysis of variance (ONEWAY procedure) (Norusis 1986). Tukey's test ($P < 0.05$) was used to determine which means were within the same range. When significant differences were determined, stepwise multiple regression ($P < 0.05$) was used to investigate relationships between mean cover (dependent variable) and the measured environmental parameters (independent variables).

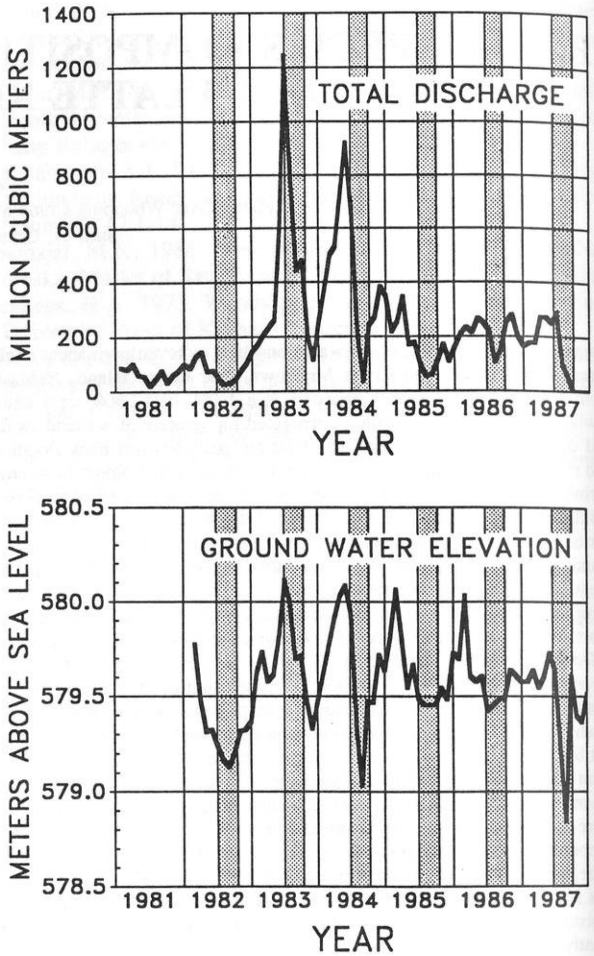


FIG. 1. Monthly river discharge and groundwater elevation during the study. Shaded areas indicate the May-August growing season.

RESULTS

During the study, precipitation and ground water elevation followed cyclical patterns with relatively low levels during fall and

Table 1. Summary of environmental parameters during the growing seasons from 1982 through 1987.

Parameters	1982	1983	1984	1985	1986	1987
	Years					
Discharge:						
Total (million m³)	182	3109	1834	395	732	696
Mean (m³/sec)	17	295	174	38	69	66
Maximum (m³/sec)	67	666	425	129	178	185
Minimum (m³/sec)	2	80	9	8	16	5
Groundwater level (cm above elevation 578.0 m):						
Mean	121	190	160	151	149	136
Maximum	132	211	208	166	160	172
Minimum	113	169	103	145	142	84
Precipitation (mm):						
Total	490	347	342	355	302	367
Deviation from Normal	+119	-8	-13	-1	-53	+11
Temperature (C):						
Mean	21.0	22.5	22.3	21.3	21.9	22.5
Deviation from Normal	-2.5	+3.8	+2.2	-1.9	+0.5	+3.0
Burning (%):						
Wet Moisture	54	54	8	46	0	0
Medium Wet Moisture	82	46	100	73	0	54
Medium Dry Moisture	23	54	54	31	46	46
Dry Moisture	100	100	100	0	0	0

winter and peaks in spring and early summer. Total precipitation was above normal in all years except 1986. Although cyclical, the timing of peak ground water levels differed between years. For instance, in 1983 and 1984, peaks occurred during the May through August growing season, while in 1985 and 1986 the peaks occurred earlier in the spring (February) and probably had little direct influence on plant growth (Figure 1). Groundwater levels in 1983 and 1984 reflected extremely high sustained flows in the Platte in mid-1983 (maximum = 666 m^3/sec) and in mid-1984 (maximum = 425 m^3/sec). Environmental conditions during the May through August growing season generally paralleled annual patterns (Table 1). Ground water and discharge were high in 1983 and 1984, while precipitation was high in 1982 and low in 1986. Temperature was relatively uniform throughout the growing season during the six years of the study.

Species Distribution

During the study, 91 species were recorded in the permanent plots. Individual species were, for the most part, distributed unimodally along a moisture gradient from swale to ridge top (Figure 2). It should be emphasized that these were general distribution patterns, since species abundance and distribution shifted along the gradient in response to environmental conditions. Water smartweed (*Polygonum amphibium* L.) was narrowly distributed in wetland sites, but other wetland species such as water sedge (*Carex aquatilis* Wahl.) and American bulrush were widely distributed. The major prairie grasses, switchgrass, indiangrass, and big bluestem had overlapping distributions in the middle of the moisture gradient, however, switchgrass was associated with wetter sites, indiangrass with intermediate sites, and big bluestem with drier sites. Redtop (*Agrostis stolonifera* L.) and smooth brome (*Bromus inermis* Leyss.), are introduced grasses that appeared along the gradient in direct competition with switchgrass and big bluestem, respectively. Many-flowered aster and common ragweed (*Ambrosia artemisiifolia* L.) were ubiquitous along the gradient. Aster was skewed towards higher elevations, while ragweed had a bimodal distribution with peaks at both high and low elevations, where disturbed sites allowed colonization.

Temporal Changes in Species Cover

Of the 91 species sampled in the study, six were chosen for detailed analysis because they showed statistically significant ($P < 0.05$, one-way ANOVA) responses from year to year (Table 2). These species included water sedge, spikerush, and American bulrush, which are characteristic of lowland sites, and indiangrass, big bluestem, and switchgrass, which dominate intermediate slopes. Species responses were similar for each of the four moisture classes (Figure 3). Sedge (+37%) and bulrush (+14%) increased substantially between 1982 and 1984, when discharge and groundwater levels also increased. Spikerush (+36%) and indiangrass (+22%) also responded positively to this wet period but they peaked early in 1983. At medium wet sites, however, sedge and spikerush continued to increase until 1985, even though groundwater and discharge levels had already declined substantially (Table 1). Following the peak cover values in 1983, 1984, and 1985;

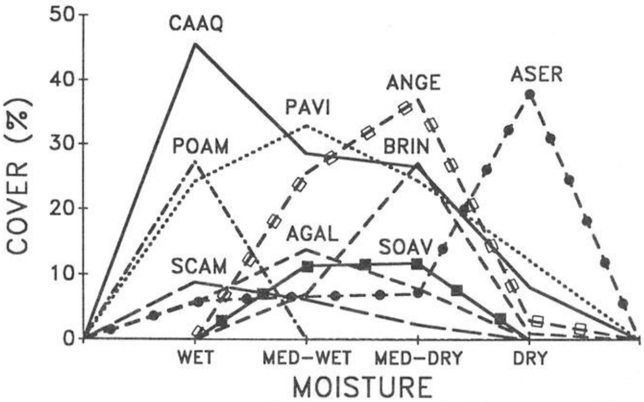


FIG. 2. Distribution of major species along the topographic (moisture) gradient. Wet represents the bottom of the swales while dry represents ridge tops. (CAAQ = water sedge, SCAM = American bulrush, POAM = water smartweed, PAVI = switchgrass, SOAV = indiangrass, ANGE = big bluestem, AGAL = redtop, BRIN = smooth brome, ASER = many-flowered aster).

Table 2. Statistically significant ($P < 0.05$, one-way ANOVA) responses of major species during the 1982-1987 period (+ = significant increase, - = significant decline). The year of peak increase or decline is provided for the overall population and for each moisture class. NS = not significant.

Species	*Overall*	*Moisture Class* Wet	*Moisture Class* Medium wet	*Moisture Class* Medium dry	*Moisture Class* Dry
Water sedge	(+) 1984	(+) 1984	(+) 1985	NS	NS
Spikerush	(+) 1983	(+) 1983	(+) 1985	(+) 1983	NS
American bulrush	(+) 1984	(+) 1984	(+) 1984	NS	NS
Indiangrass	(+) 1983	NS	(+) 1983	(+) 1983	NS
Big bluestem	(-) 1984	NS	(-) 1984	NS	NS
Switchgrass	(+) 1985	NS	(+) 1985	(+) 1984	NS

Table 3. Stepwise multiple regression equations associated with mean cover of major species during the 1982-1987 period[1]. Environmental parameters were measured during the growing season (May-August).

Water sedge	y = (27.86)(MEANGW)-(0.45)(MINQD)-18.9	$R^2 = 0.18$
Spikerush	y = (13.15)(MEANGW)-10.41	$R^2 = 0.28$
American bulrush	y = (5.57)(MAXGW)-(0.09)(MINQD)-6.39	$R^2 = 0.24$
Indiangrass	y = (7.18)(MAXGW)-8.25	$R^2 = 0.29$
Big bluestem	y = (14.68)(BURN)-(7.25)(MAXGW)+46.65	$R^2 = 0.11$
Switchgrass	y = (-0.17)(TOTPC)+(8.70)(BURN)+84.33	$R^2 = 0.20$

[1]MEANGW = mean groundwater elevation, MINQD = minimum river discharge, MAXGW = maximum groundwater elevation, BURN = percentage of plots burned, TOTPC = total precipitation.

sedge, bulrush, spikerush, and indiangrass all declined to near their former levels. Big bluestem (-28%) responded negatively to the high water period, declined until 1984, and then began to recover to its former level. Switchgrass (+24%) increased substantially between 1982 and 1985, during the high water period, but unlike the other species, it was able to maintain its increased cover after water levels declined.

Except for switchgrass, ground water parameters (mean and maximum ground water elevation) were the overriding environmental variables associated with cover changes (Table 3). Although the R^2 values for the regression equations in Table 3 are relatively low (0.11 to 0.29), the equations themselves were highly significant. This indicated that the equations could be used with confidence to identify relationships between cover changes and environmental parameters, but because of high variability (low R^2 values) in the data, the equations are not useful in predicting the exact relationship. Sedge, spikerush, bulrush, and indiangrass were positively related to high groundwater levels. Sedge and bulrush were also negatively related to minimum discharge in the river. Big bluestem was negatively related to high ground water, but positively related to burning. The decline of big bluestem from 1982 to 1984 was directly related to high ground water, but its subsequent recovery was promoted by both declining water levels and burning. Big bluestem was also negatively affected by overbank flooding in 1983 which inundated a few of the permanent plots. The duration and magnitude of the flooding, however, was not monitored.

Switchgrass cover values were not directly related to groundwater levels, but were positively related to burning and negatively related to precipitation. High ground water in 1983 and 1984 was coincident with the rapid expansion of switchgrass. When groundwater levels declined, however, there was no corresponding decline in cover. It is not immediately clear why switchgrass cover should be negatively related to precipitation.

DISCUSSION

Major changes in species cover occurred in this study following a 1-in-50 year high water period in 1983 and 1984. Unusually high soil moisture conditions were created in the wet meadows at Mormon Island during this period. Although most species responded directly to changes in mean or maximum groundwater levels, they also responded indirectly to river stage because there was a high correlation (0.89 to 0.92) between maximum, mean, and total discharge, and mean and maximum groundwater levels during the May-August growing season.

In contrast, there was little relationship between May-August precipitation and groundwater levels. Summer precipitation was fairly consistent from year to year during the study, and clearly was not the primary factor driving fluctuations in groundwater levels (Table 1). Although precipitation patterns undoubtedly affected plant growth, the high rainfall and low variability during the study probably masked any differences in species cover values.

Annual cycles in precipitation, groundwater elevation, and river discharge are common at MICM although the magnitude and timing of these fluctuations are variable and unpredictable (Figure 1). Because the elevational gradient on the island is very shallow (ranging only 1.8 m from swale to ridge top), as much as 10%-35% of the land surface can be covered by water sometime during the spring as a result of precipitation, high groundwater levels, and snowmelt. During these high moisture periods, 25% to 50% of the surface soils are saturated.

Precipitation alone, however, may have little effect on species cover depending upon the time of year and the rate of percolation and runoff. In early spring, when there is little plant growth, moisture levels may have little influence on cover values. In addition, river stage and groundwater elevation affect surface drainage and percolation, allowing water to pond on the surface of the meadows for extended periods during high water conditions. When such conditions occur during the growing season, species cover values may be significantly affected. This could be the case in this study. Some surface water ponding occurred in several areas in 1983 and 1984 when groundwater levels and river stage were high, but the duration and magnitude of these conditions were not monitored. In any case, changes in species cover were not directly related to precipitation events, but rather to the groundwater levels.

Although some level of minimal soil moisture undoubtedly is necessary to sustain wet meadow species (particularly hydrophytes such as bulrush, spikerush, and water sedge), it is uncertain whether precipitation or groundwater alone can meet this need. Further studies to determine the physiological moisture requirements of wet meadow species and the relative contributions of precipitation and groundwater are needed.

Fluctuating water levels are an important component of nearly all wetlands (Duever 1987). Because environmental conditions such as moisture levels at a site change from year to year, the vegetation is constantly adapting to a unique, new set of biological and physical conditions. Except for switchgrass, the changes observed in this study in response to the high water condition in 1983 and 1984 appear to be temporary and cyclical with species abundance returning to near pre-1983 levels within a few years. Switchgrass, in contrast, maintained its increased cover value even when water levels declined. This species may simply be more resilient to low moisture conditions and may persist for a longer period of time before declining. Between 1985 and 1987 switchgrass declined slightly (Figure 3), suggesting a slow downward trend.

Platte River wet meadows are an uncommon remnant of the once widespread complex of marshes, sloughs, and other wetlands along the river complex. Since the 1840s these wetlands have been systematically ditched, drained, and converted to cropland. The remaining wet meadows are a unique natural resource supporting lowland prairie and wetland plants, a host of vertebrate and invertebrate organisms and many species of migratory birds. Groundwater, river stage, and precipitation patterns are constantly changing, making it difficult to understand the interrelationship between these components and the response of wet meadow flora and fauna to these fluctuations. This study is a first step in outlining the complexities of the system and documenting changes in the abundance of certain wet meadow plants in relation to groundwater and surface water. Additional long-term studies to monitor surface and groundwater fluctuations and the relationships between soil moisture and the distribution and abundance of macroinvertebrates and wet meadow plants are needed before we will understand enough about the system to manage and maintain it.

ACKNOWLEDGEMENTS

The author greatly appreciates the generous contributions of Bill Whitney, Kari Lingle, Tom Labedz, Jerry Ziewitz, Maryann DeVries, John Sidle, and Mike Rodell in the collection of the field data. Thanks also to David E. Carlson, John G. VanDerwalker, and an anonymous reviewer for their constructive comments on the manuscript.

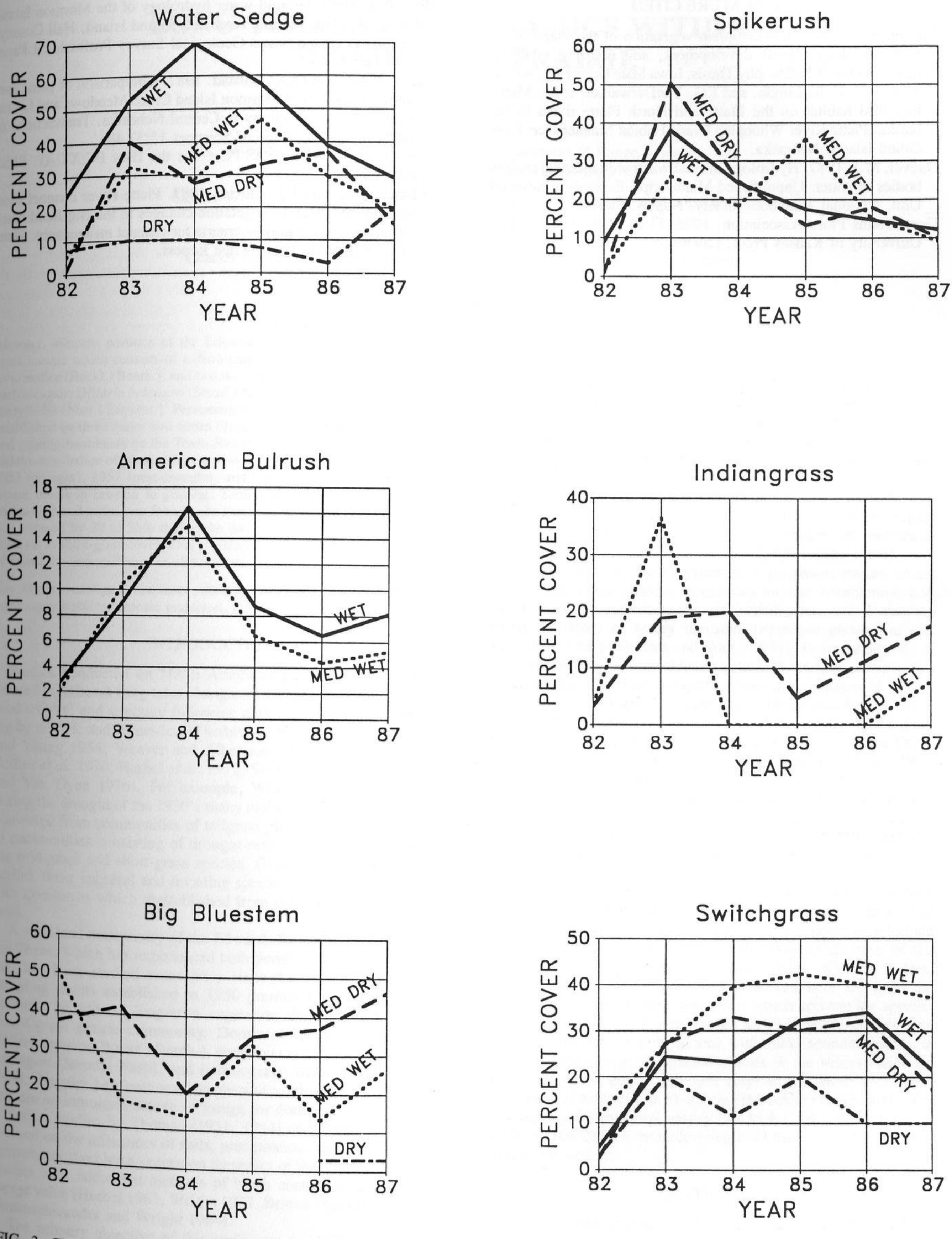


FIG. 3. Changes in percent cover of 6 major species during the study. Curves for each elevation at which a species occurred are shown.

LITERATURE CITED

Currier, P.J. 1982. The floodplain vegetation of the Platte River: phytosociology, forest development, and seedling establishment. Doctor of Philosophy Thesis, Iowa State University, Ames.

Currier, P.J., G.R. Lingle, and J.G. VanDerwalker. 1985. Migratory bird habitat on the Platte and North Platte rivers in Nebraska. Platte River Whooping Crane Habitat Maintenance Trust, Grand Island, Nebraska.

Duever, M.J. 1987. Hydrology of freshwater wetlands and shallow bodies of water. Unpublished Manuscript. Ecosystem Research Unit, National Audubon Society, Naples, Florida.

Great Plains Flora Association. 1986. Flora of the Great Plains. University of Kansas Press, Lawrence.

Hurr, R.T. 1983. Ground-water hydrology of the Mormon Island Crane Meadow Wildlife Area near Grand Island, Hall County, Nebraska. United States Geological Survey Professional Paper 1277-H.

Nagel, H.G., and O.A. Kolstad. 1987. Comparison of plant species composition of Mormon Island Crane Meadows and Lillian Annette Rowe Sanctuary in Central Nebraska. Transactions of the Nebraska Academy of Sciences 15:37-48.

Norusis, M.J. 1986. SPSS/PC+ for the IBM PC/XT/AT. SPSS Inc., Chicago.

O'Brien, J.S., and P.J. Currier. 1987. Platte River channel morphology and riparian vegetation changes in the Big Bend reach and minimum streamflow criteria for channel maintenance. Platte River Whooping Crane Trust Report.

LONG-TERM GRASS DYNAMICS WITHIN A MIXED-GRASS PRAIRIE

Brian S. Mihlbacher, Fred E. Smeins, Department of Range Science,
Texas A&M University, College Station, Texas 77843

Gerald W. Thomas, New Mexico State University, Las Cruces, New Mexico 88001

and

Charles A. Taylor, Texas Agricultural Experiment Station, Sonora, Texas 76950

Abstract. Western portions of the Edwards Plateau are dominated by a grass mosaic which consists of a rhizomatous midgrass, tobosagrass [*Hilaria mutica* (Buckl.) Benth.], and two stoloniferous short grasses, common curlymesquite [*Hilaria belangeri* (Steud.) Nash] and buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.]. Permanent 0.3 m x 6 m belt transects were established on three major soil series (Tobosa, Ozona, Valera) across several grazing treatments on the Texas Range Station near Barnhart, Texas, and the distribution of perennial grasses was mapped in 1951 (pre-drought), 1953 (drought), 1957 (post-drought), and 1987. Cover showed no consistent trends in relation to grazing. Total grass cover and composition within each soil series was found to be similar in 1951 and 1987, but cover was reduced by 20 to 56% during the drought period due primarily to a decrease in short-grass cover. This grassland mosaic exhibits a high degree of resistance and resilience to climatic variability.

Key Words. resistance, resilience, drought, tobosagrass, *Hilaria mutica*, community stability, mosaic grassland, Edwards Plateau, Texas

INTRODUCTION

Studies conducted on North American grasslands have documented significant long-term changes in community composition, productivity, and structure following periods of drought and grazing by wildlife and domesticated herbivores (Gardner 1950, Thomas and Young 1954, Weaver and Albertson 1956, Coupland 1958, Scifres *et al.* 1970, Herbel *et al.* 1972, Smeins et al . 1976, Wright and Van Dyne 1976). For example, Weaver (1961) found that during the drought of the 1930's many midwestern grasslands were converted from communities of tallgrass prairie climax dominants to communities consisting of drought-resisting and drought-evading mid-grass and short-grass species. Gradually, over a 20-year period, these subseral and invading species were replaced by climax dominants which reestablished from dormant rootstocks and seed.

A grassland community of the Edwards Plateau region of western Texas, which has experienced both periodic drought and grazing, has been studied extensively since the 1950's. Permanent sampling points established in 1950 presented an excellent opportunity to address long-term vegetation dynamics within this mixed-grass prairie community. Dominant species, tobosagrass [*Hilaria mutica* (Buckl.) Benth.], common curlymesquite [*Hilaria belangeri* (Steud.) Nash], and buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.] are common members of southwestern grasslands and are an important source of forage for domestic livestock.

Earlier studies by Thomas (1951, 1954) and Gonzalez (1957) focused on the influences of soils, precipitation, and grazing management on short-term vegetation dynamics of this grassland. Other studies have addressed methods of brush control and improving forage value (Herbel 1963, Wright 1973, Britton and Steuter 1983, Neuenschwander and Wright 1984).

The primary objective of this study was to identify long-term perennial grass dynamics of this southern mixed-grass prairie community with emphasis on the effect of periodic drought, soil type, and grazing by domestic herbivores.

STUDY AREA

The study was conducted at the Texas Range Station located 13 km south of Barnhart, Texas in the northwestern corner of Crockett County which is within the Edwards Plateau Land Resource Area. The climate is subtropical steppe, and the annual growing season averages 233 days (ESSA State Climatologist, Texas). Average annual precipitation is 52.0 cm, which occurs mostly as rainfall during spring and fall peaks. Precipitation is highly variable with annual totals as low as 19.3 cm and as high as 117.4 cm (Figure 1). Summer temperatures can be hot with temperature maxima of 37-43 C being common (ESSA State Climatologist, Texas).

The vegetation is characterized by a graminoid mosaic of the clonal rhizomatous midgrass tobosagrass and the stoloniferous short grasses common curlymesquite and buffalograss, with a scattered woody overstory of honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) (Thomas and Young 1954). Perennial grasses of lesser importance include sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], vine mesquite (*Panicum obtusum H.B.K.*), threeawns (*Aristida* spp. L.), hairy grama (*Bouteloua hirsuta* Lag.), and tumblegrass [*Schedonnardus paniculatus* (Nutt.) Trel.]. Forb species include western bitterweed (*Hymenoxys odorata* DC.), common broomweed [*Xanthocephalum dracunculoides* (DC.) Shinners], grassland croton [*Croton neomexicanus* (Muell.) Arg.], Englemann daisy (*Engelmannia pinnatifida* Nutt.), manystem evax (*Evax multicaulis* DC.), and silverleaf nightshade (*Solanum elaeagnifolium* Cav.). Various cacti (*Opuntia* spp. Mill.) are also locally abundant within the study area. Plant nomenclature follows Gould (1969).

The terrain is mostly level (0-1% slope) with scattered shallow depressions and playa lake beds. Soils on the station, mapped in 1938 by Carter, Templin, and Mowery (unpublished), were formed from underlying hard limestone of the Washita division of the Lower Cretaceous. Soil series include Ozona (Kavett), Valera, Tobosa, Randall, and Irion. Data presented here are from the Ozona, Valera, and Tobosa soil series which account for approximately 90% of the land area. Ozona series soils are shallow clay loams (<35% clay) over limestone with thick indurated caliche at 30-51 cm (Petrocalcic Calciustoll). Soils of the Valera series are moderately deep, clayey (40-50% clay) soils formed over calcic or petrocalcic horizons at 51-82 cm (Petrocalcic Calciustoll). Tobosa series soils are deep, clayey (45-55% clay) soils with solum depths of 100-215 cm to underlying hard limestone (Typic Chromustert) (Figure 2).

METHODS

Permanent belt transects (0.3 x 6 m) were established in 1950 within several grazing treatments on Ozona, Valera, and Tobosa soil series. The location of perennial vegetation within each belt transect was mapped, by species, during the summers of 1951 (pre-drought period), 1953 (drought period), 1957 (post-drought)

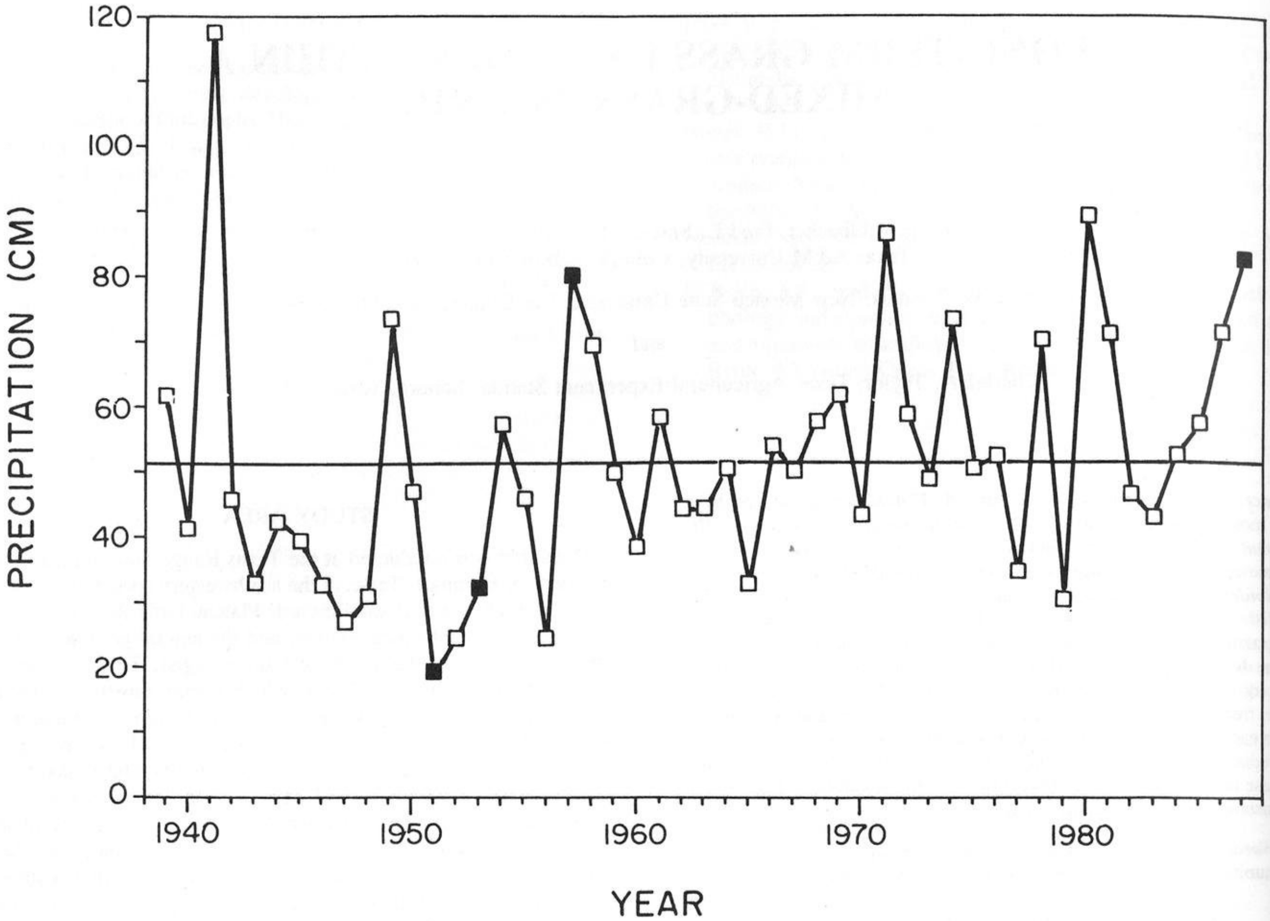


FIG. 1. Annual precipitation at the Texas Range Station, Barnhart, Texas from 1939 to 1987. The horizontal line represents the mean annual precipitation. Solid squares represent vegetation sampling years.

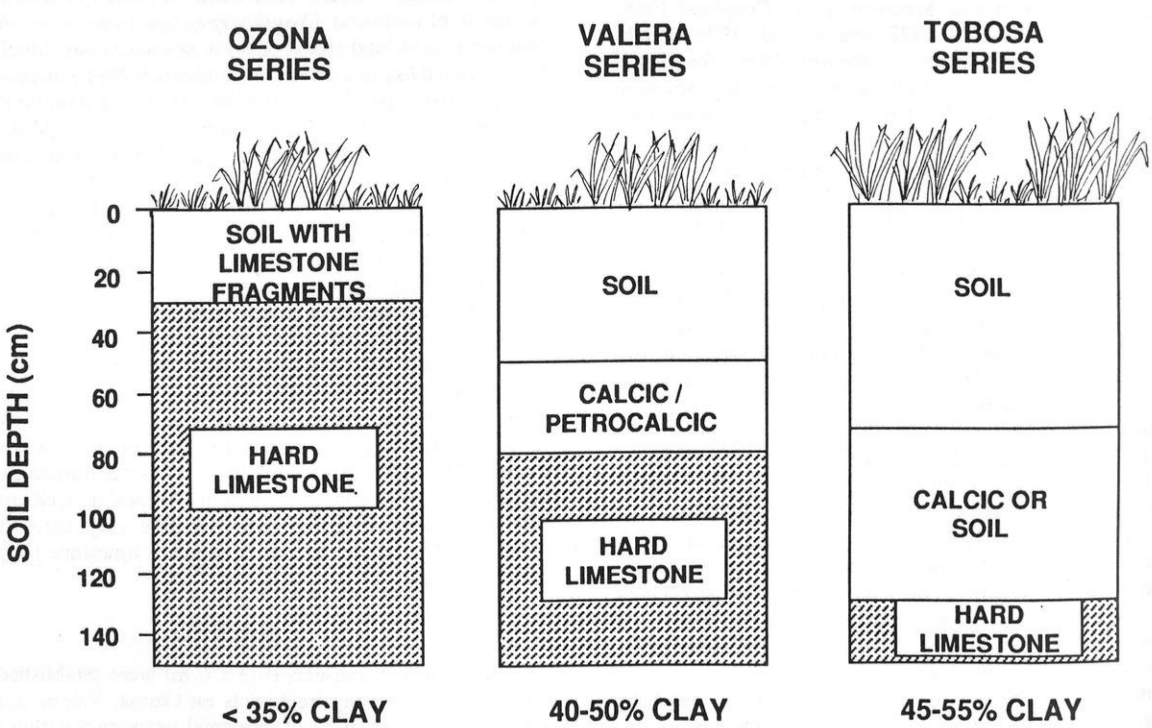


FIG. 2. Simplified schematic of typical soil profiles on Ozona, Valera, and Tobosa soil series on the Texas Range Station. The short-grass and mid-grass configuration is also illustrated for each series.

and 1987 using contiguous quadrats (30.5 x 30.5 cm) centered on 6 m belt transects (Thomas 1951, 1954). While 1951 is identified as pre-drought, it will be noted that 1951 had low rainfall (Figure 1). The two years prior to 1951 had above-normal to normal precipitation (Figure 1) and the vegetation in the early summer of 1951 still reflected the previous year's rainfall. Plant canopy cover was determined by measuring the distance of intercept, by species, along a line drawn down the center of each transect map. Fifty-two of the original belt transects were relocated and sampled in 1987 for comparison with the earlier mapping dates (n = 14, 17, and 21 for Valera, Tobosa, and Ozona soil series, respectively).

RESULTS AND DISCUSSION

The limited number of belt transects resampled within each grazing treatment/soil series combination made comparisons between grazing systems difficult. However, initial evaluation of the small data set revealed no consistent trend or difference in plant cover between the various grazing systems across years. Thomas (1954) observed that variation in vegetation composition on the station could be largely attributed to soils differences and annual precipitation rather than grazing treatment. Therefore, data collected among the grazing treatments were pooled by soil series for further analysis.

Total grass canopy cover, almost exclusively tobosagrass, common curlymesquite, and buffalograss, was found to be similar within and between soil series in 1951 and 1987 (Table 1). Both 1951 and 1987 were preceded by 2-3 years of normal to above-normal precipitation and therefore represent plant cover under favorable growth conditions. Tobosagrass cover was highest on the Tobosa soil series, while common curlymesquite and buffalograss cover were higher on the Ozona and Valera soils series prior to the drought period (1951) and in 1987. However, following a drought period which began in late summer 1951, the perennial grass canopy cover declined 56%, 43%, and 20% on the Ozona, Valera and Tobosa soil series, respectively, from 1951 to 1953 (Table 1). This decline was completely accounted for by a reduction in short-grass cover on all soil series. Large reductions in buffalograss cover, and other short-grasses, during drought periods has been previously documented in the Great Plains (Albertson and Tomanek 1965). The canopy cover of tobosagrass was unchanged or increased slightly on all soil series during the same period, however, a 24-37% decrease was observed across all soils from 1953 to 1957. No explanation has been developed to explain this decline during a period of nearly normal precipitation.

Table 1. Percent canopy cover (Mean ± S.E.) of tobosagrass and short-grass communities (common curlymesquite plus buffalograss) on the Ozona, Valera, and Tobosa soil series in 1951 (pre-drought), 1953 (drought), 1957 (post-drought), and 1987 at the Texas Range Station, Barnhart, Texas.

	Canopy Cover			
	1951	*1953*	*1957*	*1987*
	%			
Total Grass				
Ozona	92 ± .57	36 ± 1.3	56 ± 1.4	93 ± .41
Valera	95 ± .43	52 ± 1.6	58 ± 1.6	91 ± .72
Tobosa	84 ± .68	64 ± 1.4	52 ± 1.1	86 ± 1.3
Tobosagrass				
Ozona	15 ± .89	16 ± 1.0	10 ± .57	20 ± .87
Valera	32 ± 1.9	33 ± 1.9	25 ± 1.5	35 ± 1.8
Tobosa	53 ± 1.2	60 ± 1.5	38 ± 1.1	44 ± 1.3
Short-grass				
Ozona	76 ± 1.0	20 ± 1.1	45 ± 1.5	70 ± .92
Valera	62 ± 2.0	20 ± 1.2	32 ± 1.6	55 ± 2.0
Tobosa	31 ± 1.3	5 ± .63	11 ± .94	39 ± 1.5

The wide variation in reduced plant cover between the soils series is attributed to the pre-drought vegetation composition of each soil series and the response of the dominant grass species to drought conditions. Tobosagrass appears to be more tolerant of drought conditions than either of the short-grass species, therefore soils dominated by tobosagrass (Tobosa series) would be expected to maintain a higher proportion of their cover during a drought (Thomas 1954). For Ozona and Valera soils, an alterative hypothesis is that tobosagrass occupies favorable microsites which promote drought tolerance. This possibility is currently under investigation. The proportion of common curlymesquite and buffalograss present in a short-grass community will also effect plant cover during a drought, since earlier research has determined that common curlymesquite is less drought resistant than buffalograss (Thomas 1954).

Comparison of transect maps from 1951 and 1987 indicated that many transects retained the same distribution of plant species within the transect and vegetative composition over the 36-year period (Figure 3). However, several transects were found to have undergone significant changes in plant distribution and species composition during this same period (Figure 4). An evaluation of the change in relative cover of tobosagrass and short-grass from 1951 to 1987 within individual transects suggests that 59% of the transects sampled displayed less than a 15% change in the cover of these growth forms, while 23% of the transects had a 26% or greater change in relative cover of tobosagrass and/or short-grass.

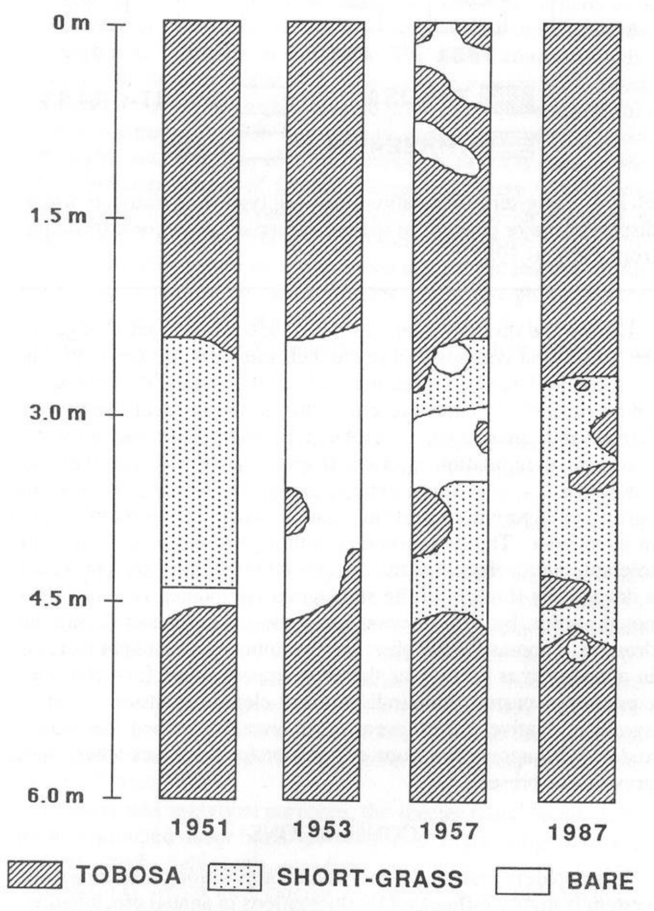


FIG. 3. Long-term vegetation mapping typical of transects which displayed no changes in species composition or distribution from 1951 to 1987.

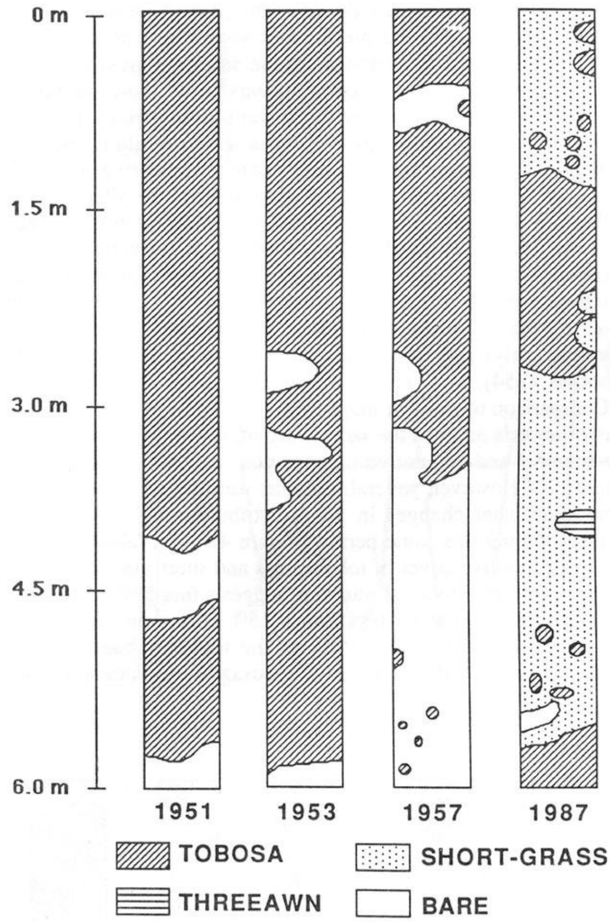


FIG. 4. Long-term vegetation mapping typical of transects which displayed major changes in species composition and/or distribution from 1951 to 1987.

During the drought interval, 1951-1956, significant changes in the vegetation composition of the belt transects occurred. Within all three soil series, areas mapped as short-grass in 1951 were found devoid of vegetative cover during the drought (Figure 3). These same areas were revegetated by short-grass species when favorable precipitation returned (Figure 3). In transects that had tobosagrass, it was found to be rather constant during the drought period, or experienced some decrease in cover, but rarely increased in abundance. This suggests that, although tobosagrass is drought tolerant, encroachment of this species into bare areas created during a drought by the loss of the short-grass component is limited. As noted earlier, by 1987 tobosagrass regained cover lost during the drought. Thomas (1954) observed that tobosagrass did not increase in abundance as quickly as the short grasses when favorable precipitation occurred. This indicates that clonal expansion of tobosagrass is relatively slow even under favorable growth conditions and/or tobosagrass is a poor competitor for resources when short grasses are present.

CONCLUSIONS

It is apparent that productivity and composition of this grassland system is highly influenced by fluctuations in annual precipitation. Nonetheless, the grassland mosaic exhibits a high degree of resistance and resilience to climatic variability. Although it is a dynamic system with a great deal of variation, after nearly 40 years following similar antecedent precipitation events, it exhibits basically the same perennial grass configuration and composition in 1987 as in 1951.

LITERATURE CITED

Albertson, F.W., and G.W. Tomanek. 1965. Vegetation changes during a 30-year period in grassland communities near Hays, Kansas. Ecology 46:714-720.

Britton, C.M., and A.A. Steuter. 1983. Production and nutritional attributes of tobosagrass following burning. Southwestern Naturalist 28:347-352.

Coupland, R.T. 1958. The effects of fluctuations in weather upon the grassland of the Great Plains. Botanical Review 24:273-317.

Gardner, J.L. 1950. Effects of thirty years of protection from grazing in desert grassland. Ecology 31:44-50.

Gonzalez, M.H. 1957. Grazing value and management of tobosa grass [*Hilaria mutica* (Buckl.) Benth.] on the Texas Range Station near Barnhart. Master of Science Thesis, Department Range Science, Texas A&M University, College Station.

Gould, F.W. 1969. Texas plants: A checklist and ecological summary. Texas Agricultural Experiment Station Miscellaneous Publication 585.

Herbel, C.H. 1963. Fertilizing tobosa on flood plains in the semi-desert grassland. Journal Range Management 16:133-138.

Herbel, C.H., F.N. Ares, and R.A. Wright. 1972. Drought effects on a semi-desert grassland range. Ecology 53:1084-1093.

Neuenschwander, L.F., and H.A. Wright. 1984. Edaphic and microclimate factors affecting tobosagrass regrowth after fire. Journal Range Management 37:116-122.

Scifres, C.J., J.H. Brock, and R.R. Hahn. 1970. Changes in a tobosagrass-buffalograss community after 27 years of protection from grazing. Texas Agricultural Experiment Station Progress Report 2809.

Smeins, F.E., T.W. Taylor, and L.B. Merrill. 1976. Vegetation of a 25-year exclosure on the Edwards Plateau, Texas. Journal Range Management 29:24-29.

Thomas, G.W. 1951. Some effects of soil differences and past grazing use on the amount and composition of vegetation on the Texas Range Station. Master of Science Thesis, Department Range Science, Texas A&M University, College Station.

Thomas, G.W. 1954. The relation of the vegetation on the Texas Range Station to soils, precipitation, and grazing. Doctor of Philosophy Dissertation, Department Range Science, Texas A&M University, College Station.

Thomas, G.W., and V.A. Young. 1954. Relation of soils, rainfall, and grazing management to vegetation, western Edwards Plateau of Texas. Texas Agricultural Experiment Station Bulletin 786.

Weaver, J.E. 1961. Return of midwestern grassland to its former composition and stabilization. Occasional Papers C.C. Adams Center for Ecological Studies 3:1-15.

Weaver, J.E., and F.W. Albertson. 1956. Grasslands of the Great Plains: their nature and use, Johnsen Publishing Company, Lincoln, Nebraska.

Wright, H.A. 1973. Fire as a tool to manage tobosa grasslands. Proceedings Tall Timbers Fire Ecology Conference 12:153-167.

Wright, R.G., and G.M. Van Dyne. 1976. Environmental factors influencing semi-desert grassland perennial grass demography. Southwestern Naturalist 21:259-274.

51-YEAR CHANGE IN THE SHORTGRASS PRAIRIE OF EASTERN WYOMING

Herbert G. Fisser
Department of Range Management, University of Wyoming

Kendall L. Johnson
Department of Range Resources, University of Idaho, Moscow, Idaho 83843

Kellie S. Moore and Glenn E. Plumb
Department of Range Management, University of Wyoming, Laramie, Wyoming 82070

Abstract. In 1936, vegetation analyses were conducted on repurchased federal lands in the Powder River Basin of eastern Wyoming. During the summer of 1987 the 74 remaining plots of 97 originally established on a 2.6 km² (1 mi²) area in Converse County were re-examined. Both surveys were conducted with the "square foot density procedure." During the past 51 years, vegetation abundance increased significantly on the saline upland site as a result of the interactive effects of favorable long-term weather patterns, annual grazing by livestock and wildlife, and reduced fire. Total vegetation cover increased significantly ($P < 0.05$) from 3% in 1936 to 11% in 1987, including a threefold increase for all grasses and a fourfold increase for all woody species. A negligible change occurred for all forbs. A shift in the cover composition occurred with grasses decreasing from 52% to 44% and non-grass species showing a corresponding increase. All growth forms, except shrubs, gained wider distribution over the study period, especially succulents and annual grasses. Continuation of current management practices probably means that this range will not return to a shortgrass-dominated prairie.

Key Words. long-term vegetation changes, grazing, drought, sampling procedures, vegetation analyses, Wyoming

INTRODUCTION

Lands in the Powder River Basin of eastern Wyoming were taken by homesteaders and other settlers in the early years of the present century. The settlers tried to establish a farming economy in the area, but many were forced off their small land holdings by drought and economic depression during the 1930's. By 1936 most farmers had abandoned their operations; only a few remained on the land and became livestock ranchers.

As a depression relief measure, many of the abandoned lands were purchased by the federal government under authority of the Land Utilization Act of 1935. Originally called L-U lands under the Resettlement Administration, they are now known as the Thunder Basin National Grassland administered by the USDA Forest Service. The area is now a patchwork of federal, state, and private ownership. Many of the repurchased federal lands have been seeded to re-establish perennial vegetative cover, usually with crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.]. Others have simply been left as "go-back" lands.

As a first step toward development of appropriate management plans, the Resettlement Administration conducted a rangeland survey in 1936. The survey included species frequency of occurrence and also estimates of vegetative ground cover as information toward determination of proper grazing capacity. These data formed the basis of grazing permits issued to private land holders for use of federal lands. Records indicate that most ranchers have practiced moderation in their utilization of federal permits for sheep and cattle. Current grazing is conducted with three and four-year rotation systems under supervision by the Forest Service.

During the 1936 survey, data were obtained from permanently marked plots on six 2.6 km² (1 mi²) sections of rangeland. One of the sections was not sampled again until the summer of 1987. This paper presents 51-year general trends based on a comparison of the 1936 and 1987 data collected from that section.

METHODS

Environment

The climate of the Powder River Basin is similar to that of Great Plains areas to the north and south. Precipitation amounts usually range from 300 to 400 mm annually, with the majority received during summer. Extreme droughts occur, as in the mid-1930's. Wet years, when precipitation exceeds 750 mm, also occur, as in the early 1980's. Temperatures are dramatically variable with extreme cold of -42 C in winter and extreme heat of 41 C during summer (Hambidge 1941). At Casper, Wyoming, with similar weather conditions to those at the study location, long-term records show monthly humidity during the two warmest months of the year, July and August, is at least 25%. The almost constant winds, with a mean monthly value of 5 m/sec, cause a desiccating effect to the native vegetation and to planted grain crops (Martner 1986). Eastern Wyoming in 1936 had already experienced several years of drought, and that year also was extremely dry. On some of the 1936 field data sheets of the area, comments were written emphasizing the extreme dryness. For example, some locations were described as having no living vegetation visible from horizon-to-horizon. In other instances it was noted that the shrubs and cactus were being killed by livestock grazing, even though shrubs are normally only a small portion of the animal's diet, especially during summer when they usually depend on native grasses and forbs for forage.

Vegetation

The Powder River Basin is a transitional zone between the shrub dominated ranges of the Great Basin and Intermountain areas to the west, and the grass-dominated ranges of the Great Plains to the east. Floristic elements common to both regions are found on the study site.

Most common plants were Wyoming big sagebrush [*Artemisia tridentata* var. *wyomingensis* (Beetle & Young) Welsh], western wheatgrass (*Agropyron smithii* Rydb.), blue grama [*Bouteloua gracilis* (H.B.K.) Lag. *ex* Griffiths], and birdsfoot sagewort (*Artemisia pedatifida* Nutt.) among a variety species listed on Table 1. Plains pricklypear (*Opuntia polyacantha* Haw.) was widely distributed but not a major component. Many annual and perennial forbs occur over the study site but were usually very sparse both during 1936 and 1987.

For study and analytical purposes, the species found on the study site were grouped under broad growth forms. Eight categories were adopted: shrub, half-shrub, mat-form, succulent, and the grasses and grasslikes which were categorized as shortgrass and grasslike, bunchgrass, rhizomatous grass and grasslike, and annual grass (Table 1).

Table 1. Plant species[1] on study site (single stem forbs excluded) grouped alphabetically by growth form.

Species	*Common Name*
Shrub Growth Form:	
Artemisia tridentata var. *wyomingensis* (Beetle & Young) Welsh	Wyoming big sagebrush
Atriplex canescens (Pursh) Nutt.	four-wing saltbush
Chrysothamnus nauseosus (Pall.) Britt.	rubber rabbitbrush
Half-shrub Growth Form:	
Artemisia frigida Willd.	fringed sagewort
Artemisia pedatifida Nutt.	birdfoot sagewort
Atriplex gardneri (Moq.) D. Dietr.	Gardner saltbush
Eriogonum microthecum Nutt.	slenderbush wildbuckwheat
Haplopappus nuttallii Torr. & Gray	toothleaf woodyaster
Hymenopappus filifolius Hook.	fineleaf hymenopappus
Xylorhiza glabriuscula Nutt.	alkali woodyaster
Mat-forming Growth Form:	
Arenaria hookeri Nutt. *ex* Torr. & Gray	Hooker sandwort
Astragalus spatulatus Sheldon	spoonleaf milkvetch
Haplopappus acaulis (Nutt.) Gray	stemless goldenweed
Phlox hoodii Richards.	Hood phlox
Succulent Growth Form:	
Coryphantha vivipara (Nutt.) Britt. & Rose	purple ballcactus
Opuntia polyacantha Haw.	plains pricklypear
Yucca glauca Nutt. *ex* Fraser	small soapweed
Shortgrass and Grasslike Growth Form:	
Bouteloua gracilis (H.B.K.) Lag. *ex* Griffiths	blue grama
Carex filifolia Nutt.	threadleaf sedge
Bunchgrass Growth Form:	
Andropogon gerardii var. *paucipilus* (Nash) Fern.	sand bluestem
Koeleria cristata (L.) Pers.	prairie junegrass
Oryzopsis hymenoides var. *contracta* (B.L. Johnson) Shechter	fine Indian ricegrass
Oryzopsis hymenoides (R. & S.) Ricker *ex* Piper	Indian ricegrass
Poa secunda Presl.	Sandberg bluegrass
Sitanion hystrix (Nutt.) J.G. Sm.	bottlebrush squirreltail
Stipa comata Trin & Rupr.	needleandthread
Stipa viridula Trin.	green needlegrass
Perennial Rhizomatous Grass and Grasslike Growth Form:	
Agropyron smithii Rydb.	western wheatgrass
Calamovilfa longifolia (Hook.) Scribn.	prairie sandreed
Carex douglasii Boott	Douglas sedge
Distichlis spicata (L.) Greene	inland saltgrass
Annual Grass Growth Form:	
Bromus japonicus Thunb. *ex* Murr.	Japanese brome
Bromus tectorum L.	cheatgrass brome
Vulpia octoflora (Walt.) Rydb.	common sixweeksgrass

[1]Nomenclature after Beetle (1970), Dorn (1988), Hitchcock and Cronquist (1973), and Kartesz and Kartesz (1980).

Initial (1936) Evaluation

The 1936 survey was based on five to ten systematically located sample plots in each 2.6 km^2 (1 mi^2) section of 250 ha (640 a). Six different sections were surveyed more intensively with about 100 plots in nine rows at about 0.16 km (0.1 mi) intervals, each with 9 to 11 plots spaced about 0.16 km (0.1 mi) apart (Lang 1945 and 1973).

Each intensively sampled section characterized a different kind of rangeland: 1) abandoned farmland, 2) sagebrush, 3) cactus, 4) shortgrass-sagebrush, 5) mixed grass, and 6) poor rangeland. The latter term was utilized for a kind of land that would currently be identified as upland saline. This study focused on the "poor rangeland" section (S3 T40N R71W of the 6th principal meridian) in northern Converse County, Wyoming.

The estimate of vegetation ground cover was conducted with a method called the "square-foot-density procedure" (Stewart and Hutchings 1936, Pickford 1940). The technique became the standard survey procedure of the U.S. Cooperative Western Range Survey Project in the 1930's (Reid and Pickford 1944).

The sampling unit, described in English units of measure, was a circular plot of 100 ft^2 (9.3 m^2) with a radius of 5.6 ft (1.7 m). The perimeter of a plot was scribed into the soil from a permanently marked center point prior to estimation of vegetation cover. Each plant species present in the plot was listed, thereby establishing frequency of occurrence. The ground cover (density) each contributed was estimated, using a 1 ft^2 (30 x 30 cm) plot as the basic unit. Data were recorded as T = trace, 0.25 ft^2 (0.9 dm^2), 0.50 ft^2 (1.8 dm^2), 0.75 ft^2 (2.7 dm^2), 1.0 ft^2 (3.7 dm^2), and larger numerical values. This rigid recording base obviously allowed for over-estimation of sparse species, especially because the trace values were often summed over multiple plots, with only seven to ten trace values being given the value of 0.25 ft^2. Many plants of the eastern Wyoming plains occur as single stems with diameters substantially less than 0.25 ft^2 or 6 x 6 inches (15 x 15 cm). This is one of the primary reasons the "square-foot-density procedure" was abandoned within a few years (Lang 1945). Also, the technique was open to personal bias or error in the estimation process, both between observers and between times, either with the same or different observers (Pickford 1940). The improper use of the term "density" for a value commonly identified in current literature as "vegetation cover" also contributed to the demise of the procedure (Reid and Pickford 1944).

1987 Evaluation

During the summer of 1987, the members of the research team worked together in recording vegetation cover values. Prior to conducting work on the permanently marked plots the authors reviewed pertinent procedural aspects as noted by Stewart and Hutchings (1936), Pickford (1940), Reid and Pickford (1944), and Lang (1945). Test plots were established to include shrubs and other plant growth forms. Only when researchers felt similarly confident of each other in conducting the procedural estimates, and of being able to conduct the work as closely as possible to the thoughts and evaluations of the 1936 workers, did estimation activities begin on the relocated permanent plots. Seventy-four of the original 97 plots (76%) were relocated.

The estimation at each plot was conducted with two, and in some cases three, observers concurrently deriving independent estimates. Inconsistencies of estimate were adjusted by re-reviewing the numbers and sizes of individual plant elements to form an adjusted value acceptable to each worker. In all cases, care was utilized to be sure that each species within a plot was listed, as was done in 1936, and that the estimated values were taken in the same manner used by the 1936 researchers. The subjectivity of the "square-foot-density procedure" does not, however, preclude statistical analysis (National Research Council 1962).

Analyses

The relationships of the 1987 data to that of 1936 were determined by comparison of the vegetation cover with two quantitative procedures. The Paired Plot t-test (Freese 1967) was used to determine differences that may have occurred over the years on the basis of: 1) individual species, 2) groups of species with similar growth forms, and 3) total vegetation. The frequency data were inspected similarly by species, groups, and total vegetation. An additional data evaluation involved inspection of the frequency data to determine the number of plots which had lost or gained specific plant elements from 1936 to 1987.

RESULTS

Total vegetation cover increased three and one-half times over the 51 year period from 3% in 1936 to 11% in 1987 (Table 2). Cover increased three times (1.6% to 5.0%) for all grasses ($P < 0.01$), and four times (1.5% to 6.3%) for woody growth forms ($P < 0.01$). The total cover of all grass species in 1936 at less than 2% was not an unusually low value for the upland saline sites currently recognized in the region.

Table 2. Mean vegetation cover (%) and plot frequency number (n = 74) of major vegetation classes for 1936 and 1987.

Vegetation	*Cover*		*Frequency*	
Class	*1936*	*1987*	*1936*	*1987*
	-----------%-----------			
Shrub	0.34	0.98	43	38
Half-shrub	0.38	0.82	63	66
Mat-form	0.72	3.58	61	66
Succulent	0.08	0.89	16	40
Bunchgrass	0.14	0.41	55	70
Rhizomatous	0.26	0.59	64	72
Shortgrass	1.24	3.91	42	48
Annual grass	0.0+	0.07	2	46
All forbs	0.0+	0.0+	57	73
All species	3.16	11.25	73	73

A shift occurred in the cover relationship between herbaceous and woody species. In 1936 grasses comprised 52% of all vegetative cover but declined to 44% in 1987, with non-grass species showing corresponding increases.

Another measure of long-term vegetation response over the 51-year period is the change in distribution indicated by frequency values on the 74 relocated plots (Table 2). With the exception of shrubs, all growth forms gained wider distribution, especially succulents and annual grasses. Increases ranged from 3 plots for half-shrubs to 44 for annual grasses. Shrubs decreased in 5 plots.

It is likely that most of the 51-year period has had substantially better growing conditions than the drought years of the 1930's. The area has undergone annual foraging by livestock and wildlife. This has affected the vegetation directly to a moderate degree and also served to reduce fire occurrence through reduction of fine fuels. Fire has been further restricted by construction of roads, which act as fire barriers, and by active fire-fighting efforts.

Some of the non-grass cover increase can be attributed to greater plant size, since many species are able to live longer than 50 years. The influence of annual grazing by livestock certainly has limited grass re-establishment, especially since most of the sampled area occurs on saline soils, restrictive to many native grasses.

CONCLUSIONS

The comparison of 1936 and 1987 vegetation shows significant increases in overall plant cover in the Powder River Basin of eastern Wyoming. These increases may reflect the fact that the initial evaluation was conducted at a time when the region was in the midst of an extreme drought, whereas conditions since that time have been more favorable thus allowing for greater plant production. Long-term grazing management and fire control, against the background of climatic influences, have apparently combined to produce: 1) a significant increase both in total ground cover and in all growth forms except forbs, 2) a decrease in the herbaceous and an increase in the woody components of total vegetative cover, and 3) an increase in the distribution of all growth forms except shrubs. Continuation of these management practices effectively ensures that this range will not return to shortgrass-dominated prairie.

ACKNOWLEDGEMENTS

The authors wish to acknowledge the support provided by the Thunder Basin National Grassland, U.S. Forest Service.

LITERATURE CITED

Beetle, A.A. 1970. Recommended plant names. University of Wyoming Agricultural Experiment Station. Research Journal 31.

Dorn, R.D. 1988. Vascular plants of Wyoming. Mountain West Publishing, Cheyenne.

Freese, F. 1967. Elementary statistical methods for foresters. United States Department of Agriculture, Forest Service. Agriculture Handbook 317.

Hambidge, G. 1941. Climate and man, 1941 yearbook of agriculture. United States Department of Agriculture, Washington, D.C.

Hitchcock, C.L., and A. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

Kartesz, J.T., and R. Kartesz. 1980. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland, Vol. II. The biota of North America. The University of North Carolina Press, Chapel Hill.

Lang, R.L. 1945. Density changes of native vegetation in relation to precipitation. Wyoming Agricultural Experiment Station. Bulletin 272.

Lang, R.L. 1973. Vegetation changes between 1943 and 1965 on the shortgrass plains of Wyoming. Journal of Range Management 26:407-409.

Martner, B.E. 1986. Wyoming climate atlas. University of Nebraska Press, Lincoln.

National Research Council. 1962. Methods of studying vegetation. Pages 45-84. *In* Basic problems and techniques in range research. National Academy of Science-Natural Resources Council Publication 890.

Pickford, G.D. 1940. Range survey methods in western United States. Herbarium Review 8:1-12.

Reid, E.H., and G.D. Pickford. 1944. An appraisal of range survey methods. Journal of Forestry 42:471-479.

Stewart, G., and S.S. Hutchings. 1936. The point-observation-plot (square-foot density) method of vegetation survey. Journal of American Society of Agronomy 28:714-722.

SPECIES COMPOSITION OF OLD SETTLER SILT-LOAM PRAIRIES

Robert F. Betz and Herbert F. Lamp
Northeastern Illinois University, 5500 N. St. Louis Avenue, Chicago, Illinois 60625

Abstract. Over the course of a decade, studies were conducted throughout northern Illinois and northeastern Indiana to locate old settler cemeteries containing prairie vegetation and to determine their species composition. Of the 824 cemeteries investigated in 42 counties in northern Illinois and in 20 counties in northwestern Indiana, 150 contained some prairie species. Of the 44 cemeteries that had sufficient prairie species to warrant study, 29 were silt-loam prairies, 14 were sand and silt-loam savannas, and one was a sand prairie. A total of 180 species of prairie plants were found in the 29 silt-loam cemetery prairies, belonging to 43 different families. The Compositae had the most representatives with 48 species (26%), followed by Gramineae with 15 (8%), Cyperaceae with 14 species (7%), and the Leguminosae had 12 (6%) species. The soils present in these cemeteries had deep A-horizons, and most showed no evidence of ever having been plowed. They represent a cross-section of the soil types found in northern Illinois and northwestern Indiana, with loess soils in the west and till soils in the east. This difference in soil type influences the relative abundance of some prairie species.

Key Words. cemetery prairies, eastern prairie, tallgrass prairie, old settler cemeteries, Illinois, Indiana

INTRODUCTION

Although the Illinois tallgrass prairie is known through historical accounts, its species composition is not well documented. Most of the early reports (Short 1845) were of a general nature, with such vague names as "goldenrods, asters, etc." Some information about the prairie's composition can be gleaned from the annotated plant list of Mead (1846) and Brendel (1887). In this century, Gleason (1910) studied the composition of the Illinois sand prairies, Gates (1912) the sand prairies of the beach area in northeastern Illinois, Evers (1955) the hill prairies along the Mississippi River, and Fell and Fell (1956) studied the hill prairies along the Rock River in northern Illinois. Both Vestal (1914) and Sampson (1921) reported on the heavier silt-loam prairies of northern Illinois, and Betz and Cole (1969) recorded the vegetational changes which occurred on a "black-soil" prairie originally studied by Paintin (1928).

Even though many ecological texts mention that remnant prairies are to be found in old settler cemeteries, They are described in relatively few papers. Lantz (1969) and Morrissey (1956) reported on the species composition of two different cemetery prairies in Iowa, and cemetery prairies were used in studies by Fay (1953) in Iowa and by Penalosa (1963) in California. Wright and Wright (1948) used these old settler cemeteries as a source of data to study the ecological relationships existing between the Palouse and Mixed-Grass prairies in south central Montana.

Since August 1961, when one of the authors accidentally found an old cemetery prairie in northern Will County, an extended search in the Chicago area began to disclose more. Since that time, especially during the 1970s,Th)Torganized searches were conducted to find cemetery prairies in northern Illinois and northwestern Indiana.

METHODS

General highway maps, prepared by the Illinois Department of Public Works and Buildings, cover individual counties and show the locations of cemeteries. Using these maps, visits were made initially to all cemeteries in a given area. However, it soon became evident that many of the cemeteries had originally been in wooded areas and did not have the potential to contain surviving prairie vegetation. Based on this consideration, it was decided to restrict exploratory visits to cemeteries which originally had been placed on the prairie or in the prairie-forest transition. Thus, it was necessary to learn the soil type or types of a cemetery to determine if it should be inspected. Accordingly, soil reports and maps, prepared by the Agricultural Experiment Station of the University of Illinois in cooperation with the Soil Conservation Service of the U. S. Department of Agriculture, were used for this purpose. Only cemeteries having soil types characteristic of prairie or prairie-forest transition were selected for exploratory visits, and the number of cemeteries designated for study was reduced substantially.

In each cemetery, certain prairie indicator species were sought, especially the warm-season grasses, such as big bluestem (*Andropogon gerardii* Vitman) and indiangrass [*Sorghastrum nutans* (L.) Nash]. These grasses often persisted around tombstones and in fence rows, even in those cemeteries which had been heavily mowed. In many cases the entire cemetery was still prairie. In others, prairie vegetation was to be found only in relatively undisturbed sections, such as areas in the front, the rear, and the sides. Those that were being regularly mowed were checked for depauperate prairie plants, such as lead plant (*Amorpha canescens* Pursh), wild bergamot (*Monarda fistulosa* L.) and yellow coneflower [*Ratibida pinnata* (Vent) Barnh.]. These sometimes were found surviving the mowing within the Kentucky bluegrass (*Poa pratensis* L.) turf. Efforts were made to urge the cemetery boards to cease mowing, so that enhanced growth would better permit the determination of the species composition still found within the cemeteries.

Vascular plants were identified and recorded at the time the cemeteries were initially evaluated. If the cemetery contained a substantial array of prairie vegetation as shown by the presence of at least 30 prairie species, a more intensive study was conducted. This necessitated revisiting the cemetery prairie at various times throughout the growing season for two or more years. Several cemetery prairies were visited more than a dozen times in order to catalog all the species. Nomenclature follows Fernald (1950) and is in conformity with that used by Swink and Wilhelm (1979). In addition to recording the species present, soil samples were taken to determine the depth of the A-horizon and to note other soil characteristics.

RESULTS

Of the 824 cemeteries in 42 counties of northern Illinois and in 20 counties in northwestern Indiana, 150 contained some prairie species. Of the 44 cemeteries that were deemed worthy of further study by having at least 30 prairie species, 29 were silt-loam prairies, one was a sand prairie, and 14 were silt-loam and sand savannas. Only the 29 silt-loam cemetery prairies are discussed in this paper.

The 180 species of prairie plants found in these silt-loam cemetery prairies belong to 43 different families (Table 1). The Compositae had the most representatives with 48 species (26%), followed by Gramineae with 15 (8%), Cyperaceae 14 (7%), and Leguminosae 12 (6%). These percentages generally correspond to the percentages reported by Curtis (1959) for the mesic prairies of

Table 1. Species composition of Illinois-Indiana silt-loam cemetery prairies.

Species	*Cemetery Prairie*[1]																													
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*Total*
Agoseris cuspidata[2]																													X	1
Allium canadense																	X	X	X	X	X	X	X		X	X				9
Amorpha canescens	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	28
Andropogon gerardii	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	29
Andropogon scoparius	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	29
Androsace occidentalis									X																					1
Anemone canadensis									X						X															2
Anemone cylindrica							X	X					X	X		X	X			X	X	X				X	X	X		12
Anemone patens wolf.																												X		1
Anemone virginiana		X															X	X												3
Antennaria neglecta	X	X	X		X				X		X	X	X	X		X	X		X	X	X	X	X	X	X	X	X	X		21
Antennaria plantaginifolia		X	X	X									X				X		X		X			X		X				9
Apios americana									X	X																				2
Apocynum cannabinum														X						X										2
Apocynum sibiricum		X		X			X	X			X		X		X		X		X		X	X	X	X			X	X		15
Asclepias amplexicaulis		X									X																			2
Asclepias sullivantii																	X			X	X	X	X	X	X					7
Asclepias tuberosa		X				X				X							X						X			X				6
Asclepias verticillata	X	X	X	X	X	X			X		X	X	X	X		X	X		X	X	X	X	X	X	X		X	X	X	23
Asclepias viridiflora	X	X	X	X							X		X	X		X	X		X	X	X	X		X			X	X	X	17
Aster azureus	X	X	X	X	X	X		X		X		X	X			X		X	X	X	X				X	X	X			18
Aster ericoides	X	X	X			X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	26
Aster laevis		X					X		X			X	X	X		X	X	X	X	X	X	X		X			X	X		16
Aster linariifolius																												X		1
Aster novae-angliae							X					X				X	X	X					X	X	X	X				9
Aster ptarmicoides																										X				1
Aster sericeus																X												X		2
Aster simplex					X				X						X								X							4
Astragalus canadensis						X		X		X			X							X										5
Baptisia leucantha																						X	X							2
Baptisia leucophaea				X			X		X			X			X	X	X			X		X	X			X		X		12
Blephilia ciliata																						X								1
Bouteloua curtipendula																											X	X	X	3
Cacalia tuberosa		X																					X							2
Calamagrostis canadensis			X									X	X	X	X						X									6
Carex bicknellii	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X			X	X		25
Carex brevior						X																								1
Carex cephaloidea								X																						1
Carex conoidea														X																1
Carex cristatella																					X	X								2
Carex gravida																							X							1
Carex meadii		X					X										X						X							4
Carex pensylvanica	X			X	X			X	X			X	X		X	X	X	X	X		X				X		X	X		16
Carex stipata																			X		X	X								3
Carex stricta															X			X												2
Carex tetanica																										X		X	X	3
Carex vulpinoidea																	X					X	X							3
Cassia fasciculata																				X				X						2
Ceanothus americanus	X	X		X	X	X	X	X	X	X	X	X			X		X		X	X			X					X	X	18
Cirsium discolor		X																		X			X							3
Cirsium hillii	X	X		X	X	X				X		X		X		X	X		X		X				X	X				14
Claytonia virginica																			X											1
Comandra richardsiana		X		X			X	X	X	X		X		X	X	X	X	X		X	X		X			X		X		17
Convolvulus sepium									X																					1
Coreopsis palmata		X				X			X	X					X	X		X		X	X	X	X			X	X	X		14
Coreopsis tripteris																	X			X		X	X			X				5
Desmodium canadense		X				X		X		X		X	X	X	X	X	X			X			X	X						13
Desmodium canescens																													X	1
Desmodium illinoense		X	X			X	X	X	X		X	X			X		X		X	X		X	X	X			X	X	X	18
Dodecatheon meadia	X				X				X	X				X		X		X	X	X	X		X		X	X	X	X		15

Table 1. Continued

	Cemetery Prairie[1]																													
Species	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*Total*
Echinacea pallida		X	X	X	X	X		X	X	X		X		X	X	X	X			X		X						X		16
Eleocharis compressa																						X								1
Elymus canadensis						X		X			X			X	X	X	X		X	X	X				X		X	X		13
Equisetum hyemale	X	X		X	X	X	X	X	X					X	X	X		X								X		X		14
Eragrostis spectabilis																													X	1
Erigeron strigosus	X	X	X	X	X	X	X	X	X	X	X		X	X			X	X	X	X	X	X	X	X	X	X	X	X	X	26
Eryngium yuccifolium	X	X	X	X		X	X	X		X		X	X	X		X	X	X	X	X		X	X			X		X		21
Eupatorium perfoliatum																		X												1
Euphorbia corollata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	29
Fragaria virginiana	X	X				X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	23
Galium obtusum						X									X				X											3
Gaura biennis																X				X		X	X							4
Gentiana puberula	X	X	X	X		X		X	X	X				X	X	X	X	X	X	X	X	X	X			X		X		20
Geum triflorum																											X	X		2
Glyceria striata																					X									1
Habenaria leucophaea		X																					X							2
Helianthemum canadense		X																												1
Helianthus grosseserratus	X	X		X	X	X		X		X		X	X	X	X	X	X	X		X	X	X	X	X	X	X		X		22
Helianthus laetiflorus rig.	X	X	X	X	X	X	X	X	X	X	X		X		X	X		X		X	X	X	X	X	X	X	X	X	X	25
Helianthus mollis																	X					X	X							3
Helianthus occidentalis	X	X							X		X			X		X										X	X			8
Heliopsis helianthoides		X	X			X	X	X		X					X		X								X			X		10
Heuchera richardsonii						X				X				X		X		X								X				6
Hieracium longipilum		X	X	X																										3
Houstonia longifolia											X										X		X							2
Hypericum sphaerocarpum																	X				X		X							3
Hypoxis hirsuta	X	X								X						X	X	X	X	X			X			X				10
Isanthus brachiatus																													X	1
Juncus dudleyi																	X													1
Koeleria cristata																			X	X	X					X				4
Krigia biflora										X													X			X				3
Kuhnia eupatorioides		X	X		X	X	X	X							X										X				X	9
Lactuca canadensis		X				X																	X							3
Leptoloma cognatum																					X									1
Lespedeza capitata		X	X	X		X	X	X		X	X	X			X	X	X	X	X	X	X	X	X	X		X			X	21
Liatris aspera		X					X	X	X				X			X		X		X		X				X	X	X		12
Liatris cylindracea																												X		1
Liatris pycnostachya																	X			X		X	X	X						5
Liatris spicata																										X				1
Lilium philadelphicum and.								X	X							X	X	X								X				6
Lilium michiganense							X																X							1
Lithospermum canescens	X	X	X			X	X	X	X	X		X		X	X	X	X	X	X	X	X	X		X		X	X	X		22
Lithospermum incisum																											X	X		2
Lobelia spicata	X	X	X	X	X				X	X		X	X	X		X	X		X	X	X	X	X	X	X	X				20
Lysimachia ciliata						X															X									2
Lysimachia lanceolata					X		X								X		X	X	X	X	X	X	X							10
Lysimachia quadriflora				X												X		X												3
Lythrum alatum																		X												1
Monarda fistulosa	X		X	X		X	X	X		X	X	X	X	X	X	X	X	X	X	X	X		X		X	X		X		22
Oenothera pilosella																							X							1
Orobanche uniflora		X																												1
Oxalis violacea	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	X	25
Panicum implicatum	X	X	X		X	X			X					X			X		X	X	X	X		X	X					14
Panicum leibergii	X			X	X	X	X	X	X	X		X	X		X	X	X	X		X	X		X			X	X	X		20
Panicum oligosanthes scrib.			X						X		X																	X	X	5

Table 1. Continued

	Cemetery Prairie[1]																													
Species	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	Total
Panicum villosissimum						X																								1
Panicum virgatum		X	X	X			X	X					X						X	X	X	X	X	X	X					13
Parthenium integrifolium	X			X	X				X	X	X	X		X		X	X	X	X	X	X	X	X	X	X	X				19
Pedicularis canadensis	X					X			X	X		X				X	X	X	X	X	X	X								12
Perideridia americana											X								X		X		X							4
Penstemon calycosus																	X		X											2
Penstemon digitalis														X																1
Petalostemum candidum	X			X	X	X	X	X	X	X		X		X		X			X	X	X		X				X	X		17
Petalostemum purpureum	X	X	X			X				X		X	X	X	X	X	X	X	X	X	X	X	X			X	X			19
Phlox glaberrima int.																							X							1
Phlox pilosa	X		X	X	X	X	X	X	X	X		X	X	X		X	X	X	X	X	X	X	X			X	X	X		23
Physalis heterophylla		X	X			X			X				X				X	X	X	X		X	X						X	12
Physalis virginiana			X		X	X	X		X	X		X	X				X	X	X	X	X	X	X		X		X	X		18
Physostegia virginiana						X	X	X				X			X	X	X			X	X			X		X				11
Polygala sanguinea	X	X																	X			X								4
Polygala senega																X											X			2
Polygala verticillata																X	X				X		X							4
Polygonum coccineum																					X									1
Potentilla arguta		X	X	X	X	X	X		X			X		X		X			X	X	X		X	X			X	X		17
Potentilla simplex																					X	X	X							3
Prenanthes aspera	X	X		X	X	X	X		X	X		X		X		X	X		X	X	X	X		X				X		18
Pycnanthemum tenuifolium											X						X					X	X							4
Pycnanthemum virginianum				X			X	X		X		X	X	X	X	X	X	X		X	X	X	X	X		X				17
Ratibida pinnata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X			26
Rosa carolina	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		27
Rudbeckia hirta	X	X	X	X		X	X		X	X		X	X	X		X	X	X	X	X	X	X	X	X		X			X	22
Ruellia humilis											X						X		X	X	X	X	X		X				X	9
Salix humilis		X	X						X	X	X			X		X	X									X				9
Scirpus atrovirens																					X									1
Scirpus lineatus																	X				X	X	X							4
Scutellaria parvula				X	X			X			X		X			X	X	X		X	X							X		11
Senecio pauperculus				X	X																									2
Senecio plattensis		X	X			X			X	X																				5
Silphium integrifolium	X	X					X	X	X	X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		21
Silphium laciniatum	X	X	X	X			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X		25
Silphium terebinthinaceum											X		X	X		X	X	X	X	X	X	X	X	X	X	X				14
Sisyrinchium albidum	X	X	X		X	X	X	X	X		X	X	X	X	X	X	X	X	X		X	X	X	X	X		X	X	X	25
Smilacina stellata														X						X										2
Solidago gigantea		X				X			X	X				X		X	X			X	X		X					X		11
Solidago graminifolia						X		X																X		X	X			5
Solidago gymnospermoides																											X			1
Solidago juncea	X	X	X	X	X		X			X		X								X	X	X	X		X	X				14
Solidago nemoralis			X						X					X					X	X	X	X	X	X		X	X	X		12
Solidago rigida	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X		26
Solidago speciosa	X			X			X		X	X																		X		6
Sorghastrum nutans	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	28
Spartina pectinata							X	X											X						X					4
Sphenopholis obtusata																			X		X		X							3
Spiranthes lacera																										X				1
Sporobolus heterolepis	X		X	X	X	X	X	X	X			X		X	X	X	X	X	X	X	X	X	X		X	X	X	X		23
Stachys palustris														X																1
Stachys tenuifolia				X		X	X			X											X			X						6
Stipa spartea	X	X		X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X		25
Strophostyles helvola																						X								1
Teucrium canadense						X		X																						2

Table 1. Continued

Species	Cemetery Prairie[1]																													
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*Total*
Thalictrum dasycarpum				X						X								X												3
Thalictrum revolutum														X							X									2
Thaspium barbinode																							X							1
Tradescantia ohiensis	X	X						X				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X			X	19
Verbena hastata										X																				1
Verbena stricta			X			X		X																					X	4
Vernonia missurica									X								X						X							3
Veronicastrum virginicum		X					X	X				X	X	X	X	X		X			X									10
Vicia americana																		X								X				2
Viola papilionacea	X		X	X	X	X	X	X	X			X		X	X	X	X	X	X	X	X	X	X	X	X		X		X	23
Viola pedata		X							X										X		X					X				5
Viola pedatifida	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		28
Viola sagittata																						X				X				2
Zizia aptera	X			X	X					X		X	X	X		X											X	X		10
Zizia aurea					X	X							X	X			X	X	X	X	X		X	X		X				12
TOTAL	52	71	47	53	45	65	54	56	60	58	36	54	47	66	49	70	84	62	70	77	86	70	89	49	41	66	49	63	30	1719

[1]The same number is used in both Tables 2 and 3 to designate a specific cemetery prairie.
[2]Authorities can be found in Fernald (1950).

Wisconsin: Compositae 26.1%, Gramineae 10.2%, and Leguminosae (7.4%), but the Cyperaceae were not listed. These similarities suggest that the sample of species obtained from the cemetery prairies is substantially representative of the species in the pre-settlement mesic prairies. Some species, such as big bluestem, were found in all of the 29 silt-loam cemetery prairies. Others, such as the prairie white fringed orchid [*Habenaria leucophaea* (Nutt.) Gray] and the prairie dandelion [*Agoseris cuspidata* (Pursh.) Raf.], were recorded only once.

The number of species found in these prairies varied between 30 in the dry prairie in the Granville Cemetery of Tippecanoe County, Indiana, to 89 in the mesic prairie in the Pine Ridge Cemetery of Iroquois County, Illinois (Table 2).

In addition to these 180 prairie species, 73 species of non-native herbaceous plants were recorded, such as Kentucky bluegrass, Queen Anne's lace (*Daucus carota* L.), and English plantain (*Plantago lanceolata* L.); 22 species of woody plants, such as gray dogwood (*Cornus racemosa* Lam.), wild black cherry (*Prunus serotina* Ehrh.), and lilac (*Syringa vulgaris* L.); and 13 species of cultivated forbs, such as spreading bellflower (*Campanula rapunculoides* L.), orange day-lily (*Hemerocallis fulva* L.), and cypress spurge (*Euphorbia cyparissias* L.). The number and kind of these non-prairie species were dependent in part on the past management of the cemetery (whether mowed, grazed, or trampled, or on the kind of decorative plants placed on the graves). In those cemetery prairies which were never mowed or in which mowing had ceased many years ago, and had been annually burned, non-prairie species were almost non-existent.

DISCUSSION

The presence of 180 different prairie species in these silt-loam cemetery prairies indicates the comparative richness of the pre-settlement Illinois-Indiana prairie. This wealth of species is probably due in part to the relatively large amount of precipitation (840 mm) generally available throughout the growing season. Yet the total number of species associated with pre-settlement Illinois and Indiana prairies may have been much higher than this study indicates, because only part of the prairie ecosystem is represented in the cemetery prairies. The settlers chose only the swells on the till plain when selecting sites for their cemeteries and not the swales. Therefore, wet-prairie and wet-mesic prairie species, such a blue-joint grass [*Calamagrostis canadensis* (Michx.) Nutt.], prairie cord grass (*Spartina pectinata* Link.), Indian plantain (*Cacalia tuberosa* Nutt.), and bottle gentian (*Genetiana andrewsii* Griseb.) were uncommon and often missing in the cemetery prairies. If present, they are usually confined to the periphery of the cemetery in an area of moist soil.

The great variability in the number and kinds of species found in these cemetery prairies is no doubt due in part to chance, i.e. individual species were not present when the pre-settlement prairie section was enclosed for use as a settler cemetery. It may also be due to human disturbances to which the cemetery has been subjected during the past century, which may have lead to the disappearance of certain species. This appears to have happened to Mead's milkweed (*Asclepias meadii* Torrey) which was reported in the Pine Hill Cemetery north of Davenport, Iowa, in 1899, but not seen a half-century later (Morrissey 1956). Broughton Cemetery (Livingston #4) contains only one clump of betony (*Pedicularis canadensis* L.) and only a few specimens of prairie gentian (*Gentiana puberula* Michx.), and hoary puccoon [*Lithospermum canescens* (Michx.) Lehm.] after two or three mowings annually for decades. Whereas, the Vermon Cemetery (Will #1), which has not been mowed but has been burned annually for more than a quarter of a century, has many specimens of these same species. Time of mowing is also important. For about 20 years, the Clyde Cemetery (Whiteside #1) was not mowed until midsummer because the farmer-caretaker liked the spring-flowering shooting stars (*Dodecatheon meadia* L.) and wanted them to set seed. Consequently, this cemetery prairie has shooting stars and prairie violets (*Viola pedatifida* G. Don) in abundance; whereas, the late-blooming smooth blue aster (*Aster laevis* L.) and prairie gentian (*Genetiana puberula* Michx.) are rarely found.

The soils present in the cemeteries represent a cross-section of the soil-types found in northern Illinois and northwestern Indiana. These range from the loess soils (Tama and Catlin) found in western Illinois to the glacial till soils (Saybrook, Elliott, Clarence, Swygert, and Parr) found in eastern Illinois and western Indiana (Table 3). In general, the loess soils were better drained and drier than the till soils. Therefore, these soils support higher populations of species such as purple coneflower (*Echinacea pallida* Nutt.), porcupine grass (*Stipa spartea* Trin.), and sky-blue aster (*Aster azur-*

Table 2. Total number of species and size (ha) of Illinois-Indiana silt-loam cemetery prairies.

Type of silt-loam and location	*Number of species*	*Area*
	-- *number* --	-- *ha* --
A. **Tama Silt-Loam**		
1. Bureau #1 (Hetzler)	52	0.4
2. Henry #1 (Munson)	71	2.0
3. Henry #2 (Hoose)	47	0.4
4. Lee #1 (Temperance Hill)	53	0.4
5. Lee #2 (DeWolf)	45	0.2
6. Mercer #1 (Brownlee)	65	0.8
7. Putman #1 (Mt. Palatine)	54	0.8
8. Warren #1 (Spring Grove)	56	0.4
9. Whiteside #1(Clyde)	60	0.4
10. Whiteside #2 (Heaton)	58	0.3
B. **Catlin Silt-Loam**		
11. Champaign #1 (Jessee)	36	0.4
12. LaSalle #1 (Four-Mile Grove)	54	0.4
13. LaSalle #2 (St.Clara)	47	0.8
C. **Saybrook Silt-Loam**		
14. DeKalb #1 (Afton)	66	1.2
15. Marshall #1 (Camp Grove)	49	0.4
16. Will #1 (Vermont)	70	0.4
D. **Elliott Silt-Loam**		
17. Ford #1 (Prospect)	84	2.0
18. DuPage #1 (Stephen's)	62	0.3
19. Livingston #4 (Broughton)	70	0.9
20. McLean #1 (Weston)	77	2.0
E. **Clarence Silt-Loam**		
21. Livingston #1 (Sunbury)	86	0.4
22. Vermilion #1 (Pellville)	70	0.4
F. **Swygert Silt-Loam**		
23. Iroquois #1 (Pine Ridge)	89	1.4
24. Livingston #2 (Nevada)	49	1.2
25. Livingston #5 (Sullivan)	41	0.4
G. **Parr Silt-Loam**		
26. Lake-Ind #1 (German Methodist)	66	0.4
H. **Dry Prairies**		
27. McHenry #1 (Queen Anne)	49	0.4
28. Ogle #1 (Beach)	63	0.8
29. Tippecanoe-Ind #1 (Granville)	30	0.4

eus Lindl.) than do the till soils. On the other hand, species such as alum root (*Heuchera richardsonii* R. Br.), Culver's root [*Veronicastrum virginicum* (L.) Farw.], and smooth blue aster (*Aster laevis* L.) usually sustain higher populations on the wetter, more poorly drained till soils of eastern Illinois and western Indiana.

In most of these cemetery prairies the depth of the A-horizon averages 36 to 48 cm and showed no evidence of ever having been plowed. However, it is possible that two of these cemetery prairies, the Hoose Cemetery (Henry #2) and the Heaton Cemetery (Whiteside #2) may have been subjected to some plowing, based on shallower A-horizons. Sunbury (Livingston #1) also had a somewhat shallower A-horizon, but the richness of species present suggested that it had not been plowed. The somewhat shallow-A horizon may have been the consequence of the sloping surface of the section where the prairie survived. Nevada Cemetery (Livingston #2) lacked certain species, such as lead plant, prairie compass plant (*Silphium laciniatum* L.), and prairie clovers (*Petalostemum* spp.), suggesting that there was an early history of plowing prior to the establishment of the cemetery. The earliest tombstone, dating from the 1880s, would have made possible the cropping of the area before the cemetery was established. In contrast, the other cemeteries dated from the 1840s and 1850s. This possible earlier period of plowing for the Nevada Cemetery would appear, however, to have been of short duration, based on the fact that the soil A-horizon is 36 to 42 cm deep and not appreciably eroded.

Some geographical differences were noted in the distribution of certain species. For example, prairie smoke (*Geum triflorum* Pursh) was found only in the more northern cemetery prairies, and long-leaved bluets (*Houstonia longifolia* Gaertn.) had a more southerly distribution.

Although these cemetery prairies are small in size (Table 2), they are perhaps the best surviving remnants of the mesic to dry-mesic pre-settlement Illinois-Indiana prairie. However, since these cemetery prairies are essentially terrestrial islands with their isolation and small populations, extinction of some species and genetic drift will occur (MacArthur and Wilson 1967). Even with adequate protection and good management, these cemetery prairies will slowly degrade without the continual introduction of new genetic material. These cemetery prairies still possess a valuable array of species which can be used in evaluating current restorations of Illinois and Indiana prairies. Further, the unplowed soils provide a measure of the extent to which erosion has taken its toll in the surrounding fields. Ten of these cemetery prairies have been designated as nature preserves by Illinois and Indiana. With their charm and beauty, these cemetery prairie remnants give a small glimpse of what the settlers of the pre-settlement Illinois-Indiana prairies first saw when they entered this region.

LITERATURE CITED

Betz, R.F., and M.H. Cole. 1969. The Peacock Prairie—A study of virgin Illinois mesic black-soil prairie forty years after initial study. Transactions of the Illinois Academy of Science 62:44-53.

Brendel, F. 1887. Flora Peoriana. The Vegetation in the climate of the middle Illinois. Peoria, Illinois.

Curtis, J.T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison.

Evers, R.A. 1955. Hill prairies of Illinois. Bulletin of the Illinois Natural History Survey 26:367-446.

Fay, M.J., and R.F. Thorne. 1953. Additions to the flora of Cedar County, Iowa. Proceedings of the Iowa Academy of Science 60:122-130.

Fell, E.W., and G.B. Fell. 1956. The Gravel-Hill Prairies of the Rock River Valley in Illinois. Transactions of the Illinois Academy of Science 49:47-62.

Fernald, M.L. 1950. Gray's manual of botany. Van Nostrand Company, New York.

Gates, F.C. 1912. The vegetation of the Beach Area in northeastern Illinois and southeastern Wisconsin. Bulletin of the Illinois State Laboratory of Natural History 9:255-372.

Gleason, H.A. 1910. The vegetation of the Inland Sand Deposits of Illinois. Bulletin of the Illinois State Laboratory of Natural History 9:23-174.

Lantz, C.W. 1969. The Clay Prairie in Butler County, Iowa. Proceedings of the Iowa Academy of Science 76:109-112.

MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Monographs in Population Biology No. 1. Princeton University Press, Princeton, New Jersey.

Mead, S.B. 1846. Catalogue of plants growing spontaneously in the state of Illinois, the principal part near Augusta, Hancock County. Prairie Farmer 6:35-36, 60, 93, 119-122.

Morrissey, T. 1956. The flora of the Pine Hill Prairie relict. Proceedings of the Iowa Academy of Science 63:201-213.

Paintin, R.D. 1928. The morphology and nature of a prairie in Cook County, Illinois. Transactions of the Illinois Academy of Science 21:152-175.

Table 3. Soils of the Illinois-Indiana silt-loam cemetery prairies.

Type of silt-loam and location	*Depth of A-horizon*	*Thickness of loess*	*Type of till*
	---------- cm ---------	------------ m ------------	
A. **Tama Silt-Loam**			
1. Bureau #1 (Hetzler)	32-35	> 1.5	none
2. Henry #1 (Munson)	25-27	> 1.5	none
3. Henry #2 (Hoose)	20-22	> 1.5	none
4. Lee #1 (Temperance Hill)	42-45	> 1.5	none
5. Lee #2 (DeWolf)	37-40	> 1.5	none
6. Mercer #1 (Brownlee)	40-42	> 1.5	none
7. Putnam #1 (Mt.Palatine)	40-42	> 1.5	none
8. Warren #1 (Spring Grove)	37-40	> 1.5	none
9. Whiteside #1 (Clyde)	32-35	> 1.5	none
10. Whiteside #2 (Heaton)	12-17	> 1.5	none
B. **Catlin Silt-Loam**			
11. Champaign #1 (Jessee)	35-40	0.9-1.5	none
12. LaSalle #1 (Four-Mile Grove)	35-40	0.9-1.5	none
13. LaSalle #2 (St. Clara)	35-40	0.9-1.5	none
C. **Saybrook Silt-Loam**			
14. DeKalb #1 (Afton)	25-27	0.45-0.9	loam
15. Marshall #1 (Camp Grove)	37-40	0.45-0.9	loam
16. Will #1 (Vermont)	35-40	0.45-0.9	loam
D. **Elliott Silt-Loam**			
17. Ford #1 (Prospect)	40-45	0.45-0.9	silty clay loam
18. DuPage #1 (St. Stephen's)	35-40	0.45-0.9	silty clay loam
19. Livingston #4 (Broughton)	40-42	0.45-0.9	silty clay loam
20. McLean #1 (Weston)	40-45	0.45-0.9	silty clay loam
E. **Clarence Silt-Loam**			
21. Livingston #1 (Sunbury)	20-22	0.45-0.9	clay drift
22. Vermilion #1 (Pellville)	35-40	0.45-0.9	clay drift
F. **Swygert Silt-Loam**			
23. Iroquois #1 (Pine Ridge)	40-45	0.45-0.9	calcareous clay
24. Livingston #2 (Nevada)	40-42	0.45-0.9	calcareous clay
25. Livingston #5 (Sullivan)	40-45	0.45-0.9	calcareous clay
G. **Parr Silt-Loam**			
26. Lake-Ind #1 (German Methodist)	30-32	< 0.45	loam
H. **Dry Prairies (Various Soils)**			
27. McHenry #1 (Queen Anne)	32-35	-----	sandy loam
28. Ogle #1 (Beach)	-----		gravel
29. Tippecanoe-Ind #1 (Granville)	30-35		none

Penalosa, J. 1963. A flora of Tiburon Peninsula, Marin County, California. The Wasman Journal of Biology 21:1-74.

Sampson, H.S. 1921. An ecological survey of the prairie vegetation of Illinois. Bulletin of the Illinois Natural History Survey 13:523-577.

Short, C.W. 1845. Observations on the botany of Illinois, more especially with reference to autumnal flora of the prairies. Western Journal of Medicine and Surgery, New Series 3:185-198.

Swink, F., and G. Wilhelm. 1979. Plants of the Chicago region. The Morton Arboretum, Lisle, Illinois.

Vestal, A.G. 1914. A Black-soil Prairie Station in northeastern Illinois. Bulletin of the Torrey Botanical Club 41:351-363.

Wright, J.C., and E.A. Wright. 1948. Grassland types of south-central Montana. Ecology 29:449-460.

THE VEGETATION HISTORY OF HEMPSTEAD PLAINS, NEW YORK

Richard Stalter and Wayne Seyfert
St. John's University, Jamaica, New York 11439

Abstract. Hempstead Plains, once encompassing 24,282 hectares, originally extended from western Suffolk County, to eastern Queens County, Long Island, New York. Hicks (1892), Harper (1918), Ferguson (1925), Cain *et al*. (1937), and Seyfert (1972), contended that Hempstead Plains was always devoid of arboreous growth, though Bailey (1949) maintained that shrubs and trees grew on the Plains. Those who have made important vegetation studies of the Plains included Hicks (1892), Harper (1918), Ferguson (1925), Conard (1935), Seyfert (1972), and Stalter and Lamont (1987). Stalter and Lamont (1987) studied a 8.5 ha remnant in the vicinity of Mitchell Field and found little bluestem (*Andropogon scoparius* Michx.) and broomsedge bluestem (*Andropogon virginicus* L.) to be the dominant species. Switchgrass (*Panicum virgatum* L.), indiangrass [*Sorghastrum nutans* (L.) Nash], and bird-foot violet (*Viola pedata* L.) are remnants of the prairie flora that dominated Hempstead Plains years ago. Invasion of alien species such as crabgrasses (*Digitaria* spp.), foxtail grass (*Setaria faberi* Herrm.), and purslane (*Portulaca oleracea* L.) on disturbed sites reflects the changing character of the Hempstead Plains flora. The small size of the Mitchell Field site, disturbance by vehicles and dumping may hasten the very slow process of old field succession at Mitchell Field.

Key Words. vegetation history, Hempstead Plains, Long Island, New York

INTRODUCTION

Hempstead Plains, once encompassing 24,282 hectares, is located on Long Island, New York. The goal of this review is to present the history of the land use of the Plains and then to interpret the floristic and vegetational changes that have occurred over the past 95 years, based on a comparison of several floristic studies. Those who have made important floristic studies of Hempstead Plains include: Hicks (1892), Harper (1918), Ferguson (1925), Seyfert (1972), and Stalter and Lamont (1987). Stalter (1981 and 1982) studied the ecology of the Plains from July 1980 through June 1981 and recorded the phenology and abundance of taxa found in 50 quadrats (m^2) at two study sites within the Hempstead Plains Nature Preserve.

Harper (1918) recognized Hempstead Plains as a genuine prairie on Long Island. Harper (1918) believed that the *Andropogon* which he found to be most abundant, little bluestem (*Andropogon scoparius* Michx.), was probably not the dominant grass in colonial times, but rather big bluestem (*Andropogon gerardii* Vitman), which is common on the prairies of western United States. Hempstead Plains is situated on outwash deposits of the last Wisconsin glacier. Two soil groups, the Haven Variant Association and Hoosic Variant Association were identified at the study sites. The Haven Variant Association occupies nearly level to gently sloping outwash plains, while Hoosic Variant soils are deep, very gravelly and well drained (Fuller 1914, Soil Conservation Service 1976).

METHODS

A comparison of native and introduced flora from 1892 through 1987 was obtained by examining species lists compiled by: Hicks (1892), Harper (1918), Ferguson (1925), Cain *et al*. (1937), Seyfert (1972), and Stalter and Lamont (1987). These data are presented in Table 1. A list of the flora identified by Stalter and Lamont (1987) appears in Table 2. Gleason and Cronquist (1963) was used as a reference to identify native and introduced species.

Table 1. A comparison of native and introduced flora, on Hempstead Plains, Long Island, New York, 1892 to 1987.

Collector	*Total Species*	*Native Species*	*Introduced Species*
Hicks (1892)	126	106 (84%)	20 (16%)
Harper (1918)	123	118 (96%)	5 (4%)
Ferguson (1925)	251	249 (99%)	2 (1%)
Cain *et al*. (1937)	69	67 (97%)	2 (3%)
Seyfert-Southeast (1972)	220	119 (54%)	102 (46%)
Seyfert-Central (1972)	185	103 (56%)	83 (44%)
Stalter and Lamont (1987)	171	106 (62%)	65 (35%)

OBSERVATIONS AND DISCUSSION

One of the earliest descriptions of Hempstead Plains was that by Denton (1670) which was reported by Seyfert (1972). Denton describes the plains as follows:

> "Toward the middle of Long-Island lyeth a plain sixteen miles long and four broad, upon which plain grows very fine grass, that makes exceeding good hay, and is very good pasture for sheep or other cattle; where you shall find neither stick nor stone to hinder the horse heels, or endanger them in their races . . ."

By 1755, 6,800 ha of plains land were held as common lands by the Town of Hempstead. Thompson (1839) reported:

> "Except for the great plains, much of the common lands of the town was anciently enclosed in large fields for the pasturing of different kinds of stock, and denominated according to the use intended, as the ox-pasture, the cow-pasture, etc."

The aforementioned accounts indicate that Hempstead Plains was primarily used for cattle and sheep raising from 1670 to 1869. That Hempstead Plains was thought to be unsuited for crops can be seen by examining the account by Prime (1845) to explain the reason why the Plains were unsuited for farming. Prime (1845) states:

> "The main difficulty lies beneath the soil. The substratum is a coarse, smooth, clean gravel, that appears as if it had been screened and washed from every particle that was capable of retaining moisture, or any other vegetable nourishment, and its depth is unfathomable. The necessary consequence is, that except in few places, where there is a small mixture of loam, a coat of manure is leached off in the coarse of a year or two; and the work must be done over again."

Table 2. The vascular flora of Hempstead Plains, Long Island, New York. Non native plants are noted with an asterisk (*). Data from Stalter and Lamont (1987).

GYMNOSPERMAE

Cupressaceae
Juniperus virginiana L.

Pinaceae
Pinus strobus L.

ANGIOSPERMAE-DICOTYLEDONEAE

Amaranthaceae
Amaranthus retroflexus L.*
Froelichia gracilis (Hook.) Mog.

Anacardiaceae
Rhus copallina L.
Rhus radicans (L.) Kuntze

Apiaceae
Daucus carota L.*

Apocynaceae
Apocynum cannabinum L.

Asclepiadaceae
Asclepias syriaca L.
Asclepias tuberosa L.

Asteraceae
Achillea millefolium L.*
Ambrosia artemisiifolia L.
Antennaria plantaginifolia (L.) Richards.
Artemisia vulgaris L.*
Aster dumosus L.
Aster pilosus Willd.
Centaurea nigra L.*
Chrysanthemum leucanthemum L.*
Cichorium intybus L.*
Cirsium arvense (L.) Scop.*
Cirsium vulgare (Savi) Tenore*
Conyza canadensis (L.) Cronq.
Erechtites hieracifolia (L.) Raf. *ex* DC.
Erigeron strigosus Muhl. *ex* Willd.
Eupatorium hyssopifolium L.
Gnaphalium obtusifolium L.
Helenium flexuosum Raf.
Hieracium floribundum Wimmer & Grab*
Hieracium pilosella L.*
Hypochaeris radicata L.*
Krigia virginica (L.) Willd.
Lactuca serriola L.
Rudbeckia hirta L.
Solidago canadensis var. *scabra* (Muhl.) Torr. & Gray
Solidago graminifolia (L.) Salisb.
Solidago juncea Ait.
Solidago nemoralis Ait.
Solidago rugosa Ait.
Solidago tenuifolia Pursh
Taraxacum officinale Weber*
Tragopogon dubius Scop.*

Brassicaceae
Arabidopsis thaliana (L.) Heynh.*
Barbarea vulgaris R.Br.*
Draba verna L.*
Lepidium virginicum L.
Raphanus raphanistrum L.*

Caesalpiniaceae
Gleditsia triacanthos L.

Caprifoliaceae
Lonicera fragrantissima Lindl. & Paxton*
Lonicera japonica Thunb.*
Sambucus canadensis L.
Viburnum dentatum L.

Caryophyllaceae
Cerastium vulgatum L.*
Dianthus armeria L.*
Scleranthus annuus L.*
Silene alba (P. Mill.) Krause
Spergula arvensis L.*
Spergularia rubra (L.) J. & C. Presl.*

Celastraceae
Celastrus orbiculatus Thunb.*

Chenopodiaceae
Chenopodium album L.

Convolvulaceae
Convolvulus sepium L.

Cornaceae
Cornus florida L.

Cuscutaceae
Cuscuta pentagona Engelm.

Elaeagnaceae
Elaeagnus angustifolia L.*

Ericaceae
Lyonia mariana (L.) D. Don
Vaccinium atrococcum (Gray) Heller

Euphorbiaceae
Euphorbia cyparissias L.*
Euphorbia supina Raf.

Fabaceae
Baptisia tinctoria (L.) R.Br.
Lespedeza capitata Michx.
Lespedeza cuneata (Dum.-Cours.) G. Don*
Lespedeza intermedia (S. Wats.) Britt.
Melilotus alba Medic.*
Strophostyles helvola (L.) Ell.
Trifolium arvense L.*
Trifolium pratense L.*

Fagaceae
Quercus coccinea Muenchh.

Hypericaceae
Hypericum gentianoides (L.) B.S.P.
Hypericum perforatum L.*

Lamiaceae
Hyssopus officinalis L.
Pycnanthemum flexuosum (Walt.) B.S.P.
Trichostema dichotomum L.

Mimosaceae
Albizia julibrissin Durz.*

Molluginaceae
Mollugo verticillata L.*

Myricaceae
Myrica asplenifolia L.

Oleaceae
Fraxinus americana L.

Onagraceae
Oenothera biennis L.

Oxalidaceae
Oxalis stricta L.

Phytolaccaceae
Phytolacca americana L.

Plantaginaceae
Plantago aristata Michx.
Plantago lanceolata L.*
Plantago major L.*

Table 2. Continued

Polygalaceae
Polygala nuttallii Torr. & Gray
Polygala polygama Walt.

Polygonaceae
Polygonum aviculare L.
Polygonum caespitosum Blume*
Polygonum scandens L.
Rumex acetosella L.*

Portulacaceae
Portulaca oleracea L.*

Primulaceae
Lysimachia quadrifolia L.

Rhamnaceae
Rhamnus frangula L.*

Rosaceae
Crataegus monogyna Jacq.
Potentilla argentea L.*
Potentilla canadensis L.
Potentilla recta L.*
*Potentilla simplex*Michx.
Prunus serotina Ehrh.
Pyrus coronaria L.*
Pyrus soulardii Bailey*
Rosa multiflora Thunb. *ex* Murr.*
Rosa virginiana P. Mill.
Rubus allegheniensis Porter *ex* Bailey
Rubus flagellaris Willd.
Rubus hispidus L.

Rubiaceae
Diodia terres Walt.

Scrophulariaceae
Agalinis acuta Pennell
Linaria canadensis (L.) Dum.-Cours.
Linaria vulgaris P. Mill.*
Verbascum blattaria L.*
Verbascum thapsus L.*
Veronica officinalis L.*

Simaroubaceae
Ailanthus altissima (P. Mill.) Swingle*

Solanaceae
Solanum dulcamara L.*

Verbenaceae
Verbena hastata L.

Violaceae
Viola fimbriatula Sm.
Viola lanceolata L.
Viola pedata L.
Viola sororia Willd.

ANGIOSPERMAE-MONOCOTYLEDONEAE

Amaryllidaceae
Hypoxis hirsuta (L.) Coville

Cyperaceae
Bulbostylis capillaris (L.) C.B. Clarke
Carex pensylvanica Lam.
Cyperus filiculmis Vahl

Iridaceae
Sisyrinchium albidum Raf.

Juncaceae
Juncus greenei Oakes & Tuckerman
Juncus secundus Beauv. *ex* Poir.
Juncus tenuis Willd.

Liliaceae
Allium vineale L.*

Poaceae
Agrostis hiemalis (Walt.) B.S.P.
Aira caryophyllea L.*
Andropogon gerardii Vitman
Andropogon scoparius Michx.
Andropogon virginicus L.
Anthoxanthum odoratum L.*
Aristida dichotoma Michx.
Aristida oligantha Michx.
Bromus japonicus Thunb. *ex* Murr.*
Dactylis glomerata L.*
Danthonia spicata (L.) Beauv. *ex* Roem. & Schult.
Digitaria ischaemum (Schreb. *ex* Scherig.) Schreb. *ex* Muhl.*
Digitaria sanguinalis (L.) Scop.*
Eragrostis spectabilis (Pursh) Steud.
Festuca elatior L.*
Festuca ovina L.*
Festuca rubra L.
Panicum auburne Ashe
Panicum capillare L.
Panicum commonsianum var. *addisonii* Stone
Panicum depauperatum Muhl.
Panicum dichotomiflorum Michx.
Panicum lanuginosum var. *fasciculatum* Fern.
Panicum lanuginosum var. *lindheimeri* Fern.
Panicum sphaerocarpon Ell.
Panicum virgatum L.
Paspalum setaceum Michx.
Poa pratensis L.*
Setaria faberi Herrm.*
Setaria geniculata (Lam.) Beauv.
Sorghastrum nutans (L.) Nash
Triodia flava (L.) Smyth
Triplasis purpurea (Walt.) Chapman

Poor soil as a detriment to cultivation is also clearly stated by Denton (1670):

> "From the first settlement of the country until within about the last thirty years it was universally believed that this great tract of land could never be cultivated-that if turned up by the plough, it was so porous, the water would at once run through it and leave the vegetation on the surface to perish from drought-that nothing would grow upon it except the tall grass which seems a native of that region."

Yet, 6,880 hectares of land in the southeastern portion of the Hempstead Plains were not plowed. By the 1840's, several influential individuals argued that this portion of plains land owned by the Town of Hempstead should be sold or cultivated. The chronology of those who argued for the cultivation of the Plains is presented by Seyfert (1972). In 1869, the Hempstead Town commissioners finally gave serious thought to selling their tracts of Hempstead Plains land. The commissioners were approached by Mr. Charles Harvey, who offered to purchase the land for $104/ha ($42/acre). Later that same year Mr. Alexander Stewart offered $136/ha ($55/acre) for a 3,035 ha tract of land. The offer was increased to $148/ha ($60/acre) by Col. Alfred Wood and Mr. C.B. Camp. After much bickering, the townspeople voted on the various offers and decided to sell 3,035 ha of land to Mr. Stewart for $394,350. On 23 November 1869, Mr. Stewart purchased an additional 809 ha of land. Additional tracts of land were sold by the Town of Hempstead in 1870, 1915, and 1927. In 1934, the last tract of Hempstead Plains was sold by the Town of Hempstead (Seyfert 1972).

Most investigators (Hicks 1892, Harper 1918, Ferguson 1925, Cain *et al.* 1937, and Seyfert 1972) were in agreement that Hempstead Plains were devoided of arboreous growth. Early descriptions of Hempstead Plains by Denton (1670) support the treeless condition of Hempstead Plains, yet Bailey (1949) maintained that shrubs and trees grew on the plains. Since the early accounts of the original flora of Hempstead Plains are contradictory, the status of the original flora is uncertain.

The first floristic study of Hempstead Plains was conducted by Hicks (1892), who reported that the most abundant plant was little bluestem. Hicks (1892) reported that big bluestem and indiangrass [*Sorghastrum nutans* (L.) Nash] might have been more abundant prior to his (1892) study.

The next serious study of the flora was published by Harper (1918). Harper reported that little bluestem was the most common component of the herbaceous vegetation. Harper stated that other important components of the flora were: big bluestem, plaintain-leaved pussy's-toes [*Antennaria plantaginifolia* (L.) Richards.], sedge (*Carex pensylvanica* Lam.), stargrass [*Hypoxis hirsuta* (L.) Coville], milkwort (*Polygala polygama* Walt.), winged sumac (*Rhus copallina* L.), indiangrass; goat's-rue [*Tephrosia virginiana* (L.) Pers.], and birdfoot violet (*Viola pedata* L.). Harper also noted that weeds were invading the once cultivated areas including: redtop (*Agrostis alba* L.), ragweed (*Ambrosia artemisiifolia* L.), heath aster, (*Aster ericoides* L.), Queen Anne's lace (*Daucus carota* L.), crab grass [*Digitaria sanguinalis* (L.) Scop.], and butter and eggs (*Linaria vulgaris* P. Mill.). Ferguson's (1925) floristic study of the Plains was one of the most complete studies of the area and included a list of 251 species (Table 1).

Conard (1935) indicated that several undisturbed tracts of 40 ha still remained within the original boundary of Hempstead Plains. Conard stated that stargrass, little bluestem, big bluestem, heath aster, wild indigo [*Baptisia tinctoria* (L.) R.Br.], Greene's rush (*Juncus greenei* Oakes & Tuckerman), grass-leaved goldenrod (*Solidago tenuifolia* Pursh), violet (*Viola fimbriatula* Sm.), and a number of other species were important components of the flora. Several of the species reported by Conard (1935) are also important components of the Plains flora today.

While Cain *et al.* 1937 did not conduct a floristic study of the Plains, his comments on the plant association "Andropogonetum Hempsteadii" are helpful in interpreting the ecology of the Plains. Cain wrote:

> "Trees, when present, usually are stunted and short-lived. The dominants included *Andropogon scoparius*, aster (*Aster linariifolius*), *Carex pensylvanica*, and *Aster ericoides* (= *Aster pilosus*). There are many other species present in the association, but they are not of high density, coverage or presence."

McManus (1968) wrote that the only remaining tracts of Hempstead Plains were located at Mitchell Field comprising approximately 243 ha of land. These small remnants have been reduced still further. Stalter (1982) noted that one site at Hofstra University that he examined in the summer of 1980 had been covered by fill in 1981. While small tracts of land supporting Plains vegetation remain, these tracts might eventually be developed.

The data in Table 1 indicate that over 80% of the species identified by Hicks (1892) were native to North America. Harper (1918), Ferguson (1925) and Cain *et al.* (1937) found over 95% of the species at Hempstead Plains were native species. Seyfert's (1972) study revealed that approximately 45% of the Plains flora were introduced while Stalter and Lamont (1987) found 38% of 171 species on a 8.5 ha tract were introduced (Table 2). The high percentage of introduced flora in the studies of Seyfert (1972) and Stalter and Lamont (1987) suggest that the areas studied by Seyfert and Stalter and Lamont were disturbed.

No accurate account of the flora of Hempstead Plains was known until the study by Hicks (1892). The flora observed by Hicks in 1892 was a product of over 150 years of intensive grazing; and, therefore, might have been different from the flora that existed when the region was first settled by Europeans. Hicks (1892) quotes early Dutch writers, "Hempstead is superior to all settlements on the Island, for it is very rich in cattle." A quotation by Thompson (1839) that appears in the Introduction section of this paper, notes the use of Hempstead Plains for the sustenance of livestock.

Little bluestem and broomsedge bluestem are the dominant vegetation at Hempstead Plains (Stalter and Lamont 1987). Poverty grass [*Danthonia spicata* (L.) Beauv. *ex* R. & S.], fescues (*Festuca* spp.), orchard grass (*Dactylis glomerata* L.), indiangrass, Kentucky bluegrass (*Poa pratensis* L.), and switchgrass (*Panicum virgatum* L.) are common the year round and are conspicuous when in flower and fruit. Important herbs are wild indigo, heath aster, grass-leaved goldenrod [*Solidago graminifolia* (Nash) Fern.], common St. John's-wort (*Hypericum perforatum* L.), hawk weeds (*Hieracium* spp.), and Queen Ann's lace (Stalter and Lamont 1987).

Harper (1918) recognizing the significance of Hempstead Plains as genuine prairie, speculated about its origin. Harper (1918) considered a number of factors (e.g., soil, fire, climate, etc.) but found each of these factors alone insufficient to explain the origin and perpetuation of the flora.

Investigators have suggested that many factors might have been important in perpetuating the vegetation. Fire (Cain *et al.* 1937, Seyfert 1972), topography (Cain *et al.* 1937), the presence of the sod producing little bluestem (Svenson 1936), the role of small mammals (Johnson 1972), soils (Svenson 1936, Stalter 1981), allelopathy (Stalter 1981), and a combination of the above factors (Stalter 1981) have been suggested to explain the presence and maintenance of the vegetation.

It is apparent that all of these factors act alone, together, or perhaps synergistically, to perpetuate the flora of Hempstead Plains. Additional work has not clarified the importance of each factor listed above although more work on the soil might provide greater insight to understanding the complexity of the flora. Of all the factors mentioned, soils are probably the most important. Permeability is moderate in the top soil and very high in the underlying sand and gravel. During years of low rainfall, or during periods of prolonged drought, the vegetation would be under severe water stress. Within the past 25 years, Hempstead Plains has experienced two dry periods. The first, the most severe of the 20th century, occurred in 1964 and 1965. In 1965, only 660 mm of rain were recorded in New York City, breaking the previous record set in 1964 by almost 150 mm. A second severe drought during the summer and early fall of 1981 killed approximately 30% of the shrubs at the study sites examined by Stalter (1981), though grasses were unaffected by the 1981 drought.

The original 24,282 ha of Hempstead Plains vegetation has now been reduced to 243 ha. Almost all of the remaining land has been altered by plowing, roads, pipelines, and mini-bike trails. Little or no portion of the original Hempstead Plains could be defined as in its "natural condition," although many of the species found on the original area still thrive there today. The presence of a high percentage of introduced species in the vegetation studies of Seyfert (1972) and Stalter and Lamont (1987) suggest that the plains remnants are highly disturbed (Table 1). While many taxa of the original flora still exist at Hempstead Plains, the composition of the vegetation today is drastically different than the vegetation that existed when Long Island was first settled by Europeans. The presence of shrubs, such as blackberry (*Rubus allegheniensis* Porter *ex* Bailey), and trees such as black cherry (*Prunus serotina* Ehrh.), crab apples (*Pyrus* spp.), and eastern redcedar (*Juniperus virginiana* L.) indicate that Hempstead Plains is undergoing very slow plant succession.

ACKNOWLEDGEMENTS

This paper is dedicated to Dr. Hugh Loveland, C.W. Post - Long Island University. The authors appreciate the contributions and assistance of Dr. Loveland toward the understanding of the flora and ecology of Long Island's plant associations. We thank Dr. Dwight T. Kincaid for helpful comments on the manuscript.

LITERATURE CITED

Bailey, P. 1949. Long Island as history of two great counties Nassau and Suffolk. Lewis Historical Publishing Company 2:144-145.

Cain, S.A., M. Nelson, and W. McLean, 1937. "*Andropogonetum Hempsteadii*: A Long Island grassland vegetation type." American Midland Naturalist 18:344-350.

Conard, H.S. 1935. The plant association of central Long Island. American Midland Naturalist 16:343,481-487.

Denton, D. 1670. Brief description of New York, formerly New Netherlands. G. Furman, New York, 1845.

Ferguson, W.C. 1925. Contributions to the flora of Long Island. Bulletin of the Torrey Botanical Club 52:133-136.

Fuller, M.L. 1914. The geology of Long Island, New York. U.S. Geologic Survey, Professional Paper #82.

Gleason, H.A., and A. Cronquist, 1963. Manual of vascular plants of northeastern North America and adjacent Canada. Willard Grant Press, Boston.

Harper, R.M. 1918. The vegetation of the Hempstead Plains. Bulletin of the Torrey Botanical Club 18:362-386.

Hicks, H. 1892. The flora of the Hempstead Plains, Long Island, unpublished manuscript presented for the degree of Bachelor of Science in Agriculture, Cornell University, Ithaca.

Johnson, R. 1972. The Hempstead Plains an eastern prairie. Unpublished report, Hofstra University, Hempstead, New York.

McManus, A.J. 1968. Surviving flora of the Hempstead Plains. Long Island Naturalist. Baldwin Bird Club, Autumn:35-43.

Prime, N.S. 1845. History of Long Island from its first settlement by Europeans to the year 1845. Robert Carter, New York.

Seyfert, W.G. 1972. A study of Hempstead Plains, Long Island, New York, and its vascular flora. Master of Science Thesis, Department of Biology, C.W. Post College.

Soil Conservation Service. 1976. General soil map and interpretation, Environmental Protection Agency Grant #002103010. USDA Soil Conservation Service, Washington, D.C.

Stalter, R. 1981. Some ecological observations of Hempstead Plains, Long Island, New York. Proceedings of the Northeastern Weed Science Society 35:101-106.

Stalter, R. 1982. Additional ecological observations at Hempstead Plains, Long Island, New York. Proceedings of the Northeastern Weed Science Society 36:76:80.

Stalter, R., and E. Lamont, 1987. Vegetation of Hempstead Plains, Mitchell Field, Long Island, New York. Bulletin of the Torrey Botanical Club 114:330-335.

Svenson, H.K. 1936. The early vegetation of Long Island. Brooklyn Botanical Garden Record 25:10-13.

Thompson, B.F. 1839. History of Long Island. E. French, New York.

INVENTORY, ASSESSMENT, AND RANKING OF NATURAL AREAS OF WALPOLE ISLAND

P. Allen Woodliffe
Ontario Ministry of Natural Resources, Chatham District, P.O. Box 1168,
Chatham, Ontario, Canada N7M 5L8

Abstract. A two-year study was begun in 1985 to document and assess the highly significant natural history features of the Walpole Island Indian Reserve in southwestern Ontario, Canada. The northern part of the island complex, where extensive prairie, savannah, and hardwood communities remain, was divided into 30 areas. The southern part, consisting of agricultural lands and wetlands was not examined. Through intensive field study and literature search, over 800 vascular plant species have been recorded from Walpole. Of the total, 12% (97) are rare in Ontario, and 1% (8) are not known elsewhere in Canada. Ninety-two species of birds have been confirmed as breeding, including 27 rare and one threatened species. An additional 44 species are probable breeders. Twenty-six species of herptiles were recorded including five of which are rare or declining. Twenty-four species of mammals have been recorded, including one rare species. Fifty-nine species of butterflies are known from Walpole Island, six of which are rare in Ontario. The results of this study confirm that Walpole Island contains the most significant tallgrass prairie and oak savannah, and associated flora and fauna remaining in Canada. Using six criteria, the 30 areas of the Island were priortized to provide the native people with a rationale for future conservation strategies.

Key Words. prairie, savannah, prairie/forest transition, inventory, Walpole Island, Ontario

INTRODUCTION

Walpole Island is part of a large delta island complex situated at the mouth of the St. Clair River at the north end of Lake St. Clair (Figure 1). Approximately one-third of the delta complex is made up of more than a dozen islands on the United States side of the border. The remaining two-thirds are made up of six islands on the Canadian side, with the St. Clair International Seaway being the main dividing line between Canada and the United States.

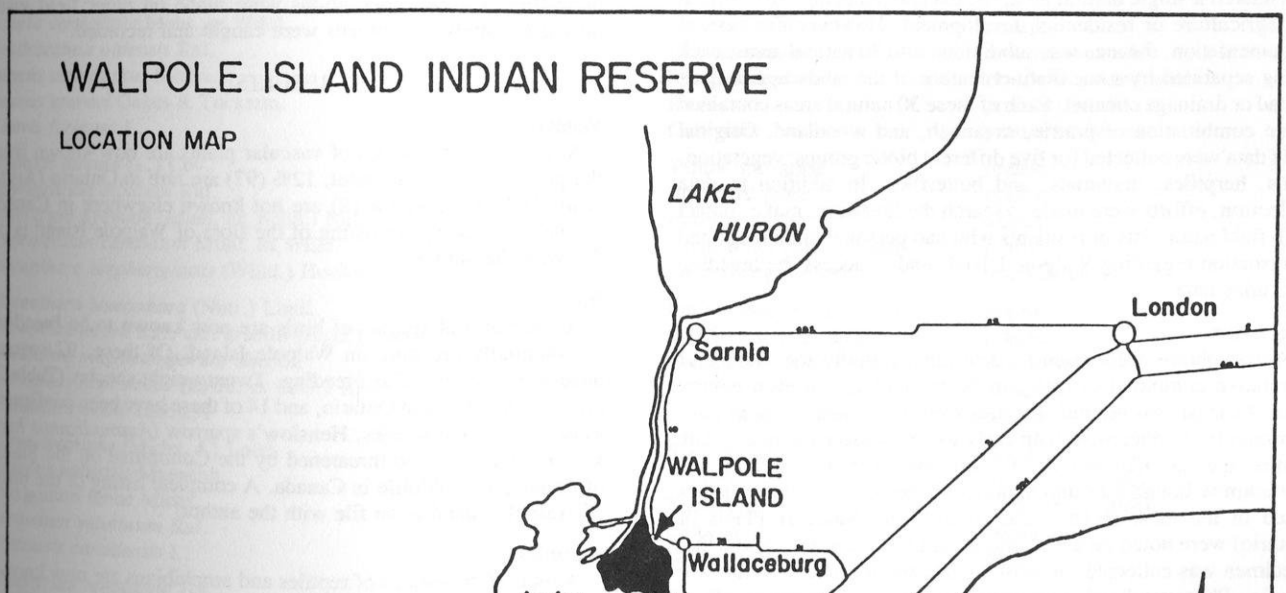


FIG. 1. Regional setting of Walpole Island Indian Reserve (from Hildebrand 1985).

The Canadian islands are wholly occupied by the Walpole Island Indian Reserve and cover approximately 24,000 ha. Almost 16,000 ha of the reserve are wetland, consisting of marshes, sloughs, channels, and the adjacent waters of Lake St. Clair. The remaining 8,000 ha, almost one-half of which are in agriculture, also include prairie, savannah, and hardwood forest. The Walpole Island Reserve is under the jurisdiction of the Walpole Island First Nation. All territory within the Reserve with the exception of public areas (ie. roads, waterways, beaches, buildings, etc.) are not generally open to the public unless otherwise posted. As a result, off-road sightseeing is strictly prohibited unless authorized by the Walpole Island Council and/or by individual private landowners.

Walpole Island has long been known for a rich mosaic of natural history features, including wetlands, wet woods, oak forest, oak savannah, and tallgrass prairie. It has been noted by the Carolinian Canada Identification Subcommittee as one of the top 36 unprotected natural areas in the Carolinian life zone of Canada (Eagles and Beechy 1985), and it was the only natural area which fulfilled all ten criteria used for selection.

Although Walpole Island is famous for its resources, no extensive surveys or documentation have taken place. Visits by naturalists have been sporadic over the decades due to the relative inaccessibility owing to its Indian Reserve status. In 1985, a two-year study was begun to carry out a natural history inventory of the terrestrial natural areas of Walpole Island was begun.

METHODS

The majority of the north one-half of Walpole Island could be considered a single natural area, the exceptions being land utilized for agriculture or residential development. However, for ease of documentation, the area was subdivided into 30 natural areas, each being separated by some distinct feature of the landscape such as a road or drainage channel. Each of these 30 natural areas contained some combination of prairie, savannah, and woodland. Original field data were collected for five different biotic groups: vegetation, birds, herptiles, mammals, and butterflies. In addition to data collection, efforts were made to search the literature, make contact with field naturalists or residents who had personal knowledge and information regarding Walpole Island, and to access the breeding bird atlas data.

Vegetation

Aerial photos were used to determine initially the variety of vegetative communities likely to be encountered in each natural area. At least two ground searches were then carried out in each community, to document both early to mid season and mid to late season species. Community descriptions were then written up. Community boundaries and significant species (i.e. those species listed in the most recent Atlas of the Rare Vascular Plants of Ontario) were noted on aerial photos and in field notes. A voucher specimen was collected for most significant or difficult to identify species. Photographic documentation was taken of significant flora and communities.

Several references were utilized for scientific names, in order to make use of recent taxonomic work. Lycopodiaceae to Dryopteridoideae followed Britton (1984 and 1985), Taxaceae to Iridaceae followed Voss (1972), except for the genus *Dichanthelium* which followed Gould and Clark (1978), and the family Orchidaceae which followed Luer (1975). Saururaceae to Cornaceae followed Voss (1975). Pyrolaceae to Compositae followed Gleason and Cronquist (1963), except for *Solidago* and *Euthamia* which followed Semple and Ringius (1983).

Birds

Aerial photos were used initially to determine the communities likely to be encountered in each natural area. Morning ground searches were then conducted at random in each natural area at least once during the breeding season. In the more significant areas, visits were made on two or more occasions in order to further document bird activity and confirm breeding. Additional observations were made during casual site visits and visits for other purposes. All species encountered were recorded with locations of significant species noted on aerial photos and in field notes. The level of breeding activity was recorded on standard atlas cards using the standard activity codes (Cadman *et al.* 1987). Most of the data were collected in 1986 only.

Herptiles

Field visits to each natural area to search for herptiles were made in conjunction with those made for vegetation and birds. Specific searches such as turning over logs and boards were made along with casual observations during field visits. Road-kills were also noted. All species were recorded with significant species being noted on air photos and in field notes.

Mammals

Field visits to each natural area to search for mammals were made in 1986 only. Trap lines using pitfall traps, snap traps, and live traps were employed to inventory small mammals. Other evidence (tracks, scats, and direct observations) were also noted during these and other field visits.

Butterflies

Each natural area was surveyed by volunteer lepidopterists primarily during the flight season in 1986 only. Random searches were made through each natural area. Efforts were also made to concentrate on some of the more significant plant host species, especially those suspected of being host to uncommon or rare butterflies. Casual observations were made on other field visits during the study. Specimens were caught and recorded.

RESULTS

Vegetation

More than 800 species of vascular plants are now known from Walpole Island. Of the total, 12% (97) are rare in Ontario (Argus *et al.* 1982-87) and 1% (8) are not known elsewhere in Canada (Table 1). A complete listing of the flora of Walpole Island is on file with the author.

Birds

A total of 138 species of birds are now known to be breeding or potentially breeding on Walpole Island. Of these, 92 species have been confirmed as breeding. Twenty-eight species (Table 2) are considered rare in Ontario, and 14 of these have been confirmed as breeding. One species, Henslow's sparrow (*Ammodramus henslowii*), is considered threatened by the Committee on the Status of Endangered Wildlife in Canada. A complete listing of the birds of Walpole Island is on file with the author.

Herptiles

A total of 26 species of reptiles and amphibians are now known from Walpole Island (Table 3). Of these, five species, queen snake (*Regina septemvittata*), eastern fox snake (*Elaphe vulpina*), Butler's garter snake (*Thamnophis butleri*), eastern spiny softshell turtle (*Trionyx spinifera*), and spotted turtle (*Clemmys guttata*), are considered to be rare or declining in Ontario (Ontario Ministry of Natural Resources 1983).

Mammals

A total of 24 species of mammals have been recorded for Walpole Island (Table 4). Of these, only the southern flying squirrel (*Glaucomys volans*) is considered rare in Ontario (Committee on the Status of Endangered Wildlife in Canada 1988).

Butterflies

A total of 59 species of butterflies were noted during the study. Of these, six species were considered to be at least rare in Ontario (Table 5). A complete listing of the butterflies of Walpole Island are on file with the author.

Table 1. Rare vascular plants of Walpole Island Indian Reserve (Allen and Oldham 1987, from Argus *et al.* 1982-87).

Scientific Name	*Common Name*	*Habitat*
Eragrostis capillaris (L.) Nees[1]	Lace grass	sandpit
Koeleria cristata (Ledeb.) Schultes	June grass	prairie/savannah
Leptoloma cognatum (Schultes) Chase	Fall witch grass	prairie
Dichanthelium clandestinum (L.) Gould & Clark	Broadleaf panic grass	woods
Dichanthelium leibergii (Vasey) Freckmann	Leiberg's panic grass	prairie
Dichanthelium praecocius Hitchcock & Chase	Early-branching panic grass	prairie
Dichanthelium meridionale Ashe[1]	Panic grass	prairie
Dichanthelium sphaerocarpon (Ell.) Gould	Panic grass	prairie/savannah
Sphenopholis obtusata (Michx.) Scribn.	Early bunchgrass	prairie/savannah
Stipa spartea Trin.	Needle grass	prairie/savannah
Bulbostylis capillaris (L.) Clarke	Hair-like bulbostylis	disturbed area
Carex bicknellii Britton	Sedge	prairie
Carex conoidea Willd.	Sedge	prairie/savannah
Carex emoryi Dewey	Sedge	prairie
Carex formosa Dewey	Sedge	prairie/woods
Carex gracilescens Steudel	Sedge	prairie
Carex meadii Dew.	Sedge	prairie
Carex muskingumensis Schw.	Sedge	wet woods
Carex suberecta (Olney) Britt.	Sedge	prairie
Carex swanii (Fern.) Mack.	Sedge	savannah
Carex tetanica Schkuhr	Sedge	prairie
Cyperus erythrorhizos Muhl.	Red-rooted cyperus	savannah
Fimbristylis spadicea (L.) Vahl[1]	Fimbristylis	prairie
Scirpus clintonii Gray	Clinton's club-rush	prairie
Scleria triglomerata Michx.	Tall nut-rush	prairie
Scleria verticillata Muhl. *ex* Willd.	Low nut-rush	prairie
Tradescantia ohiensis Raf.	Ohio spiderwort	prairie/savannah
Juncus acuminatus Michx.	Sharp-fruited rush	prairie/disturbed area
Juncus greenei Oakes & Tuckerm.	Rush	prairie/savannah
Aletris farinosa L.	Colic-root	prairie/savannah
Hypoxis hirsuta (L.) Cov.	Yellow star-grass	prairie
Sisyrinchium albidum Raf.	Blue-eyed grass	prairie
Aplectrum hyemale (Muhl. *ex* Willd.) Nutt	Putty-root	woods
Cypripedium candidum Muhl. *ex* Willd.	Small white lady's-slipper	prairie
Platanthera blephariglottis (Willd.) Hooker	White-fringed orchid	roadside ditch
Platanthera leucophaea (Nutt.) Lindl.	Prairie white-fringed orchid	prairie
Spiranthes lacera Raf. var. *gracilis* (Bigel.) Luer	Southern slender ladies'-tresses	prairie
Spiranthes magnicamporum Sheriak	Great Plains ladies'-tresses	prairie/savannah
Spiranthes ochroleuca (Rydb. *ex* Britt.) Rydb.	Yellow ladies'-tresses	savannah]
Spiranthes ovalis Lindley1	Oval ladies'-tresses	prairie
Carya laciniosa (Michx. f.) Loud.	Big shellbark hickory	woods/savannah
Quercus palustris Muenchh.	Pin oak	woods/savannah]
Polygonum tenue Michx.	Knotweed	roadside/savannah
Cerastium velutinum Raf.	Chickweed	savannah
Hydrastis canadensis L.	Golden-seal	woods
Thalictrum revolutum D.C.	Waxy meadow-rue	savannah
Liriodendron tulipifera L.	Tulip-tree	woods
Agrimonia parviflora Ait.	Agrimony	prairie
Geum vernum (Raf.) Torr & Gray	Spring avens	prairie
Rosa setigera Michx.	Prairie rose	prairie/savannah
Baptisia tinctoria (L.) R. Br.	Wild indigo	prairie/savannah
Desmodium rotundifolium (Michx.) DC.	Prostrate tick-trefoil	woods
Gymnocladus dioica (L.) K. Koch	Kentucky coffee-tree	wood edge
Lupinus perennis L.	Wild lupine	savannah
Vicia caroliniana Walt	Carolina vetch	prairie/savannah
Ptelea trifoliata L.	Hop-tree	shorelines
Polygala incarnata L[1]	Pink milkwort	prairie
Aesculus glabra Willd.[1]	Ohio buckeye	woods
Lechea pulchella Raf.	Pinweed	savannah
Lechea villosa Ell.	Hairy pinweed	savannah

Table 1. Continued

Scientific Name	*Common Name*	*Habitat*
Hibiscus moscheutos L.	Swamp rose mallow	marshes
Lythrum alatum Pursh	Wing-angled loosestrife	prairie
Nyssa sylvatica Marsh.	Black gum	roadsides
Ludwigia polycarpa Short & Peters	Many-seeded ludwigia	woods/disturbed
Bartonia virginica (L.) BSP.	Virginia bartonia	woods/disturbed areas
Gentiana alba Muhl.	White gentian	savannah
Gentiana puberulenta Pringle	Downy gentian	N/A
Gentianella quinquefolia (L). Small	Stiff gentian	prairie/savannah
Asclepias purpurascens L.	Purple milkweed	prairie/savannah
Asclepias sullivantii Engelm.	Sullivant's milkweed	prairie
Cuscuta cephalanthi Engelm.	Dodder	prairie
Cuscuta coryli Engelm.	Dodder	prairie/savannah
Phyla lanceolata Michx.	Fog fruit	
Blephilia ciliata (L.) Benth.	Downy wood-mint	prairie
Lycopus rubellus Moench	Stalked water-horehound	woods
Agalinis gattingeri (Small) Small	Gattinger's agalinis	prairie
Agalinis skinneriana (Wood) Britt.	Skinner's agalinis	prairie
Aureolaria pedicularia (L.) Raf.	Fern-leaved false foxglove	savannah
Veronicastrum virginicum (L.) Farw.	Culver's-root	prairie/savannah
Aster dumosus L. var. *strictior* T. & G.	Bushy aster	prairie/savannah
Aster praealtus Poir. var. *praealtus*	Willow aster	prairie/savannah
Bidens coronata (L.) Britt	Southern tickseed	wetlands
Cirsium hillii (Canby) Fern	Hill's Thistle	prairie
Coreopsis tripteris L.	Tall coreopsis	prairie/savannah
Eupatorium purpureum L.	Purple-jointed joe-pye weed	woods
Hieracium longipilum Torr.	Long-bearded hawkweed	N/A
Krigia biflora (Walt.) Blake	Two-flowered cynthia	prairie/savannah
Liatris aspera Michx.	Rough blazing star	savannah
Liatris spicata (L.) Willd.	Dense blazing star	prairie/savannah
Ratibida pinnata (Vent.) Barnh.	Gray-headed coneflower	prairie
Silphium terebinthinaceum Jacq.	Prairie dock	prairie
Solidago riddellii Frank	Riddell's goldenrod	prairie
Solidago rigida L.	Stiff-leaved goldenrod	prairie/savannah
Solidago speciosa Nutt.	Showy goldenrod	prairie/savannah
Vernonia gigantea (Walt.) Trel. *ex* Banner & Coville	Tall ironweed	prairie/savannah

[1]Only known Canadian location.

Table 2. Significant breeding birds of Walpole Island Indian Reserve.

Species	*Breeding Status*	*Source*[1]
Horned grebe	(+)	ORBB
Least bittern	*	ORBBP, MNR
Great egret	(*)	ORBBP
Cattle egret	+	ORBBP
Cooper's hawk	+	MNR, COSEWIC
Bald eagle	+	ORBBP, MNR, COSEWIC
Northern bobwhite	*	
Canvasback	(*)	ORBBP, MNR
Redhead	(*)	MNR
Northern shoveler	(+)	MNR
Ruddy duck	(+)	MNR
Sandhill crane	(*)	ORBBP
King rail	(*)	ORBBP, MNR, COSEWIC
Little gull	(*)	ORBBP, MNR
Forster's tern	(*)	ORBBP, MNR
Caspian tern	(+)	ORBBP, MNR, COSEWIC
Black tern	(*)	MNR
Acadian flycatcher	+	ORBBP, MNR
Tufted titmouse	*	ORBBP
Eastern bluebird	*	COSEWIC
White-eyed vireo	+	ORBBP
Prothonotary warbler	+	ORBBP, MNR, COSEWIC
Louisiana waterthrush	+	ORBBP, MNR
Hooded warbler	+	ORBBP, MNR
Yellow-breasted chat	+	ORBBP
Yellow-headed blackbird	(+)	ORBBP, MNR
Orchard oriole	*	ORBBP
Henslow's sparrow	*	ORBBP, MNR, COSEWIC

* Confirmed breeding in study area
(*) Confirmed breeding on Walpole Island, but not in study area
\+ Possible/probable breeding in study area
(+) possible/probable breeding on Walpole Island, but not in study area

[1]Sources of significance status: MNR (Ministry of Natural Resources 1983), COSEWIC (Committee on the Status of Endangered Wildlife in Canada 1988), and ORBBP (Ontario Rare Breeding Bird Program 1989).

Table 3. Reptiles and amphibians of Walpole Island Indian Reserve.

Scientific Name	*Common Name*
Notophtalmus viridescens	Eastern newt
Ambystoma tremblayi	Tremblay's salamander
Ambystoma laterale	Blue-spotted salamander
Bufo americanus	American toad
Hyla crucifer	Spring peeper
Hyla versicolor	Tetraploid gray treefrog
Pseudacris triseriata	Striped chorus frog
Rana pipiens	Northern leopard frog
Rana catesbeiana	Bullfrog
Chelydra serpentina	Common snapping turtle
Chrysemys picta	Painted turtle
Graptemys geographica	Map turtle
Emydoidea blandingi	Blanding's turtle
Clemmys guttata	Spotted turtle
Trionyx spiniferus	Spiny softshell
Eumeces fasciatus	Five-lined skink
Thamnophis sirtalis	Common garter snake
Thamnophis butleri	Butler's garter snake
Nerodia sipedon	Northern water snake
Regina septemvittata	Queen snake
Storeria dekayi	Brown snake
Opheodrys vernalis	Smooth green snake
Elaphe vulpina	Fox snake
Lampropeltis triangulum	Milk snake
Sistrurus catenatus	Massasauga

Table 4. Mammals of the Walpole Island Indian Reserve.

Scientific Name	*Common Name*
Sorex cinereus	Masked shrew
Blarina brevicauda	Short-tailed shrew
Eptesicus fuscus	Big brown bat
Lasiurus borealis	Red bat
Lepus europaeus	European hare
Sylvilagus floridanus	Eastern cottontail
Tamias striatus	Eastern chipmunk
Marmota monax	Woodchuck
Sciurus carolinensis	Grey squirrel
Tamiasciurus hudsonicus	American red squirrel
Glaucomys volans	Southern flying squirrel
Castor canadensis	Beaver
Peromyscus maniculatus	Deer mouse
Peromyscus leucopus	White-footed mouse
Microtus pennsylvanicus	Meadow vole
Ondatra zibethica	Muskrat
Canis latrans	Coyote
Vulpes vulpes	Red fox
Procyon lotor	Raccoon
Mustela erminea	Short-tailed weasel
Mustela vison	Mink
Taxidea taxus	Badger
Mephitis mephitis	Striped skunk
Odocoileus virginianus	White-tailed deer

Table 5. Significant butterfly species of Walpole Island (From Kulon et al. 1987).

Scientific Name	*Common Name*
Erynnis baptisiae	Wild indigo duskywing
Erynnis horatius	Horace's duskywing
Erynnis martialis	Mottled duskywing
Erynnis persius	Hairy duskywing
Poanes massasoit	Mulberry wing
Libytheana bachmanii	Snout

DISCUSSION

This study confirmed that outstanding natural areas remain on Walpole Island. A majority of the rare flora and fauna are directly or indirectly associated with prairie or savannah communities. These communities are generally in superb condition, due to the regular practice of setting fire to these areas by the island residents. Fully one-third of the flora is made up of grasses, sedges, and composites. This assemblage of rare and more common prairie and savannah species, combined with the excellent overall condition of the communities which they make up, gives Walpole Island undoubtedly the distinction of harboring the most significant tallgrass prairie and oak savannah vegetation remaining in Canada.

As a result of this study, the best sites have been identified and ranked in order of priority. Six hundred and thirty-eight ha of portions of the original 30 natural areas have been selected to represent the areas in most need of protection. The majority of these areas are tallgrass prairie and oak savannah communities. A feasibility study is presently underway to investigate the possibility of conserving these significant properties through leasing or other arrangements with their respective landowners.

ACKNOWLEDGEMENTS

This study was conducted with the approval of the Walpole Band Council. Funding and support was provided primarily by the World Wildlife Fund and Ontario Ministry of Natural Resources with additional assistance provided by the University of Waterloo and Lambton Wildlife Incorporated.

LITERATURE CITED

Argus, G.W., K.M. Pryer, D.J. White, and C.J. Keddy (eds.). 1982-1987. Atlas of the rare vascular plants of Ontario. Four parts. National Museum of Natural Sciences, Ottawa.

Britton, D.M. 1984. Checklist of Ontario Pteridophytes, Part 1. The Plant Press (2)4.

Britton, D.M. 1985. Checklist of Ontario Pteridophytes, Part 2. The Plant Press (3)1.

Cadman, M.D., P.F.J. Eagles, and F.M. Helleiner. 1987. Atlas of the breeding birds of Ontario. Federation of Ontario Naturalists and Long Point Bird Observatory. University of Waterloo Press.

Committee on the Status of Endangered Wildlife in Canada. 1988. Endangered species in Canada. World Wildlife Fund Canada.

Eagles, P.F.J., and T.J. Beechy. 1985. Critical unprotected natural areas in the carolinian life zone of Canada. Final report. The Nature Conservancy of Canada, The Ontario Heritage Foundation and World Wildlife Fund Canada.

Gleason, H.A. 1963. Manual of vascular plants of the northeastern United States and adjacent Canada. Van Nostrand Reinhold Company, New York.

Gould, F.W., and C.A. Clark. 1978. *Dichanthelium* (Poaceae) in the United States and Canada. Annals of the Missouri Botanical Garden 65:1132.

Kulon, B., B. Kulon, and G. Clements. 1987. Inventory of butterflies and skippers on Walpole Island. Unpublished report.

Luer, C.A. 1975. The native orchids of the United States and Canada. The New York Botanical Garden, New York.

Ontario Ministry of Natural Resources and Environment Canada. 1983. An evaluation system for wetlands of Ontario, south of the precambrian shield. Wildlife Branch, Ontario Ministry of Natural Resources and Canadian Wildlife Service, Environment Canada.

Ontario Rare Breeding Bird Program. 1989. Ontario rare breeding bird program newsletter, March 6, 1989.

Semple, J.C., and S.B. Heard. 1987. The asters of Ontario: *Aster* L. and *Virgulus* Ref. (Compositae: Astereae). University of Waterloo Biology Series Number 30.

Semple, J.C., and G.S. Ringius. 1983. The goldenrods of Ontario: *Solidago* L. and *Euthamia* Nutt. University of Waterloo Biology Series Number 26.

Voss, E.G. 1972. Michigan flora, Part I. Gymnosperms and monocots. Cranbrook Institute of Science Bulletin 55 and University of Michigan Herbarium.

Voss, E.G. 1985. Michigan flora, Part II. Dicots (Saururaceae-Cornaceae. Cranbrook Institute of Science Bulletin 59 and University of Michigan Herbarium.

THEMATIC MAPPER DIGITAL DATA FOR PREDICTING ABOVEGROUND TALLGRASS PRAIRIE BIOMASS

John M. Briggs, Division of Biology, Kansas State University, Manhattan, Kansas 66506

and

Duane Nellis, Department of Geography, Kansas State University, Manhattan, Kansas 66506

Abstract. Landsat thematic mapper digital data was found to offer an excellent potential for regular monitoring of the tallgrass prairie ecosystem by providing estimates of aboveground biomass production. Data from seven channels of a May thematic mapper scene were analyzed individually and in various combinations using stepwise regression in Statistical Analysis System (SAS). These procedures were used to determine the most appropriate multiple regression equation for estimating production of 1) total live aboveground biomass, 2) grasses, 3) forbs, 4) previous years dead, and 5) current years dead. Regression equations were based on satellite-derived estimates relative to ground level biomass values for watersheds on Konza Prairie Research Natural Area under a variety of burning treatments. Results suggest that multiple channel equations were most appropriate for measuring production of forbs and total live aboveground biomass. Channel one (0.45 to 0.52 μm) and channel four (0.76 to 0.90 μm) were applicable to estimate production of grass and levels of previous years litter, respectively. However, none of the channels were accurate in predicting current years dead. Further plans involve using thematic mapper data to estimate aboveground biomass over an entire growing season on Konza and exploring the potential of using satellite data to monitor grassland production across the Great Plains.

Key Words. tallgrass prairie, remote sensing, aboveground biomass, Landsat, thematic mapper, monitoring, Konza Prairie, Kansas

INTRODUCTION

Traditional techniques for estimating the productivity of grasslands are time consuming, destructive, costly, and do not lend themselves to evaluation of large geographical areas. Since the launch in 1972 of the first of a series of earth resources technological satellites named Landsat, the potential for utilizing remote sensing technology as a way of monitoring global resources has vastly increased. With improvement in Landsat resolution since 1982, via the onboard thematic mapper, refinements in levels of accuracy for measuring productivity with remote sensing techniques in grassland ecosystems have further increased [see Greegor (1986) for review]. The objective of this study was to determine which Landsat thematic mapper channels (Table 1) or combinations of channels would be most appropriate for predicting production of: 1) total aboveground biomass, 2) live grass, 3) forbs and woody plants, 4) current year's dead, and 5) previous year's dead (litter).

Table 1. Landsat thematic mapper bands and spectral characteristics.

Channel	*Spectral Ranges*	*Pixel Resolution*
	-------- um --------	---------- m ----------
1	0.45 to 0.52	30
2	0.52 to 0.60	30
3	0.63 to 0.69	30
4	0.76 to 0.90	30
5	1.55 to 1.75	30
6	10.40 to 12.5	120
7	2.08 to 2.35	30

METHODS

Study Site

Data were collected on Konza Prairie Research Natural Area. Konza Prairie (3,487 ha) is tallgrass prairie dominated by big bluestem (*Andropogon gerardii* Vitman) located in the Flint Hills of northeastern Kansas. Because of the steep and rocky topography, the Flint Hills include the only extensive area of unplowed tallgrass prairie remaining in North America (Hulbert 1985). Konza Prairie has a mean annual precipitation of 834 mm and a mean annual air temperature of 12.8 C (Greenland 1987). A fire management plan initiated on Konza Prairie placed different watershed units under prescribed spring burning regimes in 1971 of 1-(annual), 2-, 4- and 10-year intervals (Hulbert 1973. There are also a number of watersheds which are not burned. All watersheds used in this study have not been grazed for more than 10 years.

Ground Clipping

Abrams *et al*. (1986), Gibson and Hulbert (1987), Gibson (1988) and Knapp *et al*. (1985) have discussed the methods used to collect aboveground biomass data on Konza. Briefly, during three times in the growing season (spring, summer, and fall), all aboveground biomass in 20 quadrats (10 x 20 cm) were collected by clipping at ground level on various watersheds. The number of quadrats clipped per watershed depended on the size of the watershed, but as least 20 quadrats were sampled at each sampling interval. The clipped material was separated into forbs and woody plants, live gaminoids, standing dead, and all loose litter (dead biomass from previous years). The separated material was oven-dried at 60 C for 48 hr prior to weighing. For this study, eight treatment areas were used: two annually burned watersheds, one burned every two years, one burned every four years and four unburned watersheds. For each of the watersheds, a mean value for each aboveground component was calculated.

Satellite Digital Data and Data Analysis

An 18 May 1984, Landsat thematic mapper scene of Konza Prairie Research Natural Area was obtained. This date was selected because it corresponded to the post-spring burning period and it matched the ground clipping date. Burned watersheds were used because they are easily differentiated from unburned watersheds using digital data (Nellis and Briggs 1987). For each of the watersheds from which ground clipping the had been completed, a mean reflectance value was obtained for each of seven channels of the thematic mapper using a micro-based image processing system. These values were analyzed individually and in various combinations using multiple regression (stepwise procedure) with PC-SAS at a 0.15 significance level for entry in the regression model. The stepwise procedure is a modification of a forward-selection procedure in which, after a variable is added to the model, each variable is tested again for inclusion at the 0.05 level (SAS 1985). A 0.05 significance level for the model was used to determine the relationships between the ground clipping data and the satellite derived digital data.

RESULTS

Table 2 summarizes the aboveground biomass data separated out into the various components by watershed with the respective mean reflective value of each of the seven channels. Channel one (0.45 to 0.52 μm) was the best predictor of mean live grass on watersheds with a regression equation of: mean live grass = − 224.01 + 3.14*channel one (r^2 = 0.79; P = 0.04; Figure 1). For previous years dead, Channel four (0.76 to 0.90 μm) was the only individual channel that fit the 0.15 selection level into the model criteria. However, it was not significant (r^2 = 0.57; P = 0.14).

Table 2. Mean reflective value of each channel and aboveground biomass data by watershed.

		Channel											
Watershed	*Burned*	*One*	*Two*	*Three*	*Four*	*Five*	*Six*	*Seven*	*Total*	*Grass*	*Forbs*	*Current Year Dead*	*Previous Year Dead*
001A	YES	132.0	56.3	61.5	73.1	113.0	111.3	58.8	247.0	153.9	13.4	81.1	—
001D	YES	121.8	50.6	53.0	66.5	88.4	110.8	45.0	272.7	155.6	19.1	97.3	—
002D	YES	109.8	45.0	46.0	58.4	85.1	123.8	44.7	285.9	220.3	29.6	36.0	—
004B	NO	136.3	57.6	60.7	75.7	97.6	95.9	44.2	373.3	221.2	102.2	49.4	261.1
000B	NO	132.0	56.3	61.6	78.1	102.8	101.5	43.9	327.0	195.2	71.3	56.8	613.0
N00B	NO	114.5	47.0	52.7	62.3	101.6	123.6	44.6	280.7	139.7	86.8	54.2	714.7
N01B	NO	133.3	56.6	61.1	75.6	105.8	101.5	47.3	306.3	174.0	70.9	61.4	576.6
N04B	NO	126.1	52.7	56.2	67.9	97.4	101.5	42.5	353.7	168.2	112.4	76.7	659.8

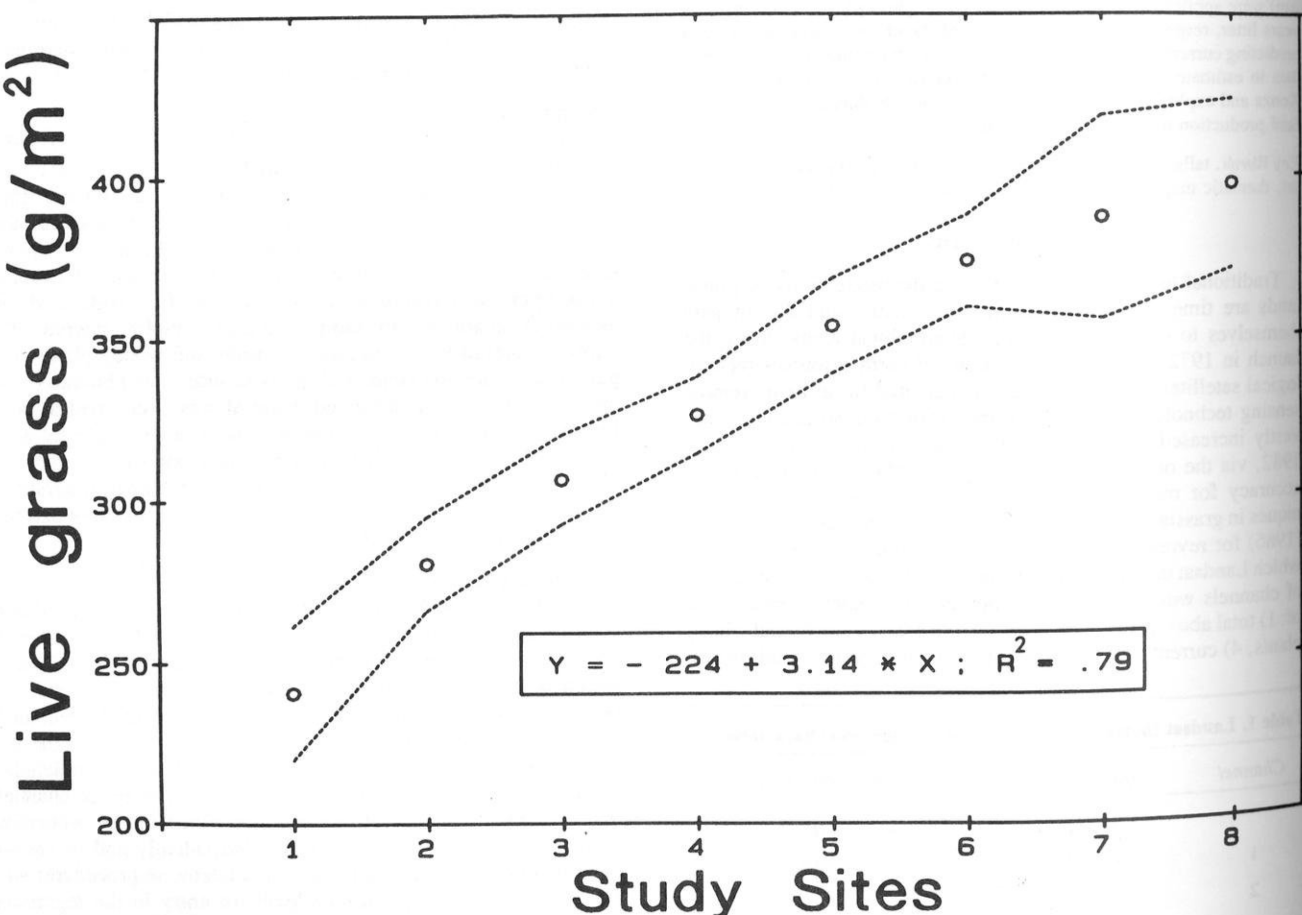


FIG. 1. Regression line and 95% confidence limits of the relationship between ground clipping data of live grass and satellite derived digital data on Konza Prairie Research Natural Area. Regression line = − 224.01 + 3.14*Channel one.

Multiple channel equations were most appropriate for measuring production of forbs and total live aboveground biomass. For forbs, the final equation was: forbs = 508.91 -1.84*channel three + 1.99*channel four biomass, the equation was total = 1016.98 + 2.79*channel two - 6.88*channel five - 1.38*channel six. However, this model only approached significance with a $P = 0.07$. The significance of combinations in the longer wavelength visible and near to mid-infrared electromagnetic energy for measuring forbs and aboveground biomass is due to the high reflectance of the healthy vegetation and low absorption in these portions of the spectrum. Obviously, the amount of infrared reflectance of the prairie canopies is going to be controlled, to a certain extent, by the stage of plant development. No individual channel or combinations of channels were applicable to predicting current years dead ($P > 0.15$). This is not surprising due to the irregular patchiness of the current years dead matter.

CONCLUSIONS

Although not all aboveground components were accurately predicated in this study, thematic mapper data were found to be valuable tools in non-destructive, large-scale assessments of important components of the tallgrass prairie. In particular, live grass, forbs and total aboveground biomass could be reasonably accurately assessed using various channel combinations.

Further plans involve monitoring the Konza tallgrass prairie over an entire growing season using remote sensing techniques and over several years to further expand and fine tune this technique. Furthermore, with the addition of bison on Konza, remote sensing will be used to study the interaction of fire and grazing at scales that could not be realized before. Remote sensing coupled with a geographical information system can address many questions that ecologists need to answer to understand the complex tallgrass prairie.

ACKNOWLEDGEMENTS

This research was funded by NSF grant BSR-8514327 for Long-term Ecological Research at Kansas State University, Division of Biology.

LITERATURE CITED

Abrams, M.D., A.K. Knapp, and L.C. Hulbert. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: Effects of fire and topographic position. American Journal of Botany 73:1509-1515.

Gibson, D.J. 1988. Regeneration and fluctuation of tallgrass prairie vegetation in response to burning frequency. Bulletin of the Torrey Botanical Club 115:1-12.

Gibson, D.J., and L.C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72:175-185.

Greegor, D.H. 1986. Ecology from space. BioScience 36:429-432.

Greenland, D. (ed.). 1987. The climate of long-term ecological research sites. INSTAAR, Occasional Paper 44, University of Colorado, Boulder.

Hulbert, L.C. 1973. Management of Konza Prairie to approximate pre-whiteman fire influences. Pages 14-19. *In* L. C. Hulbert (ed.), 3rd Midwest Prairie Conference Proceedings, Kansas State University, Manhattan, Kansas.

Hulbert, L.C. 1985. History and use of Konza Prairie Research Natural Area. The Prairie Scout 5:63-93.

Knapp, A.K., M.D. Abrams, and L.C. Hulbert. 1985. An evaluation of beta attenuation for estimating aboveground biomass in a tallgrass prairie. Journal of Range Management 38:556-558.

Nellis, M.D., and J.M. Briggs. 1987. Micro-based landsat TM data processing for tallgrass prairie monitoring in the Konza Prairie Research Natural Area. Papers and Proceedings of Applied Geography Conferences 10:76-80.

SAS. 1985. SAS/STAT guide for personal computers. Version 6 edition. SAS Institute, Cary, North Carolina.

NEBRASKA SAND HILLS: THE LAST PRAIRIE

Robert F. Whitcomb
Insect Pathology Laboratory, Agricultural Research Service, Beltsville, Maryland 20705

Abstract. Although North American grasslands are diverse and biotically rich, their conservation has never received high priority. As a result, the prairie landscape has all but disappeared. However, one prairie region has retained its essential pre-Columbian features. This is the Nebraska Sand Hills Prairie, a 4.8 million ha stabilized dune region of Holocene origin. Because the Sand Hills lie at the heart of the North American grasslands, their biota is influenced by the adjacent short- and tallgrass prairies and by northern (cool-season) and southern (warm-season) grasslands. In addition, the Sand Hills have their own distinctive sand-dependent biota. Equally important, however, is the heritage conveyed by their uninterrupted landscape and rich cultural history. Although the Sand Hills could be threatened by turning of their erodible soils for agronomic purposes that are not sustainable in the long term, implementation of the Conservation Reserve Program has reinforced historic patterns of sound land management. As a result, privately managed land in the Sand Hills serves a conservation function of global significance. In this region the optimal long-term public and private land use appears to be native prairie.

Key Words. Sandhills, prairie, Nebraska, preservation.

INTRODUCTION

> "The ranchman understood and loved the land the way he found it — grass side up. He knew, even as the Indian knew, that much of it could not be profitably farmed, that to break its thin, root-bound skin would deface and ruin it for years to come"
>
> Nellie Snyder Yost

This paper has its foundations in a series of studies (Whitcomb *et al.* 1986, 1987, and 1988, Whitcomb and Hicks 1988) that were conducted on the ecology and evolution of leafhoppers of North American grasslands. These studies pointed out both the significance of the Sand Hills and the need to make their importance known to others.

At the time of European settlement of the New World, the North American continent was rich in both mesic and semiarid grasslands. Today, the mesic grasslands that constituted the true prairie have been largely turned over to intensive agriculture. The Nebraska Sand Hills Prairie (Pool 1914, Keech and Bentall 1978, Wolfe 1984, Bleed and Flowerday 1989) is a 4.8 million ha region which has not declined in condition since European settlement. If landscape as well as grass is considered, the Nebraska Sand Hills is the last prairie. To relate the significance of the Sand Hills to others, this paper has been organized first to describe the ecosystem and then to address the issue of conservation.

DISCUSSION

Nebraska Sand Hills: The Heart of the North American Grasslands

The grassland types of the United States were mapped by Küchler (1964 and 1985). This work defined a "potential vegetation" in which vegetation was classified in terms of the natural communities that dominated the landscape before European settlement and that would reassert dominance in the absence of human disturbance. In addition to grasslands, of which 44 were described, several other formations were described, such as juniper-pinyon and ponderosa pine forests, which are in fact preponderantly grassland. The Nebraska Sand Hills lie at the heart of these North American grasslands (Figure 1).

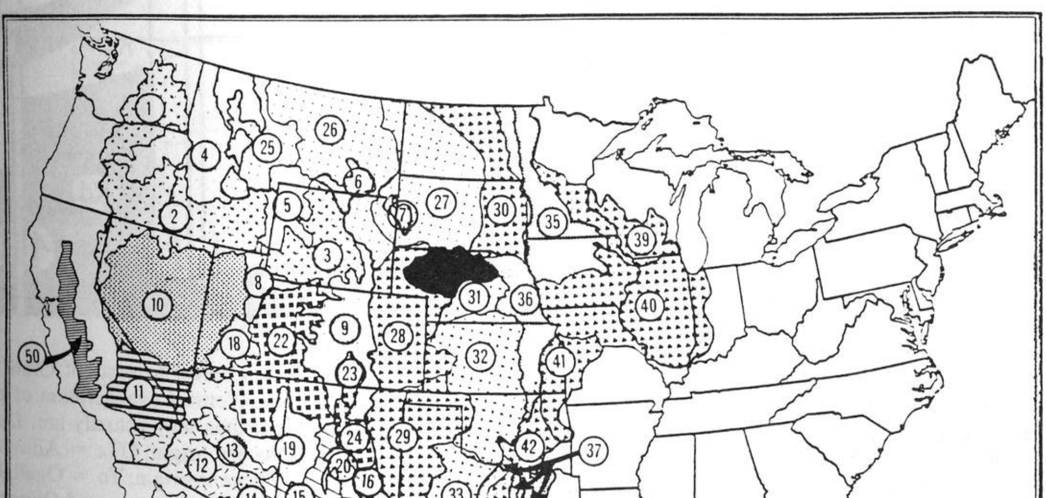


FIG. 1. Grassland regions of the United States; modified from Küchler (1964 and 1985). The Nebraska Sand Hills Prairie (solid black) lies at the heart of the North American grasslands (modified from Whitcomb *et al.* 1987); see this publication for descriptions of the illustrated regions.

East of the Sand Hills, wherever terrain permitted, the prairie has been almost quantitatively converted into cropland. Regions that were originally true prairie, or mosaics of prairie and woodland, generally receive 500 or more mm of annual precipitation, a reasonable proportion of which falls during the growing season. These prairies were dominated by tall grasses, including many warm-season (C_4) species. Principal dominant grasses of this region include big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Andropogon scoparius* Michx.), indiangrass [*Sorghastrum nutans* (L.) Nash], and switchgrass (*Panicum virgatum* L.). The regions in which these grasses were dominant include tallgrass prairie, oak savanna, deciduous forest-prairie mosaic, and the Fayette and Blackland Prairies of Texas.

South of the Sand Hills, the mixed prairie is a transitional grassland composed largely of short and tall warm-season grasses; this prairie formation receives 380-500 mm of annual precipitation. In this region, buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.] and blue grama [*Bouteloua gracilis* (Willd. *ex* H. B. K.) Lag. *ex* Griffiths] assume considerable importance. North of the Sand Hills, the transitional region between mesic and dry grassland is dominated by cool-season grasses such as western wheatgrass (*Agropyron smithii* Rydb.) and prairie junegrass [*Koeleria pyramidata* (Lam.) Beauv.]. Northwest of the Sand Hills, the semiarid prairie, although containing a minor component of short, warm-season grasses (blue grama and buffalograss) is largely a wheatgrass (*Agropyron*) prairie. To the west and southwest of the Sand Hills, the semiarid short-grass prairie, which receives 250-380 mm of annual precipitation, is dominated by blue grama and buffalograss.

With these different influences, it is small wonder that the Sand Hills have a biotic diversity that would not be predicted from their apparently monotonous physiognomy. This would be so, even if they were not composed of a seemingly infinite variety of combinations of sand and soil and water distributed along latitudinal and elevational gradients.

Climate

The Sand Hills region is large enough to exhibit considerable climatic variation. Annual precipitation in the Sand Hills ranges from about 580 mm in the east to less than 430 mm in the west (Wilhite and Hubbard 1989). As much as half of the precipitation is received during the prime growing season from May through July. Mean precipitation values for the Sand Hills can be deceiving, since precipitation varies greatly from year to year. For example, long-term records for Ewing, Nebraska show annual precipitation from as high as 960 mm to as low as 320 mm, the latter occurring in the 1936 drought. The Sand Hills were affected by the "great drought" of the 1930s, but they suffered less than many other Great Plains regions largely because the native flora is well adapted to withstand such variations in precipitation. Also, droughts, although severe, were of short enough duration that they did not severely affect the groundwater reserves. Snowfall, which ranges from 560 mm in the south to 1,440 mm in the north, is an important factor in groundwater recharge.

Mean temperatures in the Sand Hills range from 20-25 C. The freeze-free season varies from 150 days in the east to 120 in the west, primarily a reflection of elevational differences (approximately 1,220 m in the west to about 610 m in the east). Prevailing winds usually have a westerly component but frequently also are northerly or southerly; east winds are uncommon (Wilhite and Hubbard 1989).

Geology and Soils

About 98 million years before present (YBP), the present-day area of the Sand Hills was covered by Cretaceous seas (Swinehart and Diffendal 1989). Sediments of these seas were deposited for about 33 million years, until sea level fell worldwide. The Cenozoic strata found today between the recently deposited eolian (wind-deposited) sand and the underlying Jurassic and Cretaceous strata consist of either fine-grained volcanic sediments or alluvial sediments (Figure 2). Whereas the volcanic sediments originated from distant source areas, alluvial sands originated in regions immediately to the west of the Sand Hills. For example, material of the White River Group probably are derived in large part from what is now Colorado. Even in the early Tertiary, alluvial sands had begun to accumulate in the present-day Sand Hills region. A paleovalley of the White River Group with as much as 15 m of Chadron Formation sand occurs under most of Garden County (Swinehart and Diffendal 1989). The Arikaree group, formed 28-19 million YBP, covers the western third of the Sand Hills. One Arikaree paleovalley, as wide as 40 km in some places, is filled with more than 61 m of fine to medium sand.

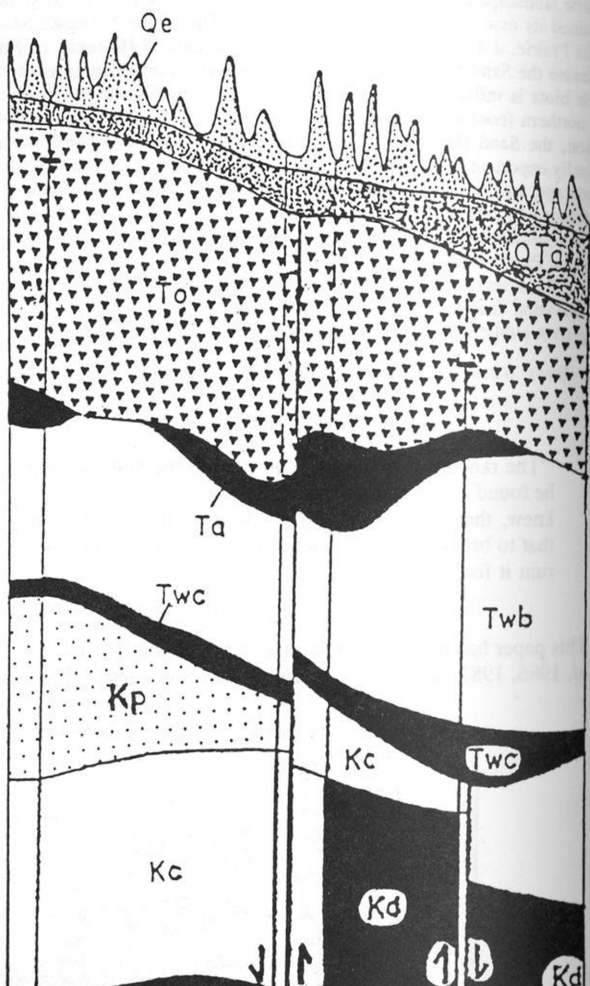


FIG. 2. Geologic section, west to east, of Grant County in the west central Sand Hills. Vertical exaggeration of diagram causes slopes to appear steeper than they actually are. Designations: Qe = Eolian sand of Holocene origin; QTa = Alluvial sand and silt of Quaternary and/or Pliocene origin; To = Ogallala Group (Miocene); Ta = Arikaree Group (Miocene and Oligocene); Twb and Twc = Brule formation and Chadron formation (respectively) of the White River Group (Oligocene); Kp and Kc = Pierre Shale and Colorado Group (respectively) of the Upper Cretaceous; and Kd = Dakota Group of the Lower Cretaceous. Two oil and gas tests are diagrammed: the end of the cased zone is indicated by a short horizontal line. Two faults are also diagrammed: arrows show direction of relative movement. Modified from a geologic section of the entire Sand Hills region of Swinehart and Diffendal (1989).

Beginning about 19 million YBP, in the Miocene, Ogallala group sediments began to accumulate in a major sedimentary basin (Figure 2). The drainage systems of this basin were diffuse. Ogallala sediments may have been deposited as alluvial fans or as sediments of braided rivers in wide shallow valleys. Thus, this group may represent an alluvial plain with a complex history (Swinehart and Diffendal 1989). Source areas of these sediments include present-day Wyoming and Colorado. These areas continued to be sources of alluvial sand in the Pliocene. Evidence for this is the presence in the sands of coarse sediments of that age consisting of uncommon materials such as anorthosite, an uncommon igneous rock of Wyoming's Laramie Mountains, or quartz pebble conglomerate from Wyoming's Snowy Range.

A scarcity of sediments between 2 million and 40,000 YBP makes assessment of the early Quaternary speculative. It is possible that significant erosion of the Ogallala and overlying younger strata occurred during the Pleistocene.

Modern drainage systems such as the Loup, as well as the Calamus and Niobrara (Figure 3), began to form about 20,000 YBP at the time of the last major pulse of continental glaciation. At that time, the area of today's Sand Hills may have been a broad alluvial plain with sandy streams flowing in valleys of low relief. Voorhies and Cormer (1985), for example, estimate that the central Niobrara valley during this period was 2-3 times wider but only half as deep as the modern Niobrara River.

Dramatic changes in the Great Plains region occurred 12,000 YBP as the last continental ice sheets retreated. By 9,000 YBP, spruce forests with prairie inclusions and aspen-pine parklands had given way to prairie (Fredlund and Jaumann 1987). But even during the Holocene, Sand Hills drainage patterns experienced dynamic changes. May and Holen (1985), for example, documented five distinct Holocene alluvial fills in the South Loup Valley. Also, Swinehart and Diffendal (1989) believe that the modern Dismal River valley is less than 1,500 years old.

But the current major geologic feature of the Sand Hills region is its stabilized eolian sand (Figure 2). In the south central and west central Sand Hills it is common to find 9-18 m of eolian sand; in other areas the thickness is 1-9 m. The sands contain between 1 and 4% silt and clay, giving the soils a cohesive property not possessed by pure sand. In many areas, vertical walled trenches can be dug in the dunes.

Although the Sand Hills are the largest eolian sand body in the western hemisphere, they are smaller than the large unstabilized sand areas of North Africa, Arabia, Asia, and Australia (Wilson, 1973). They are, however, one of the largest stabilized sand regions in the world.

Presumably, eolian activity is at least roughly correlated with dry climatic conditions. Large dunes tend to form in sandy regions when vegetation cover is less than 20% (Swinehart 1989). Under current precipitation regimes, cover in the Sand Hills greatly exceeds this percentage. Although some modern sand seas have less than 100 mm of annual precipitation, the Sand Hills may have developed with annual precipitation of nearly 250 mm per year (Swinehart 1989).

Although not obvious at the ground level, there are strong patterns in the arrays of large and small dunes. For example, satellite images of the west-central Sand Hills show strong alignments of straight to slightly curved ridges, with long axes trending west to east (Swinehart *et al.* 1989).

Further, the dunes of the Sand Hills have many forms (Smith 1965, Swinehart 1989). Parabolic dunes develop a "U" or "V" shape because their arms are anchored by vegetation. These dunes, essentially confined to the southwestern Sand Hills, have a consistent southeastern orientation. Dune-forming winds must, there-

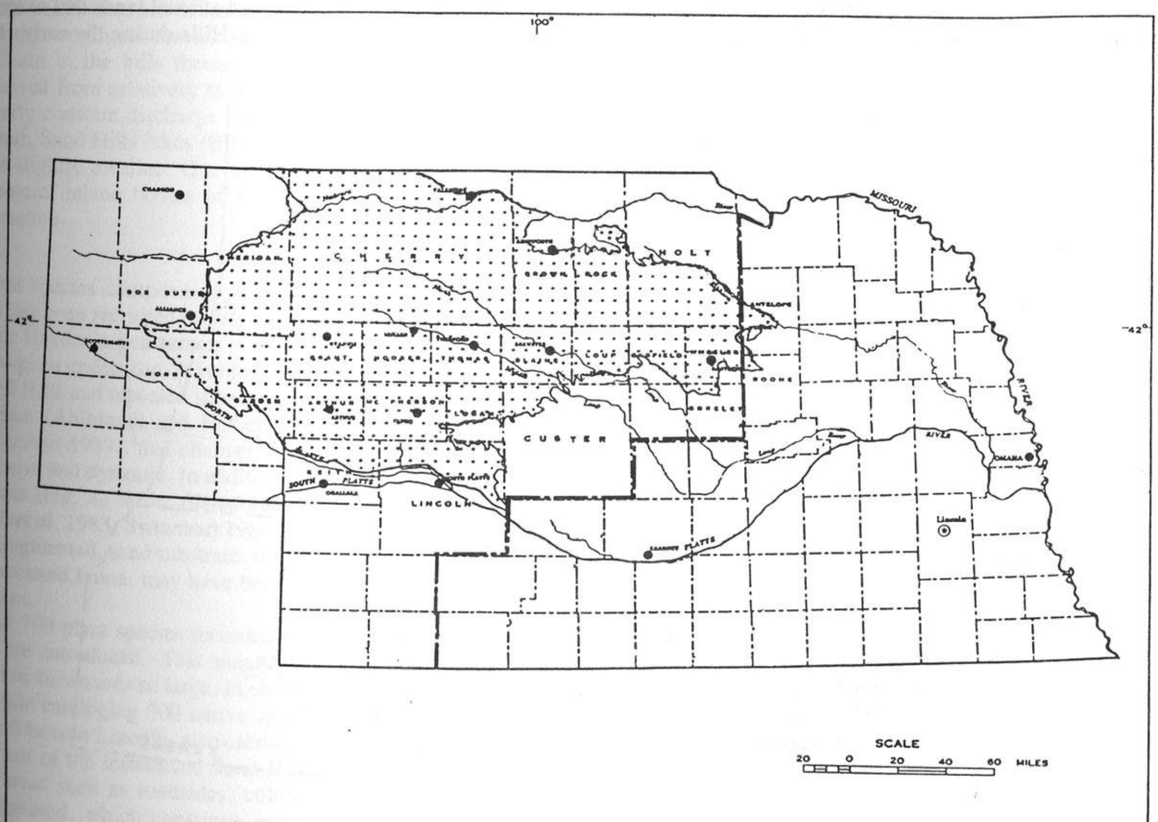


FIG. 3. The Sand Hills region of Nebraska (shaded). Kinkaid Counties (see text: European Colonization) lie to the west of the broad dashed line. A small portion of the Sand Hills extends into southern South Dakota.

fore, have blown from the northwest. In northeastern Colorado (Ramaley 1939) and southwestern Nebraska, the presence of dunes similar in age to the Sand Hills indicate that winds there must also have blown predominantly from the northwest (Muhs 1985) (Figure 4).

Most of the dunes have blowouts which, on a landscape level, impart a dimpled or pockmarked texture to large areas of the dune system. Pool (1914) described the cycle by which these depressions are generated and, eventually, revegetated. Blowouts originate on exposed upper slopes where the cover is broken or depleted from disturbances such as fire or overgrazing. During early stages, the blowout is simply a patch of bare sand a few meters wide and a few centimeters deep. Roots of deeper-rooted plants are exposed by the wind and, in time, the entire plant is blown away. When the young blowout is no more than 4-5 cm in depth the sand begins to slide into the depression, from which it is then blown away. After a number of years, the blowout may be hundreds of meters across. The inner slope that faces the wind is long and extensive. The opposite side is much steeper, in some cases nearly perpendicular. The steepness of this slope is often maintained by growth of sand-colonizing plants that are sheltered from the wind by the lee side of the blowout. Eventually the blowout reaches a size from which sand is no longer blown. Instead, the sand slides to the bottom of the blowout and remains there. At the bottom of such blowouts, numerous seeds, carried like the sand to the bottom, are able to germinate. The revegetation process initiated in this way eventually reclaims the blowout. The plant assemblages of blowouts are the most distinctive of the Sand Hills (Tolstead 1942) and include blowout grass [*Redfieldia flexuosa* (Thurb.) Vasey] and the endemic blowout penstemon (*Penstemon haydenii* S. Wats.).

At one time, it was believed that the Sand Hills dated to the Pleistocene (Lugn 1935, Swinehart 1989). However, Ahlbrandt *et al*. (1983) studied 7 sites at which radiocarbon-dated material less than 10,000 years old was overlain by eolian sand. The best documented interval of activity occurred 3,500 to 1,500 YBP. The linear dunes and most of the sand sheets, totalling about 2.1 million ha, probably formed at this time. Ahlbrandt *et al*. (1983) hypothesized that larger dunes occurred 8,000 to 5,000 YBP during the middle Holocene warm and dry period (altithermal) (Barry 1983). Corroborative evidence for Holocene origin of the Sand Hills has now come from many other sources (Bleed and Flowerday 1989). For example, Muhs (1985) found only immature soil profiles on Sand Hills dunes with thin A horizons that contain little organic matter (Lewis 1989). Even in soils of subirrigated meadows with thick A horizons, subsoils are unstructured and show no signs of clay accumulation. Thus, it appears that Sand Hills soils are in early stages of development. Many may be no more than 1,500 years old.

All available evidence, therefore, favors creation of the Sand Hills during multiple episodes of eolian activity during the last 10,000 years. Because these episodes were asynchronous, the dune fields have a complex history (Bradbury 1980). Present day eolian activity in the Great Sand Dunes area of south-central Colorado, in contrast to the pattern of stabilization in the Sand Hills, is a current example of such complexity and demonstrates that eolian activity is not necessarily correlated with contemporary climate. Nevertheless, it is reasonable to infer that appearance of the large dunes was related to the altithermal. Following about 2,000 yrs of stabilization, the climate again became dry, permitting further eolian activity. Extensive modification of crescentic dunes to domelike and domal-ridge dunes may have taken place in the central and eastern portion of the dune field at this time (Swinehart, 1989). After this eolian activity ceased, about 1,500 YBP, minor periods of drought have occurred, during which blowout processes have modified local dune structures (Swinehart 1989).

The source of the Sand Hills sand is indicated clearly by the geologic nature of its underlying sediments. As much as 60 m of Pliocene and Quaternary alluvial sand underlies the southeastern Sand Hills, and Quaternary sands are widespread in the northwest. The sand worked by Holocene eolian activity was derived, therefore, simply from unconsolidated alluvial sands that covered most of the present area of the Sand Hills during the early Holocene (Swinehart 1989).

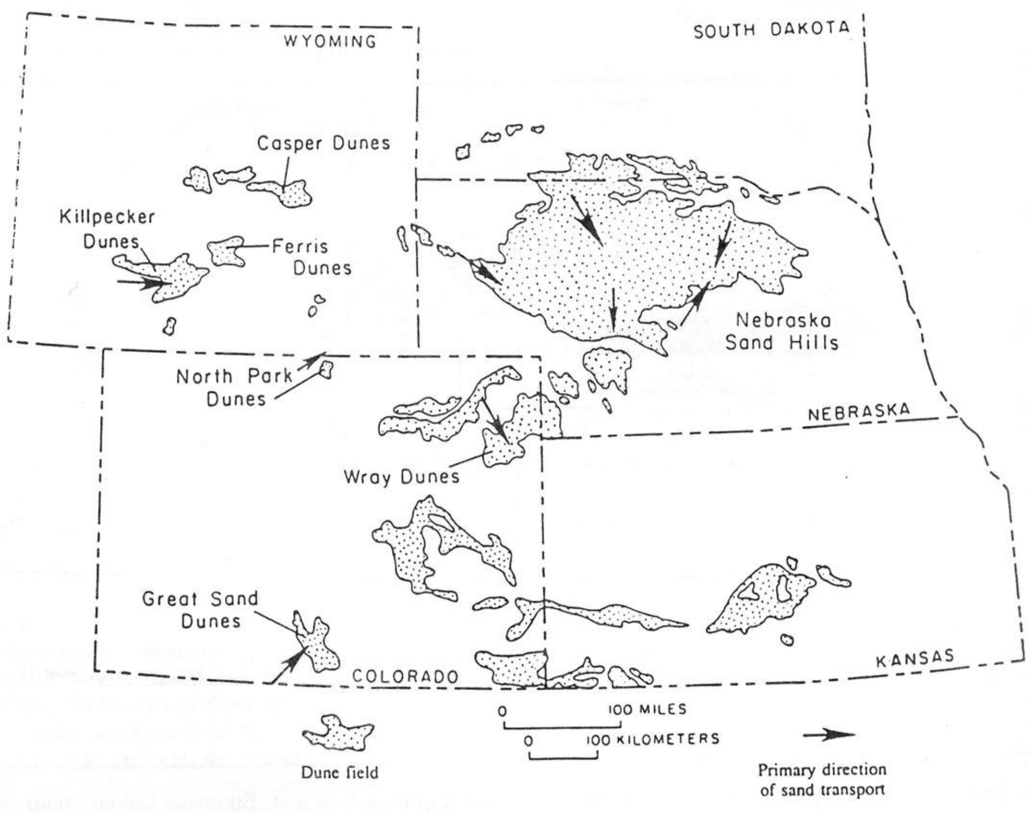


FIG. 4. Archipelago of sand regions in the west central Great Plains and central Rocky Mountain states. Figure from Ahlbrant *et al.* (1983) as modified by Swinehart (1989)

Water Resources

The Sand Hills are underlain by the High Plains Aquifer (Bleed 1989). Although the thickness of this aquifer (from 60-270 m) varies greatly, the portion underlying the Sand Hills is generally thicker than in other plains regions. The principal groundwater reservoir of the Sand Hills generally coincides with the base of the Ogallala Group. The aquifer generally slopes downward to the east, an orientation that coincides with the overall direction of the regional groundwater flow pattern. In some parts of the Sand Hills, the water table is at or near the surface, forming lakes, marshes, and subirrigated meadows.

A unique set of conditions is responsible for the rich groundwater resources of the Sand Hills. Although precipitation is only moderate and evapotranspiration rates are high, the combination of thick deposits of consolidated and gravelly sands, together with highly permeable surface sands, produces ideal conditions for aquifer recharge. Groundwater sequestered under such circumstances is mostly very low in dissolved solids.

The groundwater reserves of the Sand Hills are of national significance (Bleed 1989). Overflow from the aquifer feeds the Niobrara River and other streams and rivers. And, because the water is an important component of the Platte system, it is an important resource for downstream regions. Although large, this water resource is also fragile. Therefore, in areas where groundwater is close to the surface, extensive pumping could lower local water tables, severely impacting wetland ecosystems. High soil permeability, which facilitates recharge, would also facilitate groundwater contamination if pesticides or fertilizers were used on a large scale. Control of infiltration of such contaminants into the groundwater would be very difficult. For such reasons, the water resources of the Sand Hills require careful management (Bleed 1989).

Much of the western third of the region lacks streams and is referred to as the "Closed Basins Area" (Figure 3). The Niobrara river, whose headwaters are in eastern Wyoming, is the only Sand Hills river that originates outside the region. Other drainage systems originate in the hills themselves. Since these streams are largely derived from relatively steady groundwater seepage, they have a nearly constant discharge rate (Bentall 1989).

In general, Sand Hills lakes (Bleed and Ginsberg 1989) tend to be at least slightly alkaline. One of the lakes is among the most alkaline natural inland bodies of water known. Some lakes are also hypersaline.

Flora

The plant species composition of the Sand Hills suggests that their flora has been recruited largely from the surrounding prairie. Blowout or Hayden's penstemon is an exception to a rule of relatively low plant endemism. It is likely, given the Holocene origin of the Sand Hills and repeated subsequent pulses of eolian activity in the region (Ahlbrandt and Fryberger 1980, Ahlbrandt *et al.* 1983, Swinehart 1989), that changes in the Sand Hills biota have been extensive and dynamic. In addition, an archipelago of smaller sand regions (Fig. 4) in the plains and Rocky Mountain regions (Ahlbrandt *et al.* 1983, Swinehart 1989) has supplied an extensive, although fragmented, sand substrate. Hence, the present sand flora, and its associated fauna, may have been widely distributed during the Holocene.

Of about 700 plant species recorded from the Sand Hills, only about 50 are introduced. This number of exotic species is remarkably low for an area so large. In contrast, Kaul and Rolfsmaier (1987), while cataloging 300 native species on a tallgrass prairie of about 100 ha near Lincoln, also cataloged 60 introduced species. Further, most of the introduced Sand Hills plant species occur in disturbed areas such as roadsides, cultivated fields, and heavily grazed rangeland, which constitute a small fraction of the total Sand Hills area.

The Sand Hills Prairie, especially on xeric and mesic sites, is dominated by grasses (Sutherland 1984). There have been numerous efforts to group these grasses, and associated forbs, into communities (Pound and Clements 1900, Pool 1914, Weaver 1965, Harrison 1980, Kaul 1989). Kaul (1989) recognized 10 general types of vegetational community: bunchgrass, sand muhly, blowouts and draws, needle-and-thread, three-awn grass, short-grass, meadow, wet meadow, marsh, and aquatic. Sand Hills grasses can also be classified, more or less, on the basis of their adaptedness for soil sandiness, soil moisture, and/or alkalinity (Table 1). Particularly in a region such as the Sand Hills, where plant densities on many sites are relatively low (Pool, 1914), such a classification may be more appropriate than one based on community membership.

Table 1. Diagrammatic representation of the grasses of the Sand Hills ordinated by their position on the moisture gradient (vertical axis), soil sandiness (horizontal axis, upper portion of table) and water alkalinity (horizontal axis, lower portion).

More sandy — *Less sandy*

Redfieldia flexuosa
Muhlenbergia pungens
Triplasis purpurea
Calamovilfa longifolia — *Bouteloua hirsuta*
Buchloe dactyloides
Koeleria pyrimidata
Bouteloua gracilis
Bouteloua curtipendula
Stipa comata
Stipa viridula
Andropogon scoparius
Muhlenbergia cuspidata
Sporobolus cryptandrus
Agropyron smithii
Aristida purpurea
Paspalum setaceum
Dichanthelium oligosanthes
Dichanthelium acuminata
Dichanthelium wilcoxianum
Eragrostis spectabilis
Andropogon hallii
Eragrostis trichodes
Poa pratensis
Elymus canadensis
Elymus virginicus
Sorghastrum nutans
Andropogon gerardii

Mesic

Sporobolus airoides
Hordeum jubatum
Agrostis stolonifera
Puccinellia nutalliana
Distichlis spicata
Muhlenbergia asperifolia
Sphenopholis obtusata
Spartina gracilis
Spartina pectinata
Leersia oryzoides
Polypogon monspeliensis
Alopecurus aequalis
Phalaris arundinacea
Phragmites australis
Glyceria striata
Glyceria grandis
Catabrosa aquatica
Beckmannia syzigachne

Hydric

More alkaline — **Less alkaline**

Kaul (1989) has listed some of the important Sand Hills forbs and the communities in which they occur. Common forbs in xeric communities include Arkansas rose (*Rosa arkansana* Porter), Bush morning glory (*Ipomoea leptophylla* Torr.), leadplant (*Amorpha canescens* Pursh), lemon scurfpea (*Psoralea lanceolata* Pursh), New Jersey tea [*Ceanothus herbaceus* Raf. var. *pubescens* (T. & G.) Shinners], penstemon species (including the endemic blowout penstemon), pincushion cactus [*Coryphanta vivipara* (Nutt.) Britt. & Rose], poison ivy (*Toxicodendron rydbergii* (Small) Greene], and sand cherry [*Prunus pumila* var. *besseyi* (Bailey) Gl.]. In addition, various composites, such as asters (*Aster* spp. and sunflowers (*Helianthus* spp.) occur in these communities.

In marshes, wet meadows, and aquatic habitats, a variety of sedges, rushes, bulrushes, and reed species are found, as well as such forbs as arrowheads (*Sagittaria* spp.), clammy-weed [*Polanisia dodecandra* (L.) DC subsp. *trachysperma* (T. & G.) Iltis], cowlily [*Nuphar luteum* (L.) Sibth. & Small], duckweeds (*Lemna* spp.), floating azolla (*Azolla mexicana* Presl.), giant duckweed [*Spirodela polyrhiza* (L.) Schleid.], horned pondweed (*Zannichellia palustris* L.), water milfoil (*Myriophyllum* spp.) naiad (*Najas* spp.), pondweed (*Potamogeton* spp.), smartweed (*Polygonum* spp.), swamp milkweed (*Asclepias incarnata* L.), watercress (*Nasturtium officinale* R. Br.), waterlily (*Nymphaea* spp.), watermeal (*Wolffia* spp.), waterweed (*Elodea* spp.), water hemlock (*Cicuta* spp.), water plantain (*Alisma* spp.)., winged pigweed [*Cycloloma atriplicifolium* (Spreng.) Coult.], and widgeon grass (*Ruppia maritima* L. var. *occidentalis* (S. Wats.) Graebn.] (Great Plains Flora Association 1986).

If the vast majority of dry Sand Hills, wet meadows, and zoned aquatic niches seem to be monotonous, the flora of the Sand Hills river systems does not. This flora is recruited not only from surrounding prairie vegetation but from eastern, northern, and western floristic systems as well. For example, the vegetation of the Niobrara Valley reflects boreal, arid montane, and eastern deciduous forest elements (Kaul *et al.* 1988, Kaul 1989). Some of these elements are apparently relict populations that have persisted through the Holocene.

In general, the Sand Hills region, like much of the arid Great Plains, is now drier than it was during pluvial periods of the Pleistocene. Throughout the prairies and Great Plains there has been a tendency for complete retreat of spruce forests. In more recent time, there appears to have been a colonization by ponderosa pine (*Pinus ponderosa* Laws.) and cedars (*Juniperus* spp.) (Wells 1983), largely on scarps that are at least somewhat protected from fire. In the Sand Hills today, in the absence of periodic fire (now human controlled), there is a tendency for ponderosa pine to expand its local range, particularly in the vicinity of scarps (Steinauer and Bragg 1987).

Plant communities in the Sand Hills, like other communities, are determined in part by proximate and in part by historical determinants. Because the Sand Hills are recent in origin, there has been little time for development of soil diversity or for stochastic accumulation of species. The present-day climax communities are therefore relatively simple in terms of species numbers.

Among proximate factors, plant species occurrence is related strongly to topography. Although blowout communities have relatively few species, dune communities exceed those of the valleys and wet swales in species richness (Kaul 1989). The availability of subsurface water may be the most important factor determining plant species occurrence. The species richness of the dunes is explained by soil texture. Dune soils are coarse textured and have little organic matter. Because of the high infiltration rates, subsurface moisture is readily replenished. In contrast, in drier interdunal valleys the soils are more finely textured, and less water percolates into the soil. These soils hold more water in the spring than sandier soils but are depleted by midsummer. Thus, in dry summers these soils have less available moisture than those of the dunes (Barnes and Harrison 1982). Plants of the dune tops are deep-rooted warm-season (C_4) grasses (Barnes and Harrison 1982, Barnes and Heinisch 1984). The interdunal valleys are often dominated by cool-season (C_3) grasses such as western wheatgrass (*Agropyron smithii* Rydb.) or needlegrasses (*Stipa* spp.). The seasonal growth flush of these grasses occurs in the spring, when the subsurface moisture content of the interdunal soils is high.

Communities on north-facing slopes are often substantially different from those on south-facing slopes (Bragg 1978). Barnes (1980) felt that the temporal and spatial distribution of available water along local elevational gradients in the Sand Hills controlled such species differences through interactions with rooting morphology, photosynthetic physiology, and transpirational water loss. Competitive interactions also may play a role in the local distribution of Sand Hills grasses. For example, Heinisch (1981) demonstrated the role of root morphology in the niche partitioning of blue grama and hairy grama (*Bouteloua hirsuta* Lag.) in the western Sand Hills.

Sand Hills communities react dynamically to grazing pressures and fire disturbance and variations in precipitation. Responses to grazing pressure are rarely neutral. Plant species tend to either increase or decrease when grazed (Frolik and Shepherd 1940, Brinegar and Keim 1942, Sylvester 1957, Burzlaff 1962, Wolfe 1973, Bragg 1978, Stubbendieck 1989).

In earlier times, prairie fires were common (Pool 1914, Wolfe 1973, Richards 1980). Although there have been a few sporadic attempts to use prescribed burning on the Sand Hills range, fires have been generally feared by landowners, who believe that they are destabilizing. Indeed, rich growth flushes of the prairie after fire may be short lived if the new grass is exposed to desiccating late summer winds before the new growth has had an opportunity to regenerate a protective moisture-retaining thatch (Pool 1914). In general, the resulting changes in grassland quality after accidental fires have not suggested to land managers that burning would be a useful tool in the Sand Hills. In some reserves, however, fire has been used as a tool for increasing the content of fire-tolerant warm-season grasses at the expense of exotic cool-season grasses such as Kentucky bluegrass (*Poa pratensis* L.).

The landowners are among the best ecologists in the Sand Hills. These range managers, reinforced by specialists of the Soil Conservation Service and the University of Nebraska, are among the best in North America (Stubbendieck 1989). For this reason, and because of the close relationship between ecology and range management, advances in basic ecology will no doubt find their way rapidly into management practices in the Sand Hills.

Fauna

The Sand Hills fauna is very rich, reflecting eastern and western, northern, and southern influences.

Fish.

More than 75 species of fish have been recorded from the Sand Hills during historic times (Hrabik 1989). Only one species is presumed lost from the pre-European colonization inventory. In the Sand Hills, as elsewhere, fish diversity increases with increasing downstream position in the drainage basin. The Niobrara drainage system, in accord with its general biotic richness, has the second-highest number of fish species in the entire Missouri River basin (Bliss and Schainost 1973). In contrast to streams, Sand Hill lakes are less diverse with some playa like and others highly alkaline. Fewer species of resident fish are adapted to these limiting conditions.

Amphibians and reptiles.

Twenty seven species of amphibians and reptiles occur in the Sand Hills (Freeman 1989a).

Mammals.

In the late Pleistocene, mammoth, mastodon, horse, and camel were found in the present-day Sand Hills region. By 11,000 YBP, however, perhaps as a result of climatic change, perhaps because of activities of hunter-gatherers, or perhaps for both reasons, all became extinct. More recently, elk (*Cervus elaphus*), bison (*Bison bison*), and bighorn sheep (*Ovis canadensis*) have also been extirpated. But many species of mammals remain.

Of about 81 species of Nebraska mammals, 58 occur in the Sand

Hills (Freeman 1989b). This list includes three species that occur only in the Niobrara Valley. Moreover, two-thirds of Nebraska mammal species reach a regional, distributional limit in the state (Jones 1964) with some of these limits occurring in the Sand Hills. The Sand Hills, thus, act as a barrier that divides the range of some species. For example, a population of the eastern woodrat (*Neotoma floridana*) that occurs along the Niobrara River is disjunct from the main population to the south.

The occurrence of common species may be divided into two Sand Hills habitat zones, wet and dry. In wet areas are found opossum (*Didelphis virginiana*), masked shrew (*Sorex cinereus*), short-tailed shrew (*Blarina brevicauda*), least shrew (*Cryptotis parva*), eastern mole (*Scalopus aquaticus*), eastern cottontail rabbit (*Sylvilagus floridanus*), fox squirrel (*Sciurus niger*), gray fox (*Urocyon cinereoargenteus*), and least weasel (*Mustela nivalis*). In drier habitats, desert cottontail (*Sylvilagus audubonii*), black-tailed jackrabbit (*Lepus californicus*), spotted ground squirrel (*Spermophilus spilosoma*), Ord's kangaroo rat (*Dipodomys ordii*), silky pocket mouse (*Perognathus flavus*), western harvest mouse (*Reithrodontomys megalotis*), and northern grasshopper mouse (*Onychomys leucogaster*) occur. In addition, beaver (*Castor canadensis*) and coyotes (*Canis latrans*) are common in the Sand Hills. Raccoons (*Procyon lotor*) are common even in the absence of trees, since they can den in such habitats as burrows or clumps of cattails. Bobcats (*Lynx rufus*) are uncommon. Pronghorn antelope (*Antilocapra americana*) have been extirpated from the eastern Sand Hills, but they occur in some western parts. Mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginiana*) are common (Freeman 1989b).

Birds.

The avifauna of the Sand Hills is spectacular by any standard spectacular (Table 2). Seven special features of the region contribute to this richness. First, the numerous Sand Hills lakes (Bleed and Ginsberg 1989) serve as refugia for migratory waterfowl. Second, and even more importantly, these lakes serve as breeding areas for waterfowl, shorebirds, and other water birds. A large assemblage of breeding bird species are restricted to the vicinity of the lakes including the eared grebe (*Podiceps nigricollis*), western grebe (*Aechmophorus occidentalis*), 13 duck species, black tern (*Chlidonias niger*), American avocet (*Recurvirostra americana*), willet (*Catoptrophorus semipalmatus*), and Wilson's phalarope (*Phalaropus tricolor*). Third, an additional assemblage of seven bird species breed in fresh water marshes including the yellow-headed blackbird (*Xanthocephalus xanthocephalus*) and five rail and bittern species. Fourth, a distinctive assemblage of avifauna is made up of twenty-five species that breed in dry or mesic prairie. Of this group, those of special interest are the long-billed curlew (*Numenius americanus*), upland sandpiper (*Bartramia longicauda*), sharp-tailed grouse (*Tympanuchus phasianellus*), greater prairie chicken (*Tympanuchus cupido*), Swainson's hawk (*Buteo swainsoni*), golden eagle (*Aquila chrysaetos*), short-eared owl (*Asio flammeus*), burrowing owl (*Athene cunicularia*), and chestnut-collared longspur (*Calcarius ornatus*). Fifth, an additional feature of the Sand Hills is the Niobrara River Valley, whose riparian vegetation provides habitats for many eastern bird species. Sixth, the introduction of pine forests into the Sand Hills, now administered as two National Forest units, provides coniferous forest habitat. Seventh and last, but certainly not least, a crucial feature of the Sand Hills for faunal conservation is the large size of the region. It is now generally recognized that long-term species conservation requires large habitat units that can accommodate large populations (Soule 1986). Large population sizes serve to assure genetic diversity and to buffer against oscillations associated with climatic fluctuations, predator/parasite-prey cycles, or other periodic perturbations. The concurrent presence of all these conservation features in a single grassland region makes the Sand Hills of special interest in North American avifaunal conservation.

Table 2. Breeding bird species of the Nebraska Sand Hills; an expansion of lists by Molhoff (1985) and Labedz (1989). Alphabetic codes following common name are for (a) occurrence within the Sand Hills (codes before colon) and (b) habitat (codes after colon). Occurrence code: T = throughout; N,S,E,W = north, south, east, and west; L = local; A = accidental. Habitat: F = forest; H = habitations; L = lakes; M = marsh; P = prairie; R = riparian. * = Status uncertain. Scientific names may be obtained from American Ornithologists' Union (1983).

Pied-billed grebe, T:L; Eared grebe, T:L; Western grebe, W:L; Double-crested cormorant, W:L; American bittern, T,M; Least bittern, E,M; Great blue heron, T:L,R; Cattle egret, N:L; Green-backed heron, EN:L,R; Black-crowned night heron, T:L,R; White-faced ibis, LA:L; Trumpeter swan, W:L; Canada goose, T:L; Wood duck, T:L; Greenwinged teal, N:L; Mallard, T:L; Northern pintail, T:L; Blue-winged teal, T:L; Cinnamon teal, W:L; Northern shoveler, T:L; Gadwall, T:L; American wigeon, W:L; Canvasback, W:L; Redhead, T:L; Lesser scaup L:L; Ruddy duck, T:L; Turkey vulture, N:P,R; Northern harrier, T:P; Sharp-shinned hawk, N:R; Cooper's hawk*, L:R; Swainson's hawk, T:P; Red-tailed hawk, T:R; Ferruginous hawk, W:P; Golden eagle, L:P; American kestrel, T:R,H; Gray partridge, L:P; Greater prairie chicken, T:P; Sharp-tailed grouse, T:P; Wild turkey, N,R; Northern bobwhite, E:P,R; Ring-necked pheasant, T:P,R; Virginia rail, T,M; Sora, T:M; American coot, T:L,M; Piping plover, L:L; Killdeer, T:L,R,H; Black-necked stilt, L,L; American avocet, W:L; Willet, N:L; Spotted sandpiper, L:L,R; Upland sandpiper, T,P; Long-billed curlew, W:P; Common snipe, N:P; American woodcock*, E:R; Wilson's phalarope, T:L; Forster's tern, W:L; Least tern, L:L; Black tern, T:L; Rock dove, T:H; Mourning dove, T:L,P,R,H; Black-billed cuckoo, T:R; Yellow-billed cuckoo, T:R; Barn owl, T:H; Common screech owl, T:L,P,R,H; Great horned owl, T:P,R,H; Burrowing owl, T:P; Long-eared owl, L:R; Short-eared owl, T:P; Northern saw-whet owl, L:F; Common nighthawk, T:P; Common poorwill, W:P; Whip-poor-will, N:R; Chimney swift, T:H; Belted kingfisher, T:L,R; Red-headed woodpecker, T:R,H; Red-bellied woodpecker*, E:R,; Downy woodpecker, T:R,H; Hairy woodpecker, T:R; Northern flicker, T:R,H; Western wood pewee, W:P,R; Eastern wood pewee, E:R; Willow flycatcher*, L:P,R; Eastern phoebe, E:H; Say's phoebe, W:H; Great crested flycatcher, EN:R; Cassin's kingbird*, LW:P; Western kingbird, T:P,R; Eastern kingbird, T:P,R; Horned lark, T:P; Purple martin*, L:H; Tree swallow, E:L,R; Rough-winged swallow, T:R; Bank swallow*, L:R; Cliff swallow, T:H; Barn swallow, T:H; Blue jay, T:P,R,H; Black-billed magpie*, L:P; American crow, T:P,R; Black-capped chickadee, T:P,R; White-breasted nuthatch, E:R,H; House wren, T:H,R; Sedge wren*, L,P; Marsh wren, T:M; Eastern bluebird, T:H,R; Mountain bluebird, WL:P; Wood thrush, N:R; American robin, T:H,R; Gray catbird, T:P,R; Northern mockingbird, A:H; Brown thrasher, T:P,R; Cedar waxwing*, L:R; Loggerhead shrike, T:P; European starling, T:H; Bell's vireo, T:P,R; Warbling vireo, T:P,R; Red-eyed vireo, T:P,R; Yellow warbler, T:P,R; Black-and-white warbler, EN:R; American redstart, N:R; Ovenbird, EN:R; Common yellowthroat, T:P,R,M; Yellow-breasted chat, T:P,R; Scarlet tanager*, EN:R; Northern cardinal, E:H,R; Rose-breasted grosbeak, E:R; Black-headed grosbeak, W:R; Blue grosbeak, T:P; Lazuli bunting*, W,R; Indigo bunting, E:R; Dickcissel, T:P; Rufous-sided towhee, E:R; Chipping sparrow, N:H,R; Field sparrow, T:P,R; Vesper sparrow, N:P; Lark bunting, T:P; Savannah sparrow, N:P; Lark sparrow, T:P; Grasshopper sparrow, T:P; Song sparrow, E:L; Swamp sparrow, E:M; Chestnut-collared longspur, N:P; Red-winged blackbird, T:M,P,R,; Eastern meadowlark, TL:P, Western meadowlark, T:P; Yellow-headed blackbird, T:M,P,R; Brown-headed cowbird, T:H,M,P,R; Common grackle, T:H,R; Orchard oriole, T:P,R; No. (Baltimore) oriole, T:P,R; House finch*, SL,H; Pine siskin, N:F; American goldfinch, T:R; House sparrow, T:H

Invertebrate Fauna.

Although the invertebrates of the Sand Hills have not been intensively investigated, some groups have received attention (Hagen 1970, Whitcomb et al. 1988). The strong influence of the sandy substrate on the plant communities assures that the associated insect assemblages will be of special interest. This perspective can be illustrated with some insights from our own research.

In a comparison of the cicadellid fauna of five major grassland regions, we found the Nebraska Sand Hills assemblage to be especially diverse (Whitcomb *et al.* 1988). Because cicadellids are highly host specific, the underlying factors governing this diversity are easily surmised. Grassland leafhopper species can be classified as either generalists or specialists. Many generalists are actually broadly oligophagous species that confine their feeding to either grasses or forbs (Whitcomb *et al.* 1986 and 1987). Leafhopper diversity, therefore, directly reflects the diversity of dominant, perennial, native grasses and forbs (Whitcomb *et al.* 1986). Because the Sand Hills have recruited vegetational elements from surrounding prairie formations (east and west, north and south), and have, in addition, an assortment of plant communities dependent on a sandy substrate, they are vegetationally rich. The cicadellid species richness that we noted is therefore a direct reflection of plant species richness.

Several Sand Hills leafhoppers proved to be of special interest. These include especially species of the genus *Flexamia*. Members of this genus are closely associated with dominant, perennial, native chloridoid grasses (Whitcomb and Hicks 1988). We hypothesized that grasses fitting this description but that were only locally dominant, and therefore regionally uncommon or rare, could be hosts for undescribed *Flexamia* species. Two Sand Hills grasses appeared to fit this profile, both dominants of the blowout association; sand muhly [*Muhlenbergia pungens* Thurb.) and blowout grass, [*Redfieldia flexuosa* (Thurb.) Vasey]. It turned out that each was colonized by an undescribed *Flexamia* species. *Flexamia celata* was associated with blowout grass, and *F. arenicola* with sand muhly. These species were recently described by Lowry and Blocker (1987). The type locality for each is a research natural area of Crescent Lake National Wildlife Refuge in the western Sand Hills.

At first we thought that these new species would turn out to be endemics of the Nebraska Sand Hills. Further search, however, turned up other populations of these species (Whitcomb and Hicks 1988). In each case, however, the male genitalia of the extralimital populations show evidence of divergence from the Sand Hills populations. The case of *F. arenicola* is especially interesting, in that the recently discovered population (Anasazi form) in the Four Corners area (Arizona-New Mexico-Utah-Colorado) is clearly disjunct from the Nebraska population. The host, sand mulhy, is itself essentially disjunct, blocked on the northwest face of the Colorado Rockies by a combination of the Uinta Mountains and the dry *Agropyron* steppe of Wyoming and northern Colorado, and on the east by nonsand areas of Colorado and New Mexico (Whitcomb and Hicks 1988). Male genitalia of the Four Corners population are invariably broken, an event that presumably occurs during copulation. Therefore, it appears that the process of genetic divergence between the two populations has begun. From a conservation point of view, the important feature of the Nebraska Sand Hills population is that it is in little danger of extinction since its host reservoir is very large, and the regional population is divided into a large number of subpopulations, permitting "hedging" in the event of regional catastrophe. Populations of the Anasazi form may be stressed by increasing aridity in the Four Corners region.

For all of its sand biota, the Sand Hills provide an extent of habitat that is large enough to support viable populations. Especially because episodes of eolian activity appear to be more frequent than once supposed (Ahlbrandt *et al.* 1983, Swinehart 1989), extinction rates in small sand regions may prove to be high. Clearly, from all considerations of classical island biogeography (MacArthur and Wilson 1967), the largest sand reserve is surely the best. And for many invertebrate species, there will prove to be no extralimital populations, and the Sand Hills forms will prove to be indisputable endemics. Thus, when more complete invertebrate inventories are available, an increasingly large list of endemic invertebrates can be expected.

Finally, the very large size of the Sand Hills contributes to the diversity of its biota by permitting it to encompass geographic gradients. For example in many insect groups, such as mosquitoes (Lunt 1987), eastern or western, or northern and southern, range limits are encountered. This situation is not limited to invertebrates; many plant and animal species reach one or another range limit within the region (Jones 1964, Great Plains Flora Association 1986).

Sand Hills History

Just as an understanding of the geologic history of the Sand Hills region is vital to an understanding of its present-day physiognomy and biota, an understanding of human colonization of the Sand Hills is important to considerations of its future.

Native American colonization.

There is considerable evidence for colonization of the Great Plains at least 11,500 YBP. Indeed, many workers believe that the plains may have been colonized as early as 20,000 YBP. Thus, early native Americans were certainly on the scene at the time of formation of the Sand Hills in the Holocene. It is by no means certain that the Sand Hills were avoided by hunter-gatherers during periods of eolian activity, inasmuch as bison tracks occur in dune sand dated 7,260 YBP. These tracks suggest the presence of semipermanent water, even during dune-building episodes (Holen, 1989).

In the Paleo-Indian Period, at the close of Wisconsinan glaciation, Native Americans hunted mammoth and mastodon. After extirpation of these prehistoric mammals, bison probably served as the main prey for the hunters. Other species that were hunted included elk, deer, antelope, and smaller mammals. Waterfowl and fish were also probably hunted. Mass bison kills have been dated between 8,000 and 10,000 YBP. Steep-sided gullies were used as traps into which the bison were driven. Also, prehistoric agriculture may have been practiced on stream terraces and around some of the Sand Hills lakes.

There is abundant evident of agriculture in the Archaic period, 7,000-2,000 YBP. For example, many grinding stones for processing seeds have been recovered. Many artifacts from this period document extensive use of the Sand Hills for hunting.

In the Woodland period (2,000-1,000 YBP), ceramic vessels were used indicating a more sedentary lifestyle than that of the earlier hunter-gatherers. Pottery from this period is common along Sand Hills lakes and streams. Squash and beans were among the crops that were cultivated. Some maize was also grown late in the period.

After the Woodland period, 500-1000 YBP, Central Plains Tradition and Initial Coalescent peoples (thought to be ancestral to the Pawnee and Arikara) inhabited the plains, practicing a mixed economy of corn, beans, and squash, in addition to hunting.

In all, there is only limited evidence for permanent occupation of the Sand Hills during the Holocene. It is clear, however, that a number of the tribes that resided around the periphery of the Sand Hills used the region for seasonal hunting (Holen 1989). For example, the Plains Apache, although essentially southwestern, are well documented archaeologically in the Sand Hills, where they must have competed with the Pawnee for bison-hunting range. The Comanche appear to have been short-term occupants in the 1700s.

In historic times, a wide array of tribes utilized the Sand Hills. From 1540 to 1740, a mixed economy based on horticulture and hunting was practiced in the eastern plains. Farther west, other groups were predominantly hunter-gatherers, following a seasonal cycle in which bison were the main food supply. Both types of economy, however, led to use of the Sand Hills for hunting.

A 1718 map shows 12 villages of the Skidi-band Pawnee on the Loup River and another group of 12 villages that represented the Grand band of Pawnees (Tucker 1942). Skidi hunting territory appears to have been from the Platte River north into the Sand Hills to the Dismal River. Some of the eastern Sand Hills were hunted by the Omaha (Holen 1989).

On the northern edge, the Ponca hunted west along the Niobrara River and ventured south into the hills. But if they went too far they encountered Brule, Oglala, or Cheyenne. Some areas of the central Sand Hills (e.g., Shell Creek north to the Niobrara), may have been disputed by the Omaha and Cheyenne, as well as by the Pawnee and Ponca. Certain Sioux tribes also utilized the hills; by the 1830s the Brule Sioux were contesting the hunting grounds of the Pawnee and Omaha.

European colonization.

European colonists were slow to discover the Sand Hills. The region was known to early settlers as the "Sand Hills Desert" and was studiously avoided by early travellers. It was, in the words of B. Richards

> "avoided as no other part of the cattle country. The awe of this desert was widespread and real. Men had been known to venture into the region, lose their way and never be seen again. The hills were covered with a rather long grass [presumably prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.]; all hills looked alike; there were few landmarks; and water was uncertain, often alkaline."
>
> B. Richards Jr., 1980

The value of the region was apparently first discovered by cowboys of the N Bar Ranch, which was located 80 km east of Chadron on the Niobrara River (Figure 3). During the winter, the N Bar deployed line riders along the northern edge of the Sand Hills to prevent cattle wandering into them. In March 1879, however, an intense blizzard forced the line riders to seek shelter for survival, and some 6,000 N bar cattle drifted into the hills. An expedition was organized to rescue the lost cattle, and the N bar wagon headed into the hills on April 15.

As told by Jim Dahlman, who later became mayor of Omaha, as they entered the hills, the members of the expedition began to find native cattle:

> "as fat as any ever brought out of a feed lot; mavericks [unbranded] from one to four years old. We could hardly believe our eyes . . . Remember these cattle had no feed except native grass, and this was the month of April, after a terrific winter."
>
> Jim Dahlman, 1927

The expedition was a long one, and provisions ran low. Camping near a lake one day, the party had a dinner consisting solely of bean soup. In honor of that dinner, the lake was named Bean Soup Lake. In all, the expedition, which lasted five weeks, netted 8,000 bar N cattle and 1,000 head of "natives" that had been there for years (Dahlman 1927). It was this expedition that established the Sand Hills as exceptional cattle range.

At the time of their "discovery," the Sand Hills were almost totally in the public domain. From the time of the American Revolution, disposition of western lands had been an important issue. For many years after the Revolution, proceeds from land sales were used to reduce the national debt. Speculation in western lands became a common business enterprise. Land was cheap. For example, under the Preemption Act of 1841, 65 ha (160 A) could be purchased for $3.09/ha ($1.25/A). At such prices, most arable land east of the Mississippi River passed readily into private ownership. To encourage westward migration, President Lincoln in 1862 signed the Homestead Act, under which settlers were given title to tracts of 65 ha of surveyed public domain if they cultivated the land and lived on it for five years. However, while arable land east of the Sand Hills could often be homesteaded successfully, the Sand Hills, even more than the semiarid lands to the west, were not amenable to settlement of a mere 65 ha.

Encouraged by the construction of railroads, floods of settlers arrived in the plains in the 1880s to take up either farming or, to be lured by the open range in the public domain, cattle ranching. And, with vast acreages of public land available, the cattle business could be immensely profitable. For example, the cattle enterprise in 1895 in the northern Sand Hills was estimated to have yielded $2,000,000 (Richards 1980).

By the turn of the century, Sand Hills ranching had become a large-scale operation. For example, on a large ranch two or three windmills were established at each water station, each fitted with a 7.5-10.0 cm pump operated by a 3.7 m wooden windmill. Water from these mills flowed into reservoirs 6-9 m in diameter. The stations cost as much as $1,000 each; costs such as these were, of course, beyond the means of small operators. An indication of the size of a large operation can be obtained by measuring some of the tasks; in July, the Spade, one ranch operation, cut 15,000 tonnes of hay and plowed 644 km of fireguards. By the early 1900s, the Spade was the largest cattle company in Nebraska, running between 20,000 and 40,000 head.

Fire was a real threat, especially in the fall and winter, when the grasses became tinder dry. Fires, if not extinguished, burned over large areas, destroying range and winter feed. For this reason, large ranches like the Spade (Richards 1980) employed crews that plowed parallel fireguards that completely encircled their range. The grass between the guards was burned between August and October.

Fire, however, was not the only natural threat to ranching in the Sand Hills. Severe losses due to climatic variations, such as those experienced in the droughts and severe winters of 1885-87 made it clear that planning for winter range, good water, and hay for feed during winter snows were essential for a cattle operation. It was impossible to manage in this way without fencing. For example, it was necessary to protect lower hay meadows from untimely grazing. Under an open range system, the cattle grazed hay meadows preferentially in the summer. These hay meadows and winter pastures needed to be fenced and protected from grazing and fire during the summer months. In the winter, the cattle were given access to the protected pastures and supplied with hay during winter snows.

But throughout the semiarid grasslands, and especially in the Sand Hills, it was virtually impossible for stockmen, within the law, to obtain outright ownership of enough lands for their needs. "It took much scheming, scrambling, and perjury to assemble the acreage necessary for a sound ranching operation" (Larson 1965).

As a result of the fencing controversy, legislators from Great Plains states introduced legislation in 1901 under which federal lands adjacent to ranch holdings could be leased. But President Theodore Roosevelt, although generally sympathetic to conservation interests and no stranger to the plains, was unsympathetic to the fences. In his administration, the fencing act of 1885 was to be enforced: "Gentleman, the fences must come down." And in 1904, Congress passed the Kinkaid Act, which,. in 37 counties of western Nebraska (Figure 3), increased the size of homestead tracts from 65 to 260 ha. Unfortunately, this act combined 15 counties that were predominantly Sand Hills with 22 others of greater farming potential. Whereas some semiarid lands could be farmed in units of 260 ha, few Sand Hill tracts of that size were "proved up." Efforts to liberalize the law to permit land to pass more readily into private ownership were made. One was an amendment to the Kinkaid Act by which 194 ha (480 acre) isolated or disconnected tracts could be sold. In 1912, sale was authorized of 65 ha tracts "the greater part of which is mountainous or too rough for cultivation." In the same year, the time required to gain title under the Kinkaid Act was reduced from five to three years. By all these devices, the public domain of the Sand Hills eventually devolved into private ownership.

But the process was made no easier by the failure of Congress to devise legislation that was appropriate for the Sand Hills. As stated by Richards (1980): "The argument by Sand Hill ranchers, tirelessly reiterated, that their area was unique and should be handled as a grasslands unit . . . convinced few people in Washington."

Today's ranches, the product of numerous consolidations, are, for the most part, large enough to engage in the management practices devised by the earlier stockmen. In the east, some ranches of about 500 ha are proving to be sustainable, whereas in the west, average sizes are 1,600-2,400 ha (Miller 1989). But now, as always, the secret to effective stewardship of Sand Hills land is respect for the ecological forces that created the grassland and that are responsible for maintaining it.

Grassland conservation.

In general, interest in grassland conservation in the United States is geographically uneven (Whitcomb 1986). Predictably, greatest concern for losses of prairie come from states in which present-day destruction is nearly complete. These are, essentially, states such as Minnesota, Wisconsin, Iowa, Illinois, and Missouri that originally had extensive savannas or forest-prairie mosaics. Conservation groups in these states are very active and in some cases (e.g., Missouri) have managed to salvage small but significant preserve areas. However, in many instances, prairie destruction has gone too far, and restoration, rather than conservation, is being attempted. Unfortunately, even the botanical elements of prairie cannot be wholly reconstructed, and faunal restoration is totally hopeless.

It would certainly be helpful if states with an existing prairie inventory were to give grassland conservation the priority status it deserves. The fate of tall-grass prairie rests today on a few remnants that are managed as rangeland or hay meadows. Unfortunately, because these tracts are almost exclusively in private ownership, they will eventually be subjected to some or many of the same pressures that have already destroyed most prairie. In such regions, it is surely desirable to sequester prairie reserves. I wish to stress, however, that landowner participation should be a vital part of this process. In many instances, the public owes landowners a deep debt of gratitude, since retention of their lands as grassland has involved personal decisions that fully recognized the intrinsic value of the land as natural grassland.

In semiarid grasslands west of the Sand Hills, disappearance of native communities is less imminent, but many problems exist nonetheless. For example, there are many controversial issues regarding optimal land use. In much of the semiarid west and southwest, grasslands are under public ownership, in many cases by the USDA Forest Service or Bureau of Land Management. Although personnel of these agencies are almost unanimously concerned about proper management, they are constrained by the definition of their missions. The missions of these agencies, particularly concerning the balance between conservation and exploitation, is a proper subject for public debate. The western third of the nation is a confetti-like assortment of tiny vegetation units defined by climatic and elevational barriers and the topographies of mountain ranges, valleys, and river systems (Küchler 1985). Research on many plant or insect taxa indicates an exceptionally high species richness in this part of the United States, particularly in the southwest, where extinctions attributable to glacial cycles have been minimized by altitudinal migrations of communities. Preserve design in the face of such complexity is at present difficult or impossible (Whitcomb 1986). Rather, it is reasonable to hope that the bulk of the semiarid lands will be forever held in public ownership and managed for the common good, balancing resource needs with responsible management of biological and historical resources.

Biotic heritage.

A compelling case for conservation of Sand Hills grasslands can be made of the basis of biotic conservation. Because the Sand Hills are the largest sand dune area in the Western hemisphere and are one of the largest stabilized dune areas in the world (Bleed and Flowerday 1989), they are globally significant as a refugium for all of the plant and invertebrate species — whether or not their biologies are currently known — that evolved with the sand prairies of the Pleistocene and Holocene. Also, because the Sand Hills are the last prairie, they are of significance for many prairie animal or plant species that have vanished from, or are threatened or endangered in, prairie formations elsewhere.

The conservation significance of the Sand Hills has not gone completely unnoticed. Three national wildlife refuges have been established in the region; Valentine (28,942 ha), Crescent Lake (18,616 ha), and Fort Niobrara (7,739 ha). Also, the Nature Conservancy has acquired two preserves; the Niobrara Valley Preserve (21,853 ha) (Harrison 1980) and Arapaho Prairie (780 ha). However, given the relatively low carrying capacity of Sand Hills soils, the large acreages in these preserves are deceptive. The carrying capacity of dry Sand Hills prairie, with its thin topsoil and easily erodible soils, may be no more than a tenth of that of richer soils of, for example, eastern deciduous forest.

The small size of the Sand Hills prairie preserves seems anomalous when contrasted with its planted forests (Hunt 1965, Schmidt 1986). These units, established as experiments in type conversion of prairie to forest, occupy more than 81,000 ha. By this measure, more effort has been made to establish "reserves" that destroy prairie by replacing it with an artificial fire- and drought-sensitive formation than to preserve the native vegetational communities.

Important though they may be, the existing prairie reserves are not large enough to be self-sufficient; they are dependent on good management of surrounding range. As a result, their value would be fatally compromised if the Sand Hills around them were to be diverted to nongrassland uses. But today these grasslands stand intact. Guarantors, in a sense, of the preserves. Together, public and private lands function as a complete prairie ecosystem, not a mere remnant of one. The long-billed curlews, avocets, and phalaropes that we see in the refuges are in fact members of regional populations whose long-term existence requires not only the refuges but the privately owned grasslands that surround them.

Landscape heritage.

> "The Sand Hills are beautiful today, soft and green and dotted with flowers. . . . You feel that you are not trespassing when you stroll over the hills or lie at length on the sand, watching the shadows of the clouds drift over the dimpled hills."
>
> Joe Wing, Breeders Gazette, July, 1904

There are various fundamental criteria by which a society deserves to be judged. One of these is the degree of respect that it accords to its natural heritage. As rich and deserving as is the case for conservation of the Sand Hills on biotic grounds, unquestionably the greatest case lies in their landscape itself.

In the early years of park and forest planning in the United States, there was a clear appreciation of the value of bigness. In his tenure as President, Theodore Roosevelt ensured the sequestering of 61 million ha of public domain into the National Forest System. As exploitative as the free enterprise system was of the environment, means were found to create parks of the size of Yellowstone (about 900,000 ha), Yosemite (about 300,000 ha), and Grand Canyon (about 500,000 ha). There can be no question, in contemplating the diverse natural features of these parks, that they are the work of an ambitious nation that placed great value in its finest and unique natural features. But scenic wonders notwithstanding, the very size of these parks may be their most important characteristic.

The success of such parks could never have been achieved had they been niggardly in inception. Had the park process preserved the equivalent of Yellowstone Park in pieces (a geyser here, a hot spring there, a montane lake here, and a waterfall there) the cumulative impact of the separate pieces would not add up to a scintilla of the Yellowstone experience enjoyed by today's park visitors. Or imagine preservation of a "representative section" of the Grand Canyon.

In what we choose to conserve, we make an important statement about space. From the time of European settlement of the New World, possibility has been an open-ended process, and it has been symbolized in an important way in the relationship of Americans with unoccupied land. In a great nation, there is a national need for vastness.

Unfortunately, we have been grossly negligent in our planning for prairie space. Of the millions of km^2 of Pre-Columbian tallgrass and transitional prairie (approximately 550,000 km^2 exclusive of the Nebraska Sand Hills) and Oak savanna/deciduous forest-prairie mosaic (about 460,000 km^2), none has been saved in National Park or National Grassland, and essentially none in National Forest. The neglect of prairie grassland in our national aspiration for space represents a glaring and unacceptable omission. The national need for prairie space is supplied today by the private, not the public sector, in the Nebraska Sand Hills.

CONCLUSIONS

So the Nebraska Sand Hills Prairie today, in the vast majority (90%) of grassland that remains unplowed (Miller 1989), retains its character as native grassland. Preservation of the region has been achieved not through the park process, but as a result of natural economic forces. As reforestation of the Sand Hills was once a dream (Hunt 1965), so the concept of intensive agriculture has more recently proved again to be unsustainable, even in the short term. The Conservation Reserve Program is the most recent vehicle by which incentives for grassland maintenance are being reinforced. In the Sand Hills region, maintenance of native grassland has proven to be the best economic alternative.

I argue that Sand Hills landowners have contributed to the nation a more-or-less unrecognized public good. These landowners are good stewards of the land not only because it is in their economic interest but also because they know the land and its limitations (Stubbendieck 1989). They care for the land as no casual visitor or short-term manager could (Madson 1978). In so doing, they have regularly performed many of the vital functions of the park process; they have maintained, and are continuing to maintain, an entire vegetational region in an essentially pre-Columbian condition. It is not clear that this function has been recognized even in verbal terms, let alone in the structuring of economic incentives.

In the Sand Hills, history strongly suggests that optimal long-term public and private land use may be one and the same. Is it not possible that means can be found, by adjustments in public or private policy, to encourage this historic silent partnership between wise land managers and a nation made richer by the treasure that they have preserved? It is my hope that the future may see a new direction in conservation, one that seeks specific means to stabilize desirable land use patterns by encouraging wise private stewardship. Such an approach would pay rich dividends in the Nebraska Sand Hills.

ACKNOWLEDGEMENTS

I gratefully acknowledge discussions of Sand Hill geology with T. S. Ahlbrandt that improved the paper immeasurably. Comments of an anonymous reviewer on an earlier draft of the manuscript were also extremely valuable. I thank my wife, Judith B. Leach, for editing several versions of the manuscript. Responsibility for errors remaining after such assistance remains, however, with the author.

LITERATURE CITED

Ahlbrandt, T.S. 1973. Sand dunes, geomorphology and geology, Killpecker Creek Area, Northern Sweetwater County, Wyoming. Doctor of Philosophy Thesis, University of Wyoming, Laramie.

Ahlbrandt, T.S., and S.G. Fryberger. 1980. Eolian deposits in the Nebraska Sand Hills. United States Geological Survey Professional Paper 1120A:1-24.

Ahlbrandt, T.S, J.B. Swinehart, and D.G. Maroney. 1983. The dynamic Holocene dune fields of the Great Plains and Rocky Mountain basins, USA. Pages 379-406. *In* M.E. Brookfield and T.S. Ahlbrandt (eds.). Eolian sediments and processes, developments in sedimentology, Volume 38. Elsevier Science Publishers, Amsterdam, The Netherlands.

American Ornithologists' Union. 1983. Checklist of North American birds. 6th Edition.

Barnes, P.W. 1980. Water relations and distributions of several dominant grasses in a Nebraska Sand Hills Prairie. Master of Science Thesis. University of Nebraska, Lincoln.

Barnes, P.W., and A.T. Harrison. 1982. Species distribution and community organization in a Nebraska Sand Hills prairie as influenced by plant/soil water relationships. Oecologia 52:192-201.

Barnes, P.W., and S.P. Heinisch. 1984. Vegetation patterns in relation to topography and edaphic variation in Nebraska Sand Hills prairie. Prairie Naturalist 16:145-158.

Barry, R.G. 1983. Climatic environment of the Great Plains, past and present. Transactions of the Nebraska Academy of Sciences 11:45-55.

Bentall, R. 1989. Streams. Pages 93-114. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Bleed, A. 1989. Groundwater. Pages 67-92. *In* A.Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Bleed, A., and C. Flowerday (eds.). 1989. An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Bleed, A., and M. Ginsberg. 1989. Lakes and wetlands. Pages 115-122. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Bliss, Q.P. and S. Schainost. 1973. Niobrara River stream inventory report. Nebraska Game and Parks Commission, Lincoln.

Bragg, T.B. 1978. Effects of burning, cattle grazing and topography on vegetation of the choppy sands range site in the Nebraska Sand Hills Prairie. Pages 248-253. *In* D.N. Hyder (ed.). Proceedings of the First International Rangeland Congress, Denver.

Bradbury, J.P. 1980. Late Quaternary vegetation history of the Central Great Plains and its relationship to eolian processes in the Nebraska Sand Hills. United States Geological Survey Professional Paper 1120C:25-36.

Brinegar, R.E., and F.D. Keim. 1942. The relations of vegetative composition and cattle grazing on Nebraska range land. University of Nebraska Agricultural Experiment Station Research Bulletin 123.

Burzlaff, D.F. 1962. A soil and vegetation inventory and analysis of three Nebraska Sand Hills range sites. University of Nebraska Agricultural Experiment Station Research Bulletin 206.

Dahlman, J. 1927. Recollections of cowboy life in western Nebraska. Nebraska History Magazine 10:335-339.

Fredlund, G.G., and P.J. Jaumann. 1987. Late Quaternary paleological and paleobotanical records from the central Great Plains. Pages 167-178. *In* W.C. Johnson (ed.). Quaternary environments of Kansas. Kansas Geological Survey Guidebook Series 5.

Freeman, P. 1989a. Amphibians and reptiles. Pages 157-160. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Freeman, P. 1989b. Mammals. Pages 181-188. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Frolik, A.L., and W.O. Shepherd. 1940. Vegetative composition and grazing capacity of a typical area of Nebraska Sand Hill rangeland. University of Nebraska Agricultural Experiment Station Research Bulletin 117.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Hagen, A.F. 1970. An annotated list of grasshoppers (Orthoptera, Acrididae) from the eleven Panhandle counties of Nebraska. Nebraska Agricultural Experiment Station Research Bulletin 238.

Harrison, A.T. 1980. The Niobrara Valley Preserve: Its biogeographical importance and description of its biotic communities. Report to the Nature Conservancy. Minneapolis.

Heinisch, S.P. 1981. Water allocation and rooting morphology of two *Bouteloua* species in relation to their distribution patterns in the Nebraska Sand Hills. Master of Science Thesis. University of Nebraska, Lincoln.

Holen, S.R. 1989. Anthropology: The native american occupation of the Sand Hills. Pages 189-205. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Hrabik, R.A. 1989. Fishes. Pages 143-156. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Hunt, J.C. 1965. The forest than men made. Parts I and II. American Forests.

Jones, J.K., Jr. 1964. Distribution and taxonomy of the mammals of Nebraska. University of Kansas Publications of the Museum of Natural History 16:1-356.

Kaul, R. 1989. Plants. Pages 127-142. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Kaul, R.B., and S.B. Rolfsmaier. 1987. The characteristics and phytogeography of the flora of Nine-Mile Prairie, a western tallgrass prairie in Nebraska. Transactions of the Nebraska Academy of Sciences. XV:23-35.

Kaul, R.B., G.E. Kantak, and S.P. Churchill. 1988. The Niobrara River Valley, a postglacial migration corridor and refugium of forest plants and animals in the grasslands of central North America. Botanical Review 54:44-81.

Keech, C.F., and R. Bentall. 1978. Dunes on the plains, the Sand Hills region of Nebraska. University of Nebraska Conservation and Survey Division Resource Report Number 4.

Küchler, A.W. 1964. Potential natural vegetation of the conterminous United States. Special Publications, American Geographical Society, Washington, D.C.

Küchler, A.W. 1985. Potential natural vegetation. National Atlas of the United States of America. Department of the Interior, U.S. Geological Survey, Reston, Virginia.

Labedz, T.E. 1989. Birds. Pages 161-180. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Larson, T.A. 1965. History of Wyoming. University of Nebraska Press, Lincoln.

Lewis, D.T. 1989. Origin of Sand Hills soils. Page 57. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Lowry, J.E., and H.D. Blocker. 1987. Two new species of *Flexamia* from the Nebraska Sand Hills (Homoptera: Cicadellidae:Deltocephalinae). Proceed-ings of the Entomological Society of Washington 89:57-60.

Lugn, A.L. 1935. The Pleistocene geology of Nebraska. University of Nebraska Conservation and Survey Division Bulletin Number 10, Second Series.

Lunt, S.R. 1987. North American mosquito species with geographical distribution limits in Nebraska. Nebraska Academy of Sciences Annual Meeting 97:18-19.

MacArthur, R., and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Madson, J. 1978. Land of long sunsets. National Geographic 154:493-517.

May, D.W., and S.R. Holen. 1985. A chronology of Holocene erosion and sedimentation in the South Loup Valley, Nebraska. Geological Perspectives 56:8-12.

Miller, S.M. 1989. Land development and use. Pages 207-226. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Molhoff, W.J. 1985. The Nebraska breeding bird atlas project. Nebraska Academy of Sciences Annual Meeting 94:23.

Muhs, D. 1985. Age and paleoclimatic significance of Holocene sand dunes in northeastern Colorado. Annals of the Association of American Geographers 75:566-582.

Pool, R.J. 1914. A study of the vegetation of the Sand Hills of Nebraska. Minnesota Botanical Studies 4:189-312.

Pound, R., and F.E. Clements. 1900. The phytogeography of Nebraska. General survey. University of Nebraska Botanical Survey, Lincoln.

Ramaley, F. 1939. Sand Hill vegetation of northeastern Colorado. Ecological Monographs 9:1-51.

Raup, H.Y., and G.W. Argus. 1982. The Lake Athabasca sand dunes of northern Saskatchewan and Alberta, Canada. 1. The land and vegetation. Canadian Museum of Natural Sciences Publications in Botany 12:1-96.

Richards, B., Jr. 1980. Bartlett Richards: Nebraska Sand Hills cattleman. Nebraska State Historical Society, Lincoln.

Schmidt, T.L. 1986. Forestland resources of the Nebraska Sand Hills. *In* T.D. Wardle (ed.). University of Nebraska and Nebraska Forest Service, Lincoln.

Smith, H.T.U. 1965. Dune morphology and chronology in central and western Nebraska. Journal of Geology 73:557-578.

Soule, M. (ed.). 1986. Conservation biology. Sinauer Associates Incorporated, Sunderland, Massachusetts.

Steinauer, E.A., and T.B. Bragg. 1987. Ponderosa pine (*Pinus ponderosa*) invasion of the Nebraska Sand Hills Prairie. American Midland Naturalist 118:358-365.

Stubbendieck, J. 1989. Range management. Pages 222-233. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Sutherland, D.M. 1984. Vegetative key to grasses of the sand hills region of Nebraska. Transactions of the Nebraska Academy of Sciences 12:23-60.

Sylvester, D.D. 1957. Response of Sand Hill vegetation to deferred grazing. Journal of Range Management 10:255-292.

Swinehart, J.B. 1989. Wind-blown deposits. Pages 43-56. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Swinehart, J.B., and R.F. Diffendal, Jr. 1989. Geology of predune strata. Pages 29-42. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number 5.

Tolstead, W.L. 1942. Vegetation of the northern part of Cherry County, Nebraska. Ecological Monographs 12:255-292.

Tucker, S.J. 1942. Indian villages of the Illinois Country. Scientific Papers, Atlas, Volume 2, Part 1. Illinois State Museum, Springfield.

Voorhies, M.R., and R.G. Cormer. 1985. Small mammals with boreal affinities in Late Pleistocene (Rancholabrean) deposits of Eastern and Central Nebraska. Pages 125-141. *In* W. Dort, Jr. (ed.). TER-QUA Symposium Series: Institute for Tertiary-Quaternary Studies. Nebraska Academy of Sciences.

Weaver, J.E. 1965. Native vegetation of Nebraska. University of Nebraska Press, Lincoln.

Wells, P.V. 1983. Late Quaternary vegetation of the Great Plains. Transactions of the Nebraska Academy of Sciences XI:83-89.

Whitcomb, R.F. 1986. North American forests and grasslands: Biotic conservation. Pages 163-176. *In* D.A. Saunders, G.W. Arnold, A.A. Burbridge, and A.J.M. Hopkins (eds.). Nature conservation: The role of remnants of native vegetation. Surrey Beatty and Sons, Sydney.

Whitcomb, R.F., and A.L. Hicks. 1988. Genus *Flexamia:* New species, phylogeny, and ecology. Great Basin Naturalist Memoirs 12:224-323.

Whitcomb, R.F., A.L. Hicks, D.E. Lynn, K. Allred, and H.D. Blocker. 1987. Geographic variation in host relationships of leafhoppers (Homoptera:Cicadellidae) in North American grasslands. Pages 293-325. *In* M.R. Wilson and L.R. Nault (eds.). Proceedings of the 2nd International Workshop on Leafhoppers and Planthoppers of Economic Importance. Commonwealth Institute of Entomology, London.

Whitcomb, R.F., J. Kramer, M.E. Coan, and A.L. Hicks. 1986. Ecology and evolution of leafhopper-grass relationships in North American prairies, savanna, and ecotonal biomes. Current Topics in Vector Research 4:125-182.

Whitcomb, R.F., A.L. Hicks, H.D. Blocker, and J.P. Kramer. 1988. Host specificity: a major mechanism enhancing insect diversity in grasslands. Paper 11.06 *In* A. Davis and G. Stanford (eds.). Proceedings of the Tenth North American Prairie Conference, Denton, Texas.

Wilhite, D.A., and K.G. Hubbard. 1989. Climate. Pages 17-28. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division Resource Atlas Number

Wilson, I.G. 1973. Ergs. Sedimentary Geology 10:77-106.

Wolfe, C.W. 1973. Effects of fire on a Sand Hills grassland environment. Proceedings of the Tall Timbers Fire Ecology Conference 12:241-255.

Wolfe, C.W. 1984. Physical characteristics of the Sand Hills: Wetlands, fisheries and wildlife. Pages 54-61. *In* The Sand Hills of Nebraska - Yesterday, Today, and Tomorrow. Proceedings of the University of Nebraska Water Resources Seminar Series.

MANITOBA'S TALL-GRASS PRAIRIE CONSERVATION PROJECT

JoAnne Joyce and John P. Morgan
Manitoba Naturalists Society, 302-128 James Avenue, Winnipeg, Manitoba R3B-0N8

Abstract. Manitoba's tallgrass prairies mark the northernmost extent of that community in North America and historically comprised the most extensive area of tallgrass prairie in Canada. The Tall-Grass Prairie Conservation Project is Manitoba's first systematic inventory of this community. Potential sites were located using black-and-white aerial photography, land-use maps, and referrals from outside sources. Sites were systematically ground-checked and ranked using native species dominance, abundance and diversity, evidence of disturbance, and location. About 19% (116,600 ha) of the historic range of the true prairie was surveyed between May and October of 1987; an additional 23% (138,000 ha) was surveyed between May and July of 1988. The project has greatly heightened public awareness of the threat to Manitoba's tallgrass prairie and seeks to incorporate protection and management of prairie remnants with continued inventory.

Key Words. tallgrass prairie, inventory, prairie remnants, Manitoba

INTRODUCTION

The tallgrass prairie community in North America lies along the eastern edge of the Great Plains within the rain shadow of the Rocky Mountains (Transeau 1935) extending from Texas northward through the midwestern United States to southern Manitoba (Shelford 1963). Tallgrass prairie is bordered by the deciduous forest biome on the east, aspen parkland to the north, and mixed grass prairie to the west and south. It is the most productive and diverse of North America's grassland types, and it is the one with the richest black chernozemic soils.

Historically, Manitoba contained the largest area of tallgrass prairie in Canada with five times more than occurred in the next largest area in the azonal communities of southwestern Ontario (Johnson 1987). Manitoba's tallgrass prairie once occupied 6,000 km^2 of the south-central portion of the province (Watts 1969). Although there is some disagreement over its exact boundaries in Manitoba, this prairie is considered to have occupied the basin of ancient Glacial Lake Agassiz north of the United States border, west of the Red River, south of the Assiniboine River, and east of the Manitoba escarpment (Watts 1969, Weir 1983). Soil types, climate, and existing tallgrass prairie remnants indicate that the community comprised the dominant vegetation type for some distance east and north of the designated true tallgrass prairie zone of Manitoba (Figure 1).

Past surveys to locate remnant stands of tallgrass prairie included those of Ralston (1968), the International Biological Programme (Levin and Keleher 1969, Nero 1972), and Anderson (1986). These surveys were not systematic in nature. Documentation of sites was accomplished through random search and referrals from Department of Agriculture weed inspectors. The Manitoba Naturalists Society's Tall-Grass Prairie Conservation Project, reported in this paper, constitutes the province's first systematic inventory of the tallgrass prairie community in Manitoba.

METHODS

The inventory was conducted in the Red River Valley and its periphery in south-central Manitoba (Figure 1). The primary study area generally coincided with the basin of ancient Glacial Lake Agassiz. Topography is flat to rolling, and soils are black chernozems developed on clay and glacial till deposits. Land-use is intensive agriculture with cereal, oilseed, and domestic forage crops predominant. The secondary and tertiary (peripheral) study areas were characterized by poorer, stonier soils and rolling topography. Land-use is primarily native hay and pasture. Climate over both areas is continental temperate, characterized by long, cold winters and short, warm summers. Mean daily temperature was -17.3 C for January and 20 C for July. Mean annual precipitation was 46-51 cm with two-thirds of that amount falling in the period between May and September. Over 65% of the province's one million people live within the study area, most within the city of Winnipeg.

Black-and white aerial photographs, at a scale of 1:15,840 were analyzed to locate potential tallgrass prairie remnants larger than 1 ha in size. Potential sites included farmsteads, abandoned and existing railway lines, cemeteries, undeveloped road allowances, native pasture and hayland, and areas difficult to access with farm machinery. Locations were transferred to same-scale land-use maps for field use. Potential prairie sites were systematically ground-checked on a township-by-township basis. Additional peripheral area sites were located through referral and by reviewing unpublished data from International Biological Programme files.

Each site was evaluated on location and ranked using native species dominance and diversity, cover/abundance and sociability, relative abundance of increasers and exotics, and physical disturbance to the site. *Dominance* refers to those species with the highest cover value in a site; *diversity* is an assessment based on a combination of the number of species (species richness) and the evenness with which individuals are distributed among the species. *Cover/Abundance* was measured using an index of frequency of occurrence or the number of individuals of a given plant species on a particular site. Specific categories were: r = single occurrence, + = occasional with cover < 5%, 1 - plentiful with cover < 5%, 2 = very numerous with cover 5-25%, 3 = any number of individuals but cover 25-50%, 4 = any number of individuals but with cover 50-75%, 5 = any number of individual with cover > 75%. *Sociability* was an index of the tendency of a given plant species to "clump": 1 = growing singly; 2 = grouped with few individuals; 3 = large group with many individuals; 4 = small colonies, extensive patches, or broken mat; 5 = extensive mat. *Increasers,* as used in this study, are native plants that greatly increase in abundance or cover as a result of heavy grazing or other disturbance. For example, pussy-toes (*Antennaria* Gaertn.), wolf-willow (*Elaeagnus commutata* Bernh.), and gumweed [*Grindelia squarrosa* (Pursh) Dun.] are considered increaser species in that they tend to be over-represented in heavily grazed native pastures. *Exotics* are defined as those plants not native to North America, most having been introduced from Europe or Asia.

Indicator species, as used later in the text, are native species that are confined to or occur regularly in tallgrass prairie. These may include big bluestem (*Andropogon gerardii* Vitman), indiangrass [*Sorghastrum nutans* (L.) Nash], switchgrass (*Panicum virgatum* L.), sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], western fringed orchid (*Platanthera praeclara*), western silvery aster (*Aster sericeus* Vent.), leadplant (*Amorpha canescens* Pursh), silverleaf psoralea (*Psoralea agrophylla* Pursh), and meadow blazingstar [*Liatris ligulistylis* (A. Nels.) K. Schum].

Only sites ranked C or better were considered suitable for conservation. Location, size, present land-use, and degree of threat were the major factors considered in efforts that were initiated to secure the site through voluntary protection or by other means. Landowners of sites were contacted for access permission and to

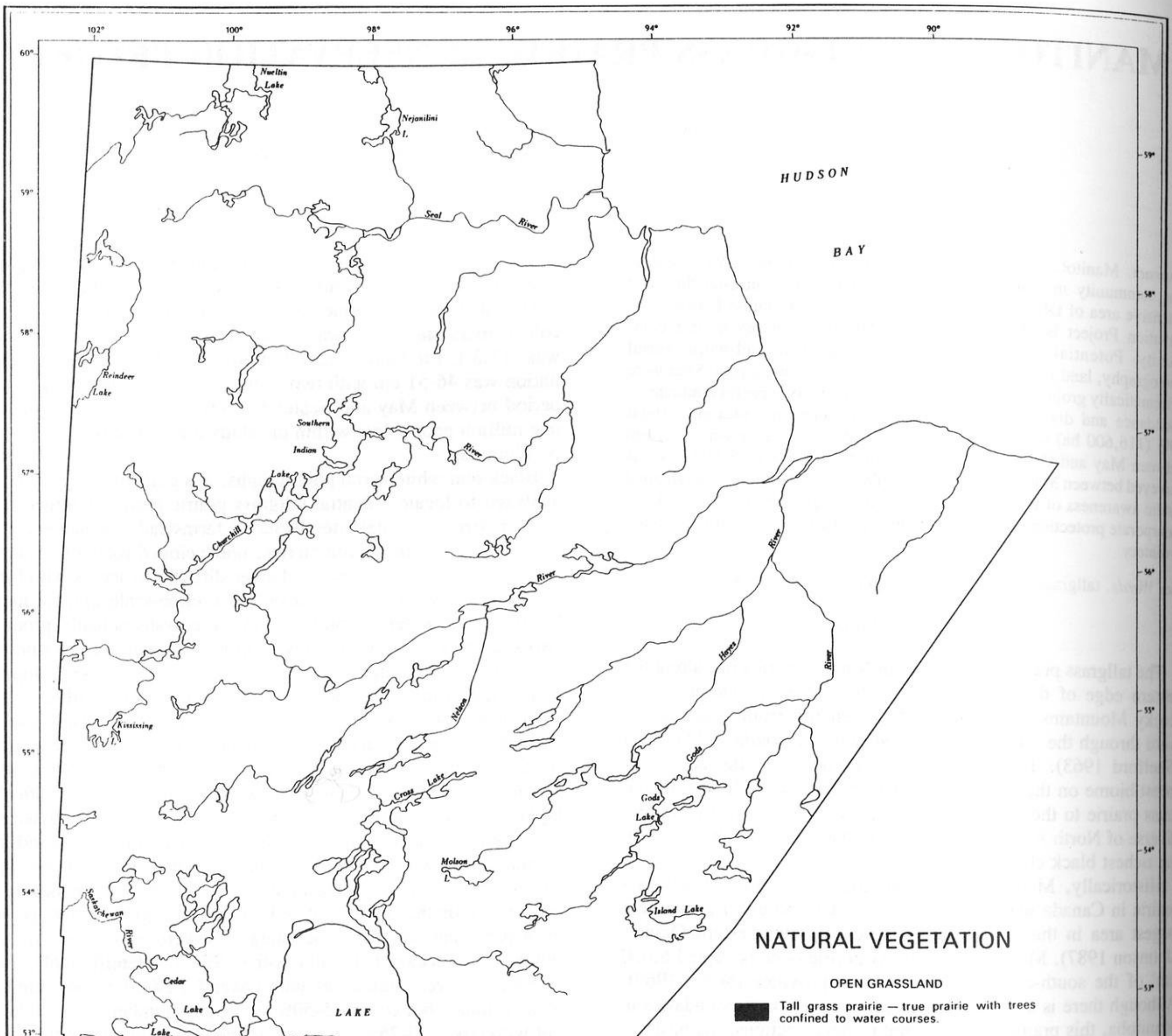


FIG. 1. Tall-Grass Prairie Conservation Project study area in Manitoba. Adapted from Weir (1983).

obtain information on site history, management, and present status. The project's purpose was explained in an effort to enlist their support for prairie conservation.

In 1988 the Tall-Grass Prairie Inventory was expanded and renamed the Tall-Grass Prairie Conservation Project. Field personnel were increased 2 to 3, and a cartographic technician and a project coordinator were hired for a year's duration. In addition, the inventory process was modified to increase inventory efficiency. All ranking criteria in 1988 were the same as those used in 1987, with the exception of cover/abundance and sociability parameters being reassigned to a later stage of the inventory. Instead, preliminary ranking of sites was based on the dominance and diversity of native indicator species. Increased emphasis was given to public education and the voluntary protection/management of prairie sites by landowners. A full-color brochure on Manitoba's tallgrass prairie was produced for distribution to landowners and the general public. A feature film on tallgrass prairie is presently in production. The narrative is being written for a wide audience in an effort to establish broad public support for tallgrass prairie conservation.

RESULTS

About 19% (116,000 ha) of the historical true prairie zone were ground-checked in the primary study area between May and October of 1987. Thirteen sites were prairies ranked between A and C (Table 1). An additional 23% (138,000 ha) of the primary area was surveyed between May and July of 1988 in which eight prairies were ranked A, B, or C. In the peripheral study areas, nine prairies were surveyed in 1987 of which all tended to be much larger than those in the primary study area. Consequently in 1988, a greater effort was directed to surveying the peripheral areas. Of the 983 peripheral sites surveyed as of 31 July 1988, ten were prairies ranked C or better.

The majority (63%) of prairie sites documented in the true prairie zone were found on railway rights-of-way (Table 2). Most of the sites located in the peripheral areas were harbored on undeveloped road allowances (32%) and pasture/hayland (32%).

Response of landowners to the prospect of site conservation has been good. Management plans are being drafted to assist both private and corporate landowners in improving or maintaining native prairies on their land, and funds have been raised through the project and its funding agencies to acquire highly threatened good-quality prairie where voluntary protection is not possible. The purchase of a 32 ha site in 1988 by the Manitoba Naturalists Society and two of its funding agencies has almost doubled the amount of protected and managed tallgrass prairie in the province.

Project findings and recommendations have stimulated the formation of two separate prairie conservation strategies recently initiated by World Wildlife Fund Canada and the Manitoba Department of Natural Resources. World Wildlife Fund's Prairie Conservation Action Plan is based on World Conservation Strategy objectives for the long-term maintenance of ecological systems and their biological diversity. It outlines specific steps to be taken by Canadian prairie provinces to protect and conserve endangered species and habitats. Data and recommendations of the Tall-Grass Prairie Conservation Project were used in the formulation of this broad strategy and in the design of specific action plans for the Manitoba Department of Natural Resources' Prairie Conservation Strategy. Both strategies are slated for implementation in late 1988. The project has raised the profile of tallgrass prairie, its value and its potential uses through tours and presentations for a variety of groups, contact with southern Manitoba landowners and widespread media attention.

DISCUSSION

This study has located less than 150 ha of tallgrass prairie in a portion of the true prairie zone where it once covered 252,000 ha. If this proportion is representative of what remains in the entire true prairie zone, tallgrass prairie now occupies an area in Manitoba 1/20 of 1% as large as it did in pre-settlement times. The majority of prairie remnants in this area occurred along railway rights-of-way which were broken for construction of the lines some 100 years ago. This fact alone attests to the extensive land-use of the area and the lack of any significant unbroken areas, even among those now dominated by native vegetation. In comparison, a greater proportion of the land in areas peripheral to the true prairie zone has been retained in its unbroken state. A high proportion of sites in these areas are found along undeveloped road allowances and on pasture and hayland.

Given that the main objective of the project is to identify and conserve as much tallgrass prairie as possible, the peripheral study areas hold the greatest potential for future work. Species diversity, which is crucial to maintenance of the prairie community, relies in part on the size of each piece conserved. Although they exist in azonal and on poor quality soils, peripheral area sites are larger and not so highly threatened as their true tallgrass zone counterparts and would be substantially less expensive to acquire. Thus, these peripheral areas present the best possibility for the establishment of a large prairie preserve. This does not lessen the importance of securing sites in the true prairie zone which are representative of a variety of conditions such as moisture regimes and soil types.

Table 1. Number and size (ha) of tallgrass prairie sites found within and adjacent to the historic range of tallgrass prairie in Manitoba.

Year	*Sites surveyed*		*Number of TGPs*		*Site size*	
	Primary	*Secondary/ Tertiary*	*Primary*	*Secondary/ Tertiary*	*Primary*	*Secondary/ Tertiary*
	number		≥ C rank		ha	
1987	311	10	13	9	79	489
1988	1,087	983	8	10	49	174
TOTAL	1,398	993	21	19	128	663

Table 2. Land-use on tallgrass prairie sites surveyed in the true prairie zone of Manitoba and its periphery as of July, 1988.

Area surveyed	*Railway right-of-way*	*Pasture/ hayland*	*Cemetery*	*Road allowance*	*Other*	*Total*
Primary	13	2	1	1	4	21
Secondary/tertiary	2	6	0	6	5	19

Because most of the province's tallgrass prairie was destroyed before it was ever documented or studied, maintenance of even the smallest remnant prairie is of high value for research and education, as habitat, and for the public good. The implementation of programs and policies that promote native prairie conservation in Manitoba is therefore of paramount importance. At present there is no public or private mechanism specific to the conservation and management of native prairies. Private landowner stewardship, management assistance, Crown land management, native prairie tax credits, and the integration of prairie maintenance into agricultural soil and water conservation initiatives are all facets of prairie conservation which should be implemented in Manitoba as soon as possible. In turn, these programs need support, wherever possible, by public education and new or amended legislation. The Tall-Grass Prairie Conservation Project will continue to strive to effect these changes towards conserving and managing Manitoba's part of a valuable national and international resource.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge the financial support of World Wildlife Fund Canada, Wildlife Habitat Canada, Manitoba Department of Natural Resources, Manitoba Habitat Heritage Corporation, Manitoba Job Training for Tomorrow, Manitoba Heritage Federation, and the Canadian Job Strategies Program, without whose support this project would not have been possible.

LITERATURE CITED

Anderson, S.M. 1986. The tall-grass prairie community in Manitoba. A report to World Wildlife Fund Canada. Unpublished.

Johnson, K.L. 1987. Tall-grass prairie in Canada; an overview and status report. Provincial Museum of Alberta, Natural History Occasional Paper #9.

Levin, M.H., and G.M. Keleher. 1969. Vegetation of a prairie near Winnipeg, Manitoba. The Canadian Field Naturalist 83:113-122.

Nero, R.W. 1972. The living prairie in a city. The Beaver, Spring:27-29.

Ralston, R.D. 1968. The grasslands of the Red River Valley. Doctor of Philosophy Thesis, University of Saskatchewan, Saskatoon.

Shelford, V.E. 1963. The ecology of North America. University of Illinois Press, Urbana.

Transeau, E.N. 1935. The prairie peninsula. Ecology 16:423-427.

Watts, R.B. 1969. The natural vegetation of the southern great plains of Canada. Pages 93-111. *In* J.G. Nelson and N.J. Chambers (eds.). Vegetation, soils and wildlife. Methuen, Toronto.

Weir, T.R. (ed.). 1983. Atlas of Manitoba. Surveys and Mapping Branch, Manitoba Department of Natural Resources. Winnipeg.

SOD SEEDED WARM-SEASON GRASS WITH AND WITHOUT SOD SUPPRESSION

B. L. Bush, S. S. Waller, B. E. Anderson, L. E. Moser, and R. M. Wozniak
Department of Agronomy, University of Nebraska, Lincoln, Nebraska 68583-0915

Abstract. Revegetation of deteriorated mixed prairie by sod seeding with a lo-till planter minimizes erosion. Critical periods of inter- and intraspecific competition must be identified to design effective methods of sod suppression and seeding rate. Sod seeding studies were conducted in two counties in south central Nebraska over a 3-year period on a silty range site (fine-silty, mixed, mesic, Typic Argiustolls). Sites were dominated by blue grama [*Bouteloua gracilis* (H.B.K.) Lag. *ex* Steud.] and buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.]. Warm-season native grasses were sod seeded with and without chemical sod suppression. Sod seeding required sod suppression for consistent stand establishment. Sod suppression during the 8-week period following seeding maximized grass seedling emergence. Seedling and stand vigor were more vigorous following sod suppression. Seedling development was independent of seeding rate, and a seeding rate of 20 PLS/0.1 m^2 resulted in an adequate stand. Spring-applied glyphosate [*N* (phosphonomethyl)-glycine] was effective at 0.8 kg/ha using a reduced carrier volume (93 l/ha). August application of glyphosate coupled with a spring application of atrazine [6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine] at the time of seeding was also an effective sod suppression treatment.

Key words. big bluestem, *Andropogon gerardii*, little bluestem, *Schizachyrium scoparium*, indiangrass, *Sorghastrum nutans*, switchgrass, *Panicum virgatum*, sideaots grama, *Bouteloua curtipendula*, glyphosate, mixed prairie, Nebraska

INTRODUCTION

The Loess Hills of south-central Nebraska is part of the mixed prairie (Weaver 1965). Improper management has caused a shift in rangeland vegetation composition from a tall and midgrass bunchgrass community to a shortgrass sod. This shortgrass community is generally considered a disclimax caused by long-term grazing mismanagement. Over 40% of the rangeland in the area was described as poor to fair range condition (Bose 1977).

Seeding native grasses generally requires a period of cropping before seeding into stubble. Erosion hazards and limited moisture often make it impractical to cultivate and grow competitive cover crops by traditional methods when seeding adapted native grasses (Dudley and Holt 1963, Schumacher 1964). Alternative range seeding practices, such as interseeding and sod seeding, have been successfully used to increase forage productivity and improve forage quality in the Great Plains (Schumacher 1964, Robertson and Box 1969, Houston and Adams 1971, Samson and Moser 1982, Hart *et al.* 1985).

The development of lo- or no-till seeding equipment and effective herbicides offers new opportunities to revegetate rangeland. Sod seeding can minimize erosion, maintain species diversity, and expedite recovery. Sod seeding studies were conducted in Furnas and Harlan counties in south central Nebraska to evaluate warm-season grass development and establishment using sod seeding with and without chemical suppression of a shortgrass sod.

METHODS

Study Area

Primary plants in the climax community are big bluestem (*Andropogon gerardii* Vitman), little bluestem [*Schizachyrium scoparium* (Michx.) Nash.], sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], needleandthread (*Stipa comata* Trin. & Rupr.), western wheatgrass (*Agropyron smithii* Rydb.), blue grama [*Bouteloua gracilis* (H.B.K.) Lag. *ex* Steud.], and buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.]. Overgrazing results in a very dense sod of buffalograss and blue grama in the study area.

Experiments were conducted on a silty range site (fine-silty, mixed, mesic, Typic Argiustolls) in two adjacent counties (Furnas and Harlan) in south-central Nebraska. Precipitation is highly variable from season to season and periodic droughts occur. The average annual precipitation is approximately 570 mm with about 80% occurring between April and September. The average growing season is 170 days from May to October. Both sites were grazed annually until initiation of the study. Species composition, based on basal cover, showed that the Furnas County site was dominated by blue grama (54%) and buffalograss (36%). Vegetation at the Harlan County site was also dominated by blue grama (34%) and buffalograss (14%).

Furnas County

Plots (4 x 10 m) were sod seeded (30 PLS/0.1 m^2) on 28 April 1981, using a modified John Deere Powr-Till Seeder (20 cm row spacing) with a mixture (% PLS) of 'Kaw' big bluestem (22%), 'Aldous' little bluestem (35%), 'Nebraska 54' indiangrass [*Sorghastrum nutans* (L.) Nash] (9%), 'Blackwell' switchgrass (*Panicum virgatum* L.) (14%), and 'El Reno' sideoats grama (20%). Glyphosate [*N* -(phosphonomethyl)glycine], a non-selective contact herbicide, was used to suppress existing shortgrass sod. Three herbicide rates (0.6, 0.8, and 1.1 kg/ha) and two carrier volumes (93, 186 l/ha) were evaluated with a seeded control and an unseeded reference. Since active growth of the warm-season shortgrass sod is generally after the optimum seeding date for warm-season grasses, it was important to delay herbicide application until after seeding but prior to seedling emergence. Plots were sprayed 6 days after seeding and excluded from grazing.

The experimental design was a randomized complete block with four replications. Blocking criteria was slope and aspect. Ten randomly located segments (1 m) of drill rows were used to estimate stand density. Stand density was evaluated the year of seeding (July 1981) and year following (June 1982). Plant and stand vigor were determined by measuring leaves/tiller, length of longest leaf, tillers/plant and total plants/unit row for each seeded species during the second growing season (June 1982). Sod suppression was determined by hand clipping (2.5 cm) five randomly located quadrats (0.2 m^2) between drill rows in June and November 1981. Treatment comparisons were made using orthogonal contrasts.

Harlan County

Plots (5 x 10 m) were sod seeded with a mixture of debearded Kaw big bluestem and Aldous little bluestem without sod suppression 24 April 1982, using the John Deere Powr-Till seeder. Three seeding rates were used: low (7 PLS/0.1 m^2), medium (20 PLS/0.1 m^2) and high (25 PLS/0.1 m^2). Big bluestem was approximately 80% of the seed mixture (% PLS) for the low rate and about half for the medium and high rates.

A second experiment evaluated the effect of sod suppression. Glyphosate (1.7 kg/ha, 78 l/ha) was applied in late summer (17 August 1982) followed with a spring (23 April 1983) application of atrazine [6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine] (1 kg/ha, 274 l/ha solution), at the time of seeding to control cool-season annuals. A second treatment was summer-applied glyphosate (4 June 1983) following a 31 May 1983, seeding (plots 2.5 x 10 m). Seeding date was delayed to increase the efficacy of the glyphosate treatment. The third treatment was no sod suppression and plots were compared to the 1982 seeding. A mixture (% PLS) of big (81%) and little bluestem (19%) was sod seeded (20 PLS/0.1 m^2).

Seedling development was determined using three permanently marked segments (1 m) of drill rows. As seedlings emerged, a 1.9 cm plastic ring was placed around the base of each seedling for permanent identification. Height, number of leaves, and vigor classification (green, wilted, or dead) was recorded. Percentage seedling emergence was based on the number of emerged seedlings as a proportion of the viable seeds planted (PLS/0.1 m^2). Measurements began 4 weeks after seeding and were repeated at weekly intervals through mid-July with two readings in August 1982. In 1983, sampling dates were once in June, August, September, and twice in July. Seedling density was determined within 7 randomly located segments (1 m) of drill row. A completely randomized design with four replications was used. Orthogonal contrasts were used to make treatment comparisons.

RESULTS AND DISCUSSION

Furnas County

Sod seeding without sod suppression.

Sod seeding with no sod suppression in 1981 resulted in a complete stand failure at the Furnas County site. However, May and June precipitation (244 mm) was very favorable for seedling development. During the period May through August, plots received about 500 mm of precipitation. Chemical sod suppression resulted in satisfactory stands, suggesting that sod competition rather than equipment, seed, or weather was responsible for seeding failure.

Sod seeding with sod suppression.

Plots treated with the higher glyphosate rates (0.8 and 1.1 kg/ha) had greater seedling density than the 0.6 kg/ha rate (Table 1). The lower carrier volume was more effective than the higher. Buhler and Burnside (1983) determined that decreasing carrier volume reduced or eliminated inhibition of glyphosate phytotoxicity due to high ion content of carrier water. The highest glyphosate rate used with the lowest carrier volume resulted in a successful (> 1.0 seedling/0.1 m^2, Launchbaugh and Owensby 1978) stand (1.4 seedlings/0.1 m^2). Stand counts in 1982 were generally higher than the 1981 counts, primarily due to tillering.

Above-ground sod biomass in the untreated area was greater in June (1970 kg/ha, $P = 0.01$) and November (1850 kg/ha, $P = 0.03$) than the average of the treated areas. Above-ground sod biomass was not significantly different between rates or carrier volumes in June of the seeding year (Table 2). In November, the medium glyphosate rate had less sod biomass than the highest rate (1090 and 1530 kg/ha, respectively). An inverse relationship existed between seedling density and June sod biomass ($r = -0.41$, $P = 0.07$). Spring-applied glyphosate suppressed rather than killed the sod. Treated plots were suppressed for approximately 8 weeks

Table 1. Seedling density (number/0.1 m²) of a warm-season grass mixture sod seeded April 28, 1981, at Furnas County, Nebraska, and evaluated July 1981 and June 1982. Glyphosate was applied at three rates in two carrier volumes 6 days after seeding.

		Carrier volume (l/ha)			*Glyphosate rate (kg/ha)*			*Contrasts (PR > F)²*	
Species	*Year*	*93*	*186*	*PR > F¹*	*0.6*	*0.8*	*1.1*	*0.6 vs. 0.8, 1.1*	*0.8 vs. 1.1*
		no./0.1 m²				no./0.1 m²			
Big bluestem	1981	3.4	2.4	.18	1.5	3.0	4.2	.02	.20
	1982	6.4	5.1	.25	2.5	7.1	7.6	<.01	.74
Sideoats grama	1981	0.2	0.3	.53	0.1	0.2	0.6	.12	.03
	1982	0.5	0.1	.05	0.2	0.4	0.3	.65	.70
Switchgrass	1981	2.3	1.4	.06	0.7	2.4	2.4	<.01	.93
	1982	2.4	1.7	.35	0.5	2.2	3.4	<.01	.16
Little bluestem	1981	2.7	1.1	<.01	0.7	1.9	3.1	<.01	.06
	1982	3.0	2.1	.20	0.9	3.4	3.4	<.01	.95
Indiangrass	1981	0.8	0.6	.06	0.1	0.7	0.9	<.01	.28
	1982	1.3	1.5	.54	0.4	1.7	2.1	<.01	.40
Total	1981	9.4	5.6	<.01	3.2	8.1	11.1	<.01	.06
	1982	13.6	10.6	.21	4.6	14.9	16.7	<.01	.51

¹PR > F is the significance probability value for the F value for the comparison of carrier volume within year.
²Orthogonal contrasts of the lowest glyphosate rate with the average of the two higher rates and the comparison of the medium rate with the highest rate.

Table 2. Above-ground sod biomass (kg/ha) of plots sod seeded 28 April 1981, at Furnas County, Nebraska. Glyphosate was applied at three rates in two carrier volumes 6 days after seeding and yields were determined in June and November of the seeding year.

		Carrier volume (l/ha)			*Glyphosate rate (kg/ha)*			*Contrasts (PR > F)²*	
Month	*Year*	*93*	*186*	*PR > F¹*	*0.6*	*0.8*	*1.1*	*0.6 vs. 0.8, 1.1*	*0.8 vs. 1.1*
		kg/ha							
June	1981	1,190	1,090	.64	1,280	990	1,160	.38	.54
November	1981	1,300	1,354	.75	1,360	1,090	1,530	.79	.04

¹PR > F is the significance probability value for the F value for the comparison of carrier volume within year.
²Orthogonal contrasts of the lowest glyphosate rate with the average of the two higher rates and the comparison of the medium rate with the highest rate.

and then the sod recovered. The herbicide treatment resulted in a more vigorous sod than in controls at the end of the treatment year, apparently due to the chemical fallow. The timing and completeness of sod suppression was critical for seedling establishment rather than total biomass reduction.

Higher rates of glyphosate and lower carrier volume generally resulted in more vigorous seeded plants the year after seeding. Sprague *et al.* (1962) demonstrated that germination and emergence of seeded species were not affected by sod suppression but growth and development were. The response of little bluestem was representative of all seeded species (Table 3). Tiller and plant vigor was greater following application of the higher glyphosate rates and lower carrier volume.

Harlan County

Sod seeding without sod suppression.

The 1982 sod seeding without sod suppression at Harlan County was successful (Table 4). Despite differences in seeding mixture, end-of-season stand density and seedling vigor were not affected by seeding rate. Seedling mortality probably resulted from interspecific competition with existing sod during periods of low soil moisture rather than intraspecific competition. The 1982 precipitation pattern was favorable and minimized sod competition. May and June precipitation (220 mm) was adequate for seedling growth. The summer precipitation (May-August) was 294 mm.

Approximately 90% of big and little bluestem emergence occurred by the eighth week after seeding (Figure 1). Big and little bluestem seedling mortality increased sharply 8 weeks after seeding to approximately 80 and 60% survival, respectively (Fig. 2).

Stand persistence was determined by comparing the number of tillers in 1983 (mid-July) with live seedlings at the end of the seeding year (1982). Big bluestem had 87% stand persistence for the low seeding rate, 82% for the medium and 89% for the high seeding rate. Little bluestem had 39% stand persistence for the low seeding rate, 54% for the medium rate and 23% for the high rate.

Stand establishment in 1983 failed (Table 5, untreated). Little bluestem had minimal establishment in plots seeded in April and May (Table 4). Big bluestem did not survive the growing season with either seeding date. Plots seeded 23 April received about 130 mm of precipitation during May. Plots seeded 31 May only received 50 mm during June. July was extremely dry (< 10 mm) with high temperatures which resulted in seedling mortality.

Table 3. Effect of carrier volume and glyphosate rate on tiller and plant vigor of seed seeded little bluestem determined June 1982. Seeding was done 28 April 1981, at Furnas County, Nebraska.

	Carrier volume (l/ha)			*Glyphosate rate (kg/ha)*			*Contrasts (PR > F)*[2]	
Variable	*93*	*186*	*PR > F*[1]	*0.6*	*0.8*	*1.1*	*0.6 vs. 0.8, 1.1*	*0.8 vs. 1.1*
Tiller vigor								
Leaves/tiller (number)	3.6	3.5	.92	2.1	4.2	4.3	.01	.89
Longest leaf/tiller (cm)	19.7	16.4	.41	11.0	20.6	22.7	.02	.66
Plant vigor								
Tillers/plant (number)	5.6	3.3	.06	1.4	4.9	7.1	<.01	.13

[1]PR > F is the significance probability value for the F value for the comparison of carrier volume within year.
[2]Orthogonal contrasts of the lowest glyphosate rate with the average of the two higher rates and the comparison of the medium rate with the highest rate.

Table 4. Seedling density (number/0.1 m²) of big bluestem (6, 9, and 11 PLS/0.1 m²) and little bluestem (1, 11, and 13 PLS/0.1 m²) sod seeded in a mixture at three seeding rates (low, medium, high) on 24 April 1982, in Harlan County, Nebraska, without sod suppression.

	Weeks after seeding										
Seeding rate	*4*	*5*	*6*	*7*	*8*	*10*	*11*	*12*	*14*	*16*	*18*
						big bluestem					
Low	0.6	0.2	0.5	0.5	1.0	0.9	0.8	0.2	0.1	0.2	0.4
Medium	0.4	0.2	0.9	1.3	1.7	0.8	0.7	0.9	0.8	0.3	0.6
High	0.3	0.5	1.0	1.5	1.2	1.7	0.8	0.4	0.6	0.5	0.2
Contrasts (PR > F)[1]											
Low *vs.* medium, high	0.37	0.13	0.05	0.04	0.37	0.04	0.93	0.15	0.02	0.28	0.98
Medium *vs.* high	0.74	0.02	0.41	0.70	0.43	<0.01	0.67	0.21	0.35	0.30	0.20
						little bluestem					
Low	0.6	0.5	0.5	0.4	1.0	1.0	0.6	0.1	0.3	0.1	0.5
Medium	1.4	1.1	1.1	1.4	3.0	1.6	1.8	1.7	1.7	1.5	1.7
High	1.9	1.1	1.2	1.4	1.9	1.9	1.3	1.0	1.0	0.6	0.8
Contrasts (PR > F)											
Low *vs.* medium, high	0.04	0.04	0.2	<0.01	0.05	0.09	0.01	0.01	0.02	0.03	0.22
Medium *vs.* high	0.42	0.96	0.80	1.0	0.17	0.59	0.19	0.11	0.10	0.06	0.21

[1]PR > F is the significance probability value for the F value for the comparisons of seeding rate by species within a sampling date. The lowest seeding rate was compared to the average of the highest two and the medium seeding rate was compared to the highest seeding rate.

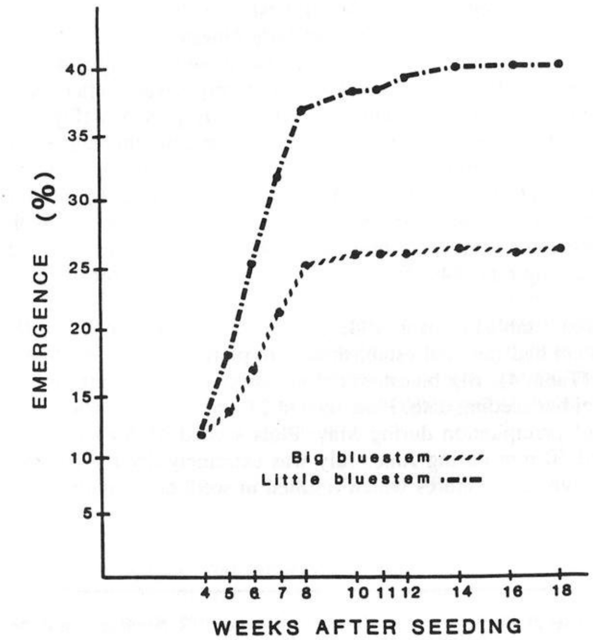


FIG. 1. Emergence (%) during the growing season of big and little bluestem, averaged over seeding rate at Harlan County, Nebraska. Emergence was based on a percent of PLS sod seeded on 24 April 1982.

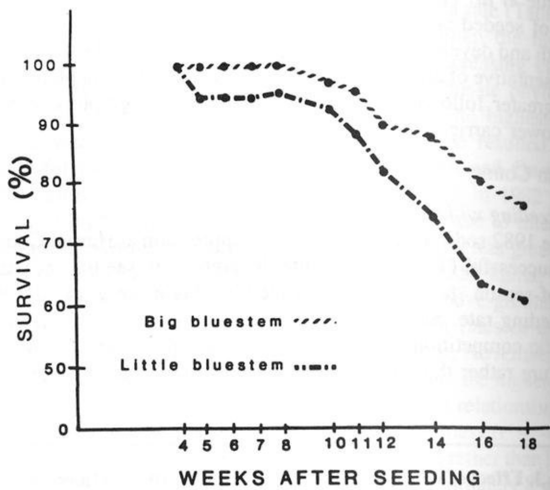


FIG. 2. Survival (%) for big and little bluestem averaged over the medium and high seeding rates at Harlan County, Nebraska. Percent survival was based on emerged seedlings following an 24 April 1982, sod seeding.

Table 5. Seedling density (number/0.1 m²) of big bluestem and little bluestem sod seeded (20 PLS/0.1 m²) in a mixture at Harlan County, Nebraska. Plots seeded 23 April 1983, had received glyphosate (1.7 kg/ha) the preceding late summer and atrazine (1 kg/ha) at the time of seeding. Plots seeded 31 May 1983, received glyphosate June 4.

	Date after seeding									
Species/Treatment	*July 5*	*PR > F*[1]	*July 18*	*PR > F*	*Aug 5*	*PR > F*	*Aug 18*	*PR > F*	*Sept 18*	*PR > F*
Seeded April 23										
Big bluestem Untreated	0.1	0.35	0.0	0.02	0.1	0.07	0.0	0.05	0.0	0.11
Late summer glyphosate spring atrazine	0.2		0.7		1.0		0.2		0.3	
Little bluestem Untreated	0.1	0.37	0.0	0.01	0.0	0.02	0.0	0.08	0.0	0.07
Late summer glyphosate spring atrazine	0.2		0.4		0.3		0.2		0.2	
Seeded May 31										
Big bluestem Untreated	—[2]		0.0		0.0	0.77	0.0	0.56		0.87
Early summer glyphosate	0.1		0.0		0.2		0.1		0.0	
Little bluestem Untreated	—		—		0.1	0.52	0.0	0.54	0.1	0.86
Early summer glyphosate	0.3		0.0		0.2		0.1		0.1	

[1]PR > F is the significance probability value for the F value for the comparison of with and withoutchemical sod suppression by species.
[2]No seedlings emerged.

Sod seeding with sod suppression.

Seedling development in 1983 was poor and inconsistent. However, stand density 18 September of the seeding year was greater ($P = 0.09$) with an August application of glyphosate plus an April application of atrazine (0.5 seedlings/0.1 m^2) compared to June applied glyphosate (<0.5 seedlings/0.1 m^2) (Table 5). The success of the early May applied glyphosate (1.1 kg/ha) at Furnas County and results of a 1979 sod seeding (Hart *et al.* 1985) suggested that other factors influenced glyphosate efficacy at Harlan County. The residue accumulation resulting from 1 year of non-use could have interfered with herbicide activity or been detrimental to seedling development. Andrews *et al.* (1974) determined that summer and fall glyphosate applications were more effective than spring for perennial weed control.

CONCLUSIONS

Sod seeding without sod suppression was not successful in 1981 at Furnas County nor 1983 at Harlan County using two different seeding dates. While a stand was established without sod suppression in 1982 at Harlan County, the risk of stand failure warrants the use of sod suppression. In both cases where stands failed without sod suppression, stands were established with chemical sod suppression. Approximately 90% of the warm-season seedlings emerged within 8 weeks of seeding, defining a critical period for sod suppression. Stand vigor increased with increased sod suppression. Glyphosate was an effective herbicide for control of the warm-season shortgrass sod. It should be applied in a minimum carrier volume (93 l/ha) and the rate should be at least 0.8 kg/ha for a spring application. Timing of spring-applied glyphosate was a problem because the warm-season sod did not green-up appreciably until after the optimum seeding date for warm-season grasses. A late summer glyphosate application the year prior to seeding was a feasible alternative. It provided better sod suppression due to sod mortality which was apparently associated with the downward carbohydrate translocation during this period. However, in this study (50% shortgrass sod) a spring application of atrazine was required to control cool-season annuals, limiting the warm-season seeded species to big bluestem and switchgrass. Dense sods may not require a follow-up spring application of atrazine.

ACKNOWLEDGMENTS

At the time of the research Bush and Wozniak were graduate research assistants. Research was funded by the Anna H. Elliott Fund, and the Lower Republican, Middle Republican, and Tri-Basin Natural Resources Districts. Sincere appreciation is extended to Mr. Terry Woollen and Mr. Paul Schroeder for providing the study areas and Mr. Ron Wunibald for advice and coordination of the projects. Published as Paper Number 8737, Journal Series, Nebraska Agriculture Research Station. Mention of trade names does not imply an endorsement by the grantors or the Nebraska Agricultural Research Station.

LITERATURE CITED

Andrews, O.N., Jr., R.C. Billman, and F.D. Timmons. 1974. Glyphosate control of railroad right-of-way vegetation in the southeast. Proceedings of the Southern Weed Science Society 27:251-258.

Bose, D.R. 1977. Rangeland resources of Nebraska. Society of Range Management, Old West Regional Range Program, Denver.

Buhler, D.D., and O.C. Burnside. 1983. Effect of water quality, carrier volume, and acid on glyphosate phytotoxicity. Weed Science 31:163-169.

Dudley, D.I., and E.C. Holt. 1963. Establishment of warm-season grasses on the grand prairie. Texas Agriculture Experiment Station Miscellaneous Publication 672.

Hart, M., S.S. Waller, S.R. Lowry, and R.N. Gates. 1985. Discing and seeding effects on sod bound prairie. Journal of Range Management 38:121-125.

Houston, W.R., and R.E. Adams. 1971. Interseeding for range improvement in the northern great plains. Journal of Range Management 24:457-461.

Launchbaugh, J.L., and C.E. Owensby. 1978. Kansas rangelands-their management based on a half century of research. Kansas Agriculture Experiment Station Bulletin 622.

Robertson, T.E., Jr., and T.W. Box. 1969. Interseeding sideoats grama on the Texas High Plains. Journal of Range Management 22:243-245.

Samson, J.F., and L.E. Moser. 1982. Sod-seeding perennial grasses into eastern Nebraska pastures. Agronomy Journal 74:1055-1060.

Schumacher, C.M. 1964. Range interseeding in Nebraska. Journal of Range Management 17:132-137.

Sprague, M.A., R.D. Ilnicki, R.W. Chase, and A.H. Kates. 1962. Growth of forage seedlings in competition with partially killed grass sods. Crop Science 2:52-55.

Weaver, J.E. 1965. Native vegetation of Nebraska. University of Nebraska Press, Lincoln.

ESTABLISHING WARM-SEASON GRASSES AND FORBS USING HERBICIDES AND MOWING

Thomas B. Bragg and David M. Sutherland
Department of Biology, University of Nebraska at Omaha, Omaha, Nebraska 68182-0040

Abstract. The objective of this study was to provide a preliminary assessment of the use of selected herbicides in establishing a diverse stand of prairie grasses and forbs. An upland and a lowland site in eastern Nebraska, consisting of well-drained, fine-silty clay, loess-derived soils, were seeded with 23 native prairie grass and forb species and subsequently mowed or treated at rates of 0.6, 1.1, 1.7, and 2.2 kg/ha with atrazine [6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine] or 2,4-D (2,4-dichlorophenoxyacetic acid). Treatments were applied at one and two-year intervals. Canopy cover in unreplicated treatment areas (12 x 30 m) was evaluated in ten randomly located plots (0.5 x 1.0 m). In the lowland, four species of seeded forbs were established only in mulch-mowed plots. In the upland, the number of successfully established, seeded forb species was greatest in the control plot (9 species). While forb establishment was not maximized with herbicide use, such use did contribute to the rapid establishment of some warm-season grasses such as switchgrass (*Panicum virgatum* L.), 77% cover, and eastern gammagrass [*Tripsacum dactyloides* (L.) L.], 21% cover, in the lowland and blue grama [*Bouteloua gracilis* (H.B.K.) Lag. *ex* Griffiths], 11% cover with 2,4-D, and little bluestem (*Andropogon scoparius* Michx.), 60% cover with atrazine. Comparisons of fall total standing crop biomass (1.11 kg/m^2 for lowlands and 0.47 kg/m^2 for uplands) and seedling establishment suggested that high standing crop biomass, regardless of species composition, was likely to affect the establishment of a diverse stand of grasses and forbs. Where stand diversity is the primary objective, methods that prevent high biomass accumulations, particularly the first year or two, will be most successful.

Key Words. grassland reestablishment, forbs, grasses, atrazine, 2,4-D, herbicides, Nebraska

INTRODUCTION

Native prairie species have been seeded for a multitude of purposes including stabilization of disturbed areas, such as abandoned fields, roadsides, and flood-control dams (Landers 1972, MacLauchlan 1973, Brakeman 1975), as well as to reestablish grasslands for preservation efforts (Bland 1970, Bragg 1978). Depending on specific climatic and site conditions, however, these species may require several years to become well established, at least in part because of competition with undesirable (e.g. weedy) species (Cornelius and Atkins 1946, Martin *et al*. 1982). Herbicide application is one of the more common methods used to counter the effect of such undesirable species and thus to speed the rate of establishment. Atrazine [6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine] and 2,4-D (2,4-dichlorophenoxyacetic acid) are among herbicides often used. Both herbicides are sold under various trade names.

Atrazine

Atrazine is a preplanting, pre- and post-emergence herbicide for the control of undesirable broadleaf plants and certain grasses. In grassland reestablishment efforts, atrazine at rates varying from 1.1 to 4.5 kg/ha, resulted in well established stands of warm-season grasses such as switchgrass (*Panicum virgatum* L.) and big bluestem (*Andropogon gerardii* Vitman), particularly at higher rates (McCarty 1976, Martin *et al*. 1982, Vogel 1987). Switchgrass was particularly favored, thriving even under high concentrations of atrazine (Morrow and McCarty 1976). On the other hand, substantial reductions were reported for cool-season species (Plumb 1988), and poor establishment was reported for indiangrass [*Sorghastrum nutans* (L.) Nash], sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], and sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood] even at rates as low as 1.1 kg/ha (Vogel *et al*. 1981, Bahler, *et al*. 1984, Weimer *et al*. 1988). Atrazine carryover in reestablishment studies has been shown to last for 6 to 12 months (Martin *et al*. 1977) and thus may also have some effect on late-germinating seeds.

In range improvement studies, atrazine also increased warm-season grasses, often at the expense of cool-season species (Houston 1977, Morrow *et al*. 1977, Baker and Powell 1978, Samson and Moser 1982, Waller and Schmidt 1983, Rehm 1984, Gillen *et al*. 1987). For example, atrazine, at a rate of 3.3 kg/ha, was effective in recovering warm-season species on previously seeded but overgrazed pastures that had been invaded by cool-season species (Dill *et al*. 1986); lower application rates, however, were not as effective.

2,4-D

2,4-D is a growth regulating phenoxy herbicide for broadleaf weed control in grass crops (McCarty *et al*. 1974, Furrer *et al*. 1981). It also is used to control woody plants (Morrow and McCarty 1975, Wilson *et al*. 1984, Sturges 1986), which often occur during reestablishment efforts. In reestablishment studies, 2,4-D applied at rates from 0.6 to 1.1 kg/ha did not significantly increase switchgrass, indiangrass, or 'Champ' bluestem [a cross between big bluestem and sand bluestem (*Andropogon hallii* Hack.)] (McCarty 1976) although it has been shown to effectively control some undesirable forbs (Quimby *et al*. 1978) and to increase warm-season grass establishment in some areas (Cox and McCarty 1958).

Different responses, however, were obtained from range improvement studies using 2,4-D. For example, a single application of 2,4-D at rates of 0.6 and 1.1 kg/ha significantly increased overall warm-season grass yields in Oklahoma (Elwell and McMurphy 1973). One community-level effect of using auxin-type herbicides, such as 2,4-D, is that the increased number of grasses and the reduced number of broadleaf herbs results in a persistent simplification of community type (Tomkins and Grant 1977) which is counter to the goals of some reestablishment studies.

Of the various studies on native plant reestablishment, most have focused primarily on warm-season grasses with little research on the concurrent establishment of perennial forbs. Forbs, however, are an integral part of the diversity of natural ecosystems and, since many reestablishment efforts are designed to recreate such diversity, it is particularly important to include them when developing such grassland reestablishment procedures. The successful establishment of forbs in an already established grassland is particularly difficult, thus it is desirable to seed both grasses and forbs at the same time. The use of herbicides in such grassland reestablishment efforts has been considered to be important to improve the successful establishment of seeded species. However, herbicides are also designed to deter broadleaf plant (i.e. forb) establishment, and, thus is likely to be counter productive.

This study was designed to assess problems associated with the establishment of both native prairie forbs and grasses. In particular, the focus was on forb establishment in areas likely initially to have a substantial cover of undesirable (e.g. weedy) species that, therefore, may need to be controlled with herbicides. The focus of the study was to assess the net effect of treatment on grass and forb establishment. While essential to a full understanding of the effect of herbicides on native plant establishment, the proximal causes of any observed effects were not part of the design. The study, therefore, implies, but does not attempt to determine, whether the results are a consequence of direct effects of the herbicide on seeds or seedlings, of excessive biomass resulting in reduced solar radiation reaching the prairie seedlings, of effects of allelochemicals that are known to be produced by several of the species identified in this study (Rice 1984), or of any other possible causes.

METHODS AND MATERIALS

Study Site

The study was conducted from 1975 through 1978 on two, previously cultivated fields located at a recently developed flood-control dam site situated about 20 km northwest of Omaha, Nebraska. This area is locally designated Dam Site 11 or Cunningham Reservoir. Soils of the site are mostly of the Mollisol soil order. One field, the Lowland Site (SE1/4 of SE1/4, Section 22, T16N, R12E), was located on a Colo/Kennebec Series (Ck) soil complex (Cumulic Haplaquolls and Hapludolls). These soils are deep, nearly level, somewhat poorly drained to well-drained fine-silty clay loam soils that typify the occasionally-flooded bottomlands along major streams of this portion of eastern Nebraska. The second field, the Upland Site (SW1/4 of SW1/4, Section 22, T16N, R12E), was situated on a Monona/Ida Series (MoD and MsE2) soil complex (Typic Hapludolls and Typic Udorthents the latter of the Entisol Soil Order). These are deep, well-drained, sloping fine-silty and silty loam soils (7-11% slopes) formed over 9-15 m of loess. Climate of the region varies from average high temperatures of 31 C in July to -11 C in January; annual precipitation averages 71 cm with 75% falling from April to September. The growing season averages 167 days. Soil and climatic data are from Bartlett (1975).

Treatments

At each of the two sites, a 0.82 ha study plot was permanently marked and divided into 22 treatment plots (12 x 30 m). The study plots were disked and harrowed just prior to seeding to provide a weed-free seed bed (Cox and McCarty 1958). From 21 to 23 May 1975, 16 species of native prairie forbs and 7 of native prairie grasses were seeded in each study site at rates averaging 19 pure live seed (PLS) per m² for grasses and 28 seeds per m² for forbs (Table 1). Seeds were obtained from the Soil Conservation Service's Plant Materials Center in Manhattan, Kansas. Seeding was accomplished using a Nesbit drill and planting at a depth of 0.6 cm. Forb seeds were mixed with bran to prevent size-sorting during drilling. The bran-forb seed mixture was uniformly drilled across both upland and lowland sites on 21 May 1975 at a rate of 26 kg/ha.

Grasses were drilled evenly across each study site on 22 and 23 May 1975, but the species seeded varied for each topographic location (Table 1). Eastern gammagrass [*Tripsacum dactyloides* (L.) L.] was an exception. It was broadcast, followed by harrowing, because of the large size of the seed.

Atrazine and 2,4-D treatments were applied at rates of 0.6, 1.1, 1.7, and 2.2 kg/ha. All treatment plots evaluated, including untreated controls, were separated by buffer plots of equal size to reduce the effects of pesticide drift or edge effect. In 1975, atrazine was applied in the 80% wettable powder form on 23 May, the time of grass seeding, while 2,4-D was applied as a liquid spray on 10 July 1975. Mowed plots were mulch-mowed to a height of approximately 5-10 cm on 17 July and 8 August 1975 for the lowland site, and 24 July and 8 August 1975 on the upland site. Untreated control plots were not treated in any way. One half of each treatment plot was retreated in 1976 at the same rate applied the previous year. Atrazine was applied in the wettable powder

Table 1. Seeded species coding and application rates. Species indicated with an asterix (*) were seeded but not found in any treatment plot.

Code	*Scientific and Common/Varietal Name*	*Quantity*
Forbs - upland/lowland seeding:		% trt[1]
AscTub	*Asclepias tuberosa* L. (butterfly milkweed)	0.7*
CeaHer	*Ceanothus herbaceous* Raf. var. *pubescens* T. & G. (inland ceanothus; New Jersey Tea)	5.7
DalCan	*Dalea candida* Michx. ex Willd. (white prairie clover)	11.4
DalPur	*Dalea purpurea* Vent. (purple prairie clover)	12.1*
DesIll	*Desmanthus illinoensis* (Michx.) MacM. (Illinois bundleflower)	1.8*
EchAng	*Echinacea angustifolia* DC. (purple coneflower)	2.9
HelMax	*Helianthus maximilianii* Schrad. (Maximilian sunflower)	3.8
HelHel	*Heliopsis helianthoides* (L.) Sweet var. *scabra* (Dun.) Fern. (false sunflower)	3.1
LesCap	*Lespedeza capitata* Michx. (round-head lespedeza)	8.0
LiaAsp	*Liatris aspera* Michx. (rough gay-feather)	7.2
LiaPun	*Liatris punctata* Hook. (dotted gay-feather)	4.8*
LiaPyc	*Liatris pycnostachya* Michx. (thickspike gay-feather)	7.7*
PenGra	*Penstemon grandiflorus* Nutt. (shell-leaf penstemon)	12.0
RatPin	*Ratibida pinnata* (Vent.) Barnh. (grayhead prairie coneflower)	21.9
SalAzu	*Salvia azurea* Lam. (Pitcher sage)	2.7
SchNut	*Schrankia nuttallii* (DC.) Stand. (catclaw sensitive brier)	0.7
Grasses upland seeding:		kg PLS/ha
AndSco	*Andropogon scoparius* Michx. ('Aldous' little bluestem)	1.74
BouCur	*Bouteloua curtipendula* (Michx.) ('El Reno' sideoats grama)	2.56
BouGra	*Bouteloua gracilis* (H.B.K.) Lag. *ex* Griffiths ('Nature' blue grama)	1.27
Grasses lowland seeding:		
AndGer	*Andropogon gerardii* Vitman ('Kaw' big bluestem)	1.39
AndSco	*Andropogon scoparius* Michx. ('Aldous' little bluestem)	2.16
PanVir	*Panicum virgatum* L. ('Blackwell' switchgrass)	1.68
SorNut	*Sorghastrum nutans* (L.) Nash ('Oto' indiangrass)	2.73
TriDac	*Tripsacum dactyloides* (L.) L. (eastern gammagrass)	2.12

[1]Based on estimates of counts of disseminules of each species; total estimate = 442,500 disseminules.

form on 12 March 1976, and 2,4-D was sprayed on 25 May 1976. In 1976, mowing was completed on 30 March. Information on effects of mowing was limited due to inadvertent mowing of the lowland site just prior to the scheduled sampling date in 1978 and early mowing of some treatment plots in 1977.

Evaluations

Evaluations were conducted 30 August to 10 September 1976, 21 September to 6 October 1977, and, for upland only, on 15 September 1978. Evaluations in 1976 were conducted using 10 microplots (0.5 x 1.0 m) randomly located within each treatment plot. For 1977 and 1978, five circular microplots (1 m^2) were used; this increase in size and reduction in number was needed to accommodate the reduced size of the treatment plots resulting from herbicide retreatment of half of each of the original plots. Within each microplot, canopy cover by species was estimated using seven canopy cover categories: 0%, < 5%, 5-25%, 25-50%, 50-75%, 75-95%, and > 95% (Daubenmire 1959). In addition, from 1 to 20 September 1976, biomass was clipped from 3 microplots (0.5 x 1.0 m) from within each treatment plot and separated into grasses, forbs, and woody plants.

RESULTS AND DISCUSSION

Responses to herbicide application rates were adequately reflected in 1.1 and 2.2 kg/ha treatments thus, for the sake of clarity, only these two rates are addressed in this study. The effects of all four herbicide application rates, however, are available from the authors.

Effects on Overall Diversity

In the lowland site, where standing crop biomass was highest (1.11 kg/ha), mowing resulted in the establishment of the most diverse stand of seeded grasses and forbs. No seeded forbs were found in any plot treated with either atrazine or 2,4-D (Figure 1, Table 2) due to either the effect of the herbicide or the strong favoring of a seeded species, such as switchgrass, which resulted in high standing crop biomass. In the upland, however (standing crop biomass = 0.47 kg/m^2), seeded grass and forb diversity was highest in the untreated plots (Table 3). In combination, these results suggest that herbicides are is not necessary when the objective is to establish a diverse stand of perennial forbs. However, while herbicides did adversely affect overall forb establishment, some forbs were able to become established in treated plots. In those instances, a single application of 2,4-D at any concentration was more successful than was any atrazine treatment or any retreatment.

While 2,4-D and atrazine adversely affected forb establishment, a result that was consistent with the normal use of these herbicides, they were beneficial when the need for rapid grass establishment was the principal objective. Overall results of this study show that, at certain rates, atrazine or 2,4-D were useful in encouraging the rapid establishment of big bluestem, little bluestem, switchgrass, eastern gammagrass, sideoats grama, and blue grama (Figure 2, Tables 2 and 3). Results for individual species were consistent with the findings of others (McCarty 1976, Morrow and McCarty 1976, Martin *et al.* 1982, Bahler *et al.* 1984, Vogel 1987). While forbs may be absent following application of atrazine or 2,4-D, grass diversity can be high even though one species may dominate. For example, first-year, lowland grass stands with atrazine were dominated by switchgrass (ave. cover = 60%) but also contained eastern gammagrass (ave. cover = 19%), big bluestem (ave. cover = 18%), and little bluestem (ave. cover = 10%). However, retreatment, particularly with high concentrations of atrazine, tended to reduce diversity by strongly favoring switchgrass over other species (Table 2). Switchgrass was the only lowland seeded grass to show a consistent increase as atrazine application rates increased from 0.6 to 2.2 kg/ha.

Differences between conditions for the successful establishment of prairie species (mowing in the lowland, control in the upland) and between average standing crop biomass (0.47 kg/m^2 in the upland, 1.11 kg/m^2 in the lowland) (Figure 2), suggest that the amount of standing crop biomass, regardless of the species from which derived (i.e. whether ruderal or seeded), may be at least one factor that adversely affects the establishment and success of seeded forbs. This effect is in addition to any direct effect of herbicides. The relationship between biomass and the number of established species was supported by a weak correlation between total standing biomass and the number of established, seeded species ($R = 0.40$; $P < 0.05$).

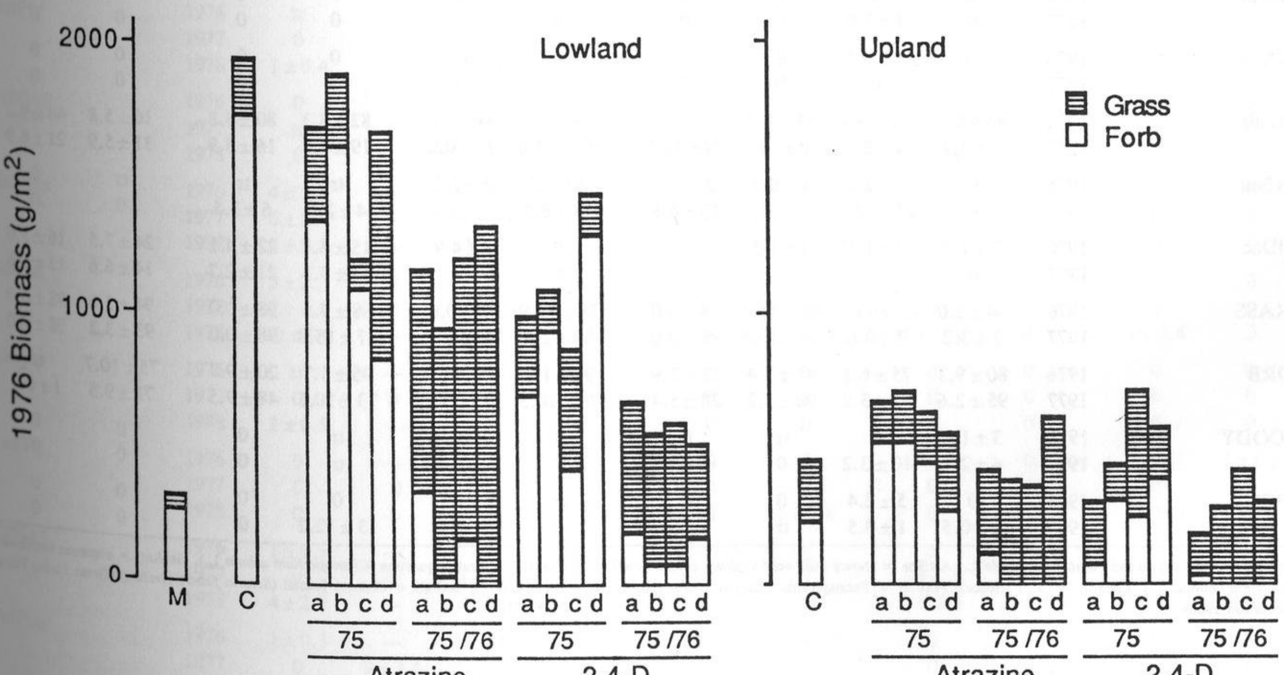


FIG. 1. Biomass for 1976 for upland and lowland sites. M = mowed, C = control, 75 = treated in 1975, 75/76 = treated in both 1975 and 1976, a-c are rates of herbicide application: a = 0.6, b = 1.1, c = 1.7, and d = 2.2 kg/ha.

Table 2. Canopy cover (% ± S.E.) of selected Lowland Site species for 1976 and 1977, two and three growing seasons following seeding and treatment with 2,4-D and atrazine. Selected species are those specifically seeded or those with either at least one average cover value > 25% or a frequency > 70%. See Table 1 or below for species coding. OPEN = bare soil, "tr" = <0.5% cover; "-" = not evaluated.

				Treatment (Rate and Number of Years Applied)							
				2,4-D				*Atrazine*			
				1.1 kg/ha		*2.2 kg/ha*		*1.1 kg/ha*		*2.2 kg/ha*	
Species	*Year*	*Control*	*Mow*	*1 yr*	*2 yr*	*1 yr*	*2 yr*	*1 yr*	*2 yr*	*1 yr*	*2 yr*
		%									
AmbTri[1]	1976	44 ± 13.2	0	0	0	4 ± 3.7	0	64 ± 13.3	6 ± 6.2	31 ± 12.1	0
	1977	56 ± 23.2	0	0	0	0	0	0	12 ± 12.4	6 ± 3.7	0
AndGer	1976	1 ± 0.3	0	2 ± 1.5	11 ± 3.6	2 ± 1.5	8 ± 3.7	3 ± 1.4	24 ± 3.6	12 ± 4.6	31 ± 4.1
	1977	0	25 ± 16.6	11 ± 7.1	48 ± 9.5	50 ± 14.1	38 ± 7.4	19 ± 7.9	33 ± 8.7	26 ± 7.3	1 ± 0.5
AndSco	1976	1 ± 0.3	0	2 ± 1.5	15 ± 3.0	8 ± 4.8	15 ± 4.0	1 ± 0.3	14 ± 3.1	9 ± 2.3	17 ± 3.8
	1977	1 ± 0.5	19 ± 4.4	4 ± 2.7	26 ± 14.8	12 ± 3.0	4 ± 2.7	19 ± 4.4	3 ± 2.9	0	0
AscSpe[1]	1976	2 ± 1.5	0	10 ± 4.8	15 ± 8.7	2 ± 1.5	0	4 ± 2.3	2 ± 1.5	tr	2 ± 1.5
	1977	tr	1 ± 0.5	3 ± 3.0	9 ± 3.7	3 ± 3.0	0	4 ± 2.8	3 ± 2.9	tr	1 ± 0.5
CheAlb[1]	1976	tr	0	2 ± 1.5	0	2 ± 1.5	0	0	0	0	0
	1977	4 ± 2.8	tr	0	0	0	0	0	0	0	0
HelAnn[1]	1976	30 ± 9.9	0	59 ± 6.7	0	54 ± 8.6	2 ± 1.5	40 ± 13.4	tr	21 ± 7.8	0
	1977	40 ± 18.5	31 ± 13.0	76 ± 5.6	21 ± 7.2	68 ± 13.0	57 ± 13.7	58 ± 17.3	35 ± 9.9	71 ± 9.5	0
HelMax	1976	0	4 ± 3.7	0	0	0	0	0	0	0	0
	1977	0	20 ± 12.7	0	0	0	0	0	0	0	0
HelHel	1976	0	0	0	0	0	0	0	0	0	0
	1977	0	tr	0	0	0	0	0	0	0	0
LacSpp[1]	1976	3 ± 2.0	3 ± 2.0	3 ± 2.0	0	7 ± 3.9	0	0	0	0	0
	1977	0	18 ± 8.3	10 ± 7.2	0	10 ± 7.2	0	0	0	0	0
PanVir	1976	0	0	tr	3 ± 2.0	2 ± 1.5	6 ± 3.8	8 ± 4.9	66 ± 8.5	70 ± 12.5	97 ± 1.3
	1977	0	3 ± 3.0	tr	0	6 ± 3.7	3 ± 2.9	3 ± 3.0	59 ± 15.6	59 ± 15.2	95 ± 2.6
Polpen[1]	1976	3 ± 2.0	48 ± 7.4	87 ± 4.6	27 ± 5.6	87 ± 5.9	45 ± 7.1	5 ± 2.3	0	56 ± 11.6	0
	1977	6 ± 3.7	33 ± 8.7	9 ± 3.7	10 ± 7.2	9 ± 3.7	16 ± 5.9	10 ± 3.4	3 ± 3.0	6 ± 3.7	0
RatPin	1976	0	tr	0	0	0	0	0	0	0	0
	1977	0	3 ± 3.0	0	0	0	0	0	0	0	0
SalAzu	1976	0	2 ± 1.5	0	0	0	0	0	0	0	0
	1977	0	0	0	0	0	0	0	0	0	0
SetFab[1]	1976	88 ± 8.3	52 ± 9.4	81 ± 8.2	98 ± 0.0	69 ± 7.9	94 ± 3.6	82 ± 8.3	80 ± 5.8	16 ± 5.8	44 ± 9.2
	1977	7 ± 3.4	4 ± 2.7	69 ± 14.7	79 ± 12.5	47 ± 12.0	98 ± 0.0	19 ± 4.4	16 ± 5.9	31 ± 5.9	21 ± 6.9
SorNut	1976	tr	7 ± 2.2	1 ± 0.3	2 ± 1.5	2 ± 1.5	5 ± 2.2	tr	tr	tr	0
	1977	0	23 ± 18.9	0	13 ± 6.8	18 ± 8.3	7 ± 3.4	4 ± 2.8	6 ± 3.5	0	0
TriDac	1976	2 ± 1.5	2 ± 1.5	2 ± 1.5	2 ± 1.5	0	9 ± 4.9	15 ± 6.3	22 ± 4.1	24 ± 7.5	16 ± 5.0
	1977	tr	0	0	0	0	tr	11 ± 7.1	21 ± 2.7	14 ± 6.6	13 ± 6.8
GRASS	1976	94 ± 2.0	63 ± 11.8	83 ± 11.1	98 ± 0.0	78 ± 10.9	98 ± 0.0	88 ± 9.5	98 ± 0.0	94 ± 3.6	98 ± 0.0
	1977	7 ± 3.2	2 ± 0.0	78 ± 10.5	98 ± 0.0	88 ± 2.6	98 ± 0.0	47 ± 15.8	98 ± 0.0	93 ± 3.2	98 ± 0.0
FORB	1976	80 ± 9.3	75 ± 6.3	95 ± 2.4	27 ± 7.9	98 ± 1.8	44 ± 11.0	95 ± 1.7	20 ± 9.7	75 ± 10.7	tr
	1977	95 ± 2.6	93 ± 3.2	90 ± 3.2	28 ± 5.4	78 ± 10.5	57 ± 13.7	73 ± 10.5	48 ± 9.5	71 ± 9.5	1 ± 0.5
WOODY	1976	3 ± 1.4	0	tr	0	0	0	tr	0	0	0
	1977	4 ± 2.7	10 ± 3.2	0	0	tr	0	tr	0	0	0
OPEN	1976	0	5 ± 2.4	0	tr	tr	tr	0	0	0	0
	1977	1 ± 0.5	1 ± 0.5	tr	0	0	0	13 ± 12.2	0	0	0

[1]AmbTri = giant ragwweed (*Ambrosia trifida* L.) AscSpe = showy milkweed (*Asclepias speciosa* Torr.), CheAlb = lamb's quarters (*Chenopodium album* L.), HelAnn = common sunflower (*Helianthus annuus* L.), LacSpp = (wild lettuce), PolPen = Pennsylvania smartweed (*Polygonum pensylvanicum* L.), SetFab = Chinese foxtail (*Setaria faberi* Herrm.) (Great Plains Flora Association 1986).

Table 3. Canopy cover (% ± S.E.) of selected Upland Site species for 1976, 1977, and 1978, two, three, and four growing seasons following seeding and treatment with 2,4-D and Atrazine. Selected species are those specifically seeded or those with either at least one average cover value > 25% or a frequency > 70%. See Table 1 or below for species coding. OPEN = bare soil, "tr" = < 0.5% cover; "-" = not evaluated.

				Treatment (Rate and Number of Years Applied)							
				2,4-D				*Atrazine*			
				1.1 kg/ha		*2.2 kg/ha*		*1.1 kg/ha*		*2/2 kg/ha*	
Species	*Year*	*Control*	*Mow*	*1 yr*	*2 yr*	*1 yr*	*2 yr*	*1 yr*	*2 yr*	*1 yr*	*2 yr*
		%									
AndGer	1976	0	—	0	0	0	0	tr	2±1.5	tr	0
	1977	0	0	0	0	0	0	0	0	0	0
	1978	0	—	0	0	0	0	0	0	3±2.7	0
AndSco	1976	1±0.3	—	1±0.3	1±0.3	2±1.4	6±2.1	7±2.1	6±2.1	17±3.8	13±3.4
	1977	16±5.9	9±3.7	tr	9±3.7	12±3.0	9±3.4	17±5.6	12±2.6	33±4.4	28±5.4
	1978	28±4.9	—	9±3.3	20±4.0	12±2.7	24±8.5	30±9.6	43±8.0	71±8.4	48±8.5
BouCur	1976	14±3.2	—	8±2.3	4±1.8	3±1.4	15±3.0	15±5.1	14±5.7	16±4.8	10±3.7
	1977	16±5.9	19±4.4	19±4.4	43±13.6	19±4.4	19±4.4	15±0.0	15±0.0	29±9.3	9±3.7
	1978	38±11.4	—	38±0.0	43±8.0	34±7.9	34±10.4	21±6.5	34±7.9	21±6.5	21±6.5
BouGra	1976	3±1.4	—	1±0.2	4±1.8	4±1.8	13±4.4	4±1.9	4±1.9	2±1.4	tr
	1977	6±3.7	4±2.7	12±2.6	12±3.0	15±0.0	12±2.6	3±3.0	0	3±2.9	3±3.0
	1978	2±0.4	—	4±2.5	4±2.6	12±2.7	10±3.0	0	1±0.4	0	0
CeaAme	1976	tr	—	0	tr	tr	0	0	0	0	0
	1977	tr	0	tr	0	0	0	0	0	0	0
	1978	1±0.4	—	3±2.7	0	0	0	0	0	0	0
CheAlb[1]	1976	31±8.3	—	68±9.5	0	72±8.4	0	70±6.7	0	14±6.6	0
	1977	0	tr	0	0	0	0	0	0	0	9±3.4
	1978	0	—	0	0	1±0.5	1±0.5	4±2.4	4±2.4	4±2.5	10±3.0
ConCan[1]	1976	5±2.3	0	5±2.3	tr	4±3.6	0	13±3.4	0	5±3.8	0
	1977	83±5.8	6±3.5	88±2.6	88±2.6	74±7.5	85±0.0	88±2.6	90±3.2	54±14.2	76±5.6
	1978	24±4.9	—	53±10.7	76±4.9	38±9.5	34±10.4	7±3.0	20±4.0	6±3.3	29±8.4
DalCan	1976	tr	—	0	2±1.5	tr	tr	0	0	0	0
	1977	0	0	0	3±2.9	0	3±2.9	0	0	0	0
	1978	0	—	0	1±0.4	0	4±2.6	0	0	0	0
DalPur	1976	tr	—	0	tr	tr	1±0.3	0	0	tr	0
	1977	0	tr	0	0	0	0	0	0	0	0
	1978	1±0.4	—	1±0.4	0	1±0.4	1±0.4	0	0	0	0
EchAng	1976	0	—	tr	0	0	0	0	0	0	0
	1977	tr	0	0	0	0	0	0	0	0	0
	1978	0	—	0	1±0.4	0	0	1±0.4	0	0	0
HelMax	1976	4±3.7	—	2±1.5	0	3±2.0	0	0	0	0	0
	1977	6±3.7	tr	3±2.9	0	6±3.7	0	3±3.0	0	0	0
	1978	4±2.5	—	15±0.0	4±2.5	3±2.7	0	6±3.3	3±2.7	0	0
HelHel	1976	5±2.3	0	tr	0	tr	0	tr	0	tr	0
	1977	1±0.5	0	1±0.5	0	7±7.4	0	0	0	0	0
	1978	10±3.0	—	14±5.7	1±0.5	16±5.4	1±0.4	1±0.4	0	1±0.4	0
LiaAsp	1976	tr	—	0	0	0	0	0	0	0	0
	1977	0	0	0	0	0	0	0	0	0	0
	1978	1±0.5	—	0	0	0	0	0	0	0	0
PanVir	1976	0	—	0	0	0	0	0	0	4±3.7	2±1.5
	1977	0	0	0	0	0	0	0	0	0	0
	1978	0	—	0	0	0	1±0.4	0	0	1±0.4	0
PenGra	1976	1±0.5	—	tr	tr	2±1.5	0	tr	0	tr	0
	1977	tr	tr	1±0.5	0	6±3.7	0	3±2.9	0	tr	0
	1978	4±2.5	—	4±2.6	0	1±0.5	0	4±2.6	0	6±3.3	0
PolPen[1]	1976	1±0.3	—	11±4.7	9±2.4	tr	tr	0	0	0	0
	1977	0	9±3.4	0	0	0	0	0	0	0	0
	1978	0	—	6±3.1	4±7.5	6±3.1	1±0.4	0	1±0.4	0	3±2.7

Table 3. Continued

				Treatment (Rate and Number of Years Applied)							
				2,4-D				Atrazine			
				1.1 kg/ha		2.2 kg/ha		1.1 kg/ha		2/2 kg/ha	
Species	Year	Control	Mow	1 yr	2 yr	1 yr	2 yr	1 yr	2 yr	1 yr	2 yr
		%									
RatPin	1976	5±2.2	—	2±1.5	0	2±1.5	0	1±0.3	0	1±0.3	0
	1977	3±2.9	4±2.8	1±0.5	0	6±3.5	0	9±3.4	0	tr	0
	1978	1±0.4	—	4±2.6	1±0.5	10±3.0	1±0.4	9±3.3	0	0	0
SalAzu	1976	2±1.5	—	tr	0	0	0	0	0	0	0
	1977	0	0	1±0.5	0	0	0	0	0	4±2.8	0
	1978	1±0.5	—	0	0	0	0	0	0	1±0.4	0
SetFab[1]	1976	0	0	79±5.4	92±2.2	78±9.3	89±3.6	89±2.0	98±0.0	73±7.2	95±1.7
	1977	0	88±7.0	0	tr	0	0	0	0	0	0
	1978	1±0.4	—	7±0.3	10±3.0	7±3.0	10±3.0	4±2.5	20±4.0	8±2.7	14±5.9
SchNut	1976	0	—	0	0	0	0	0	0	0	0
	1977	0	0	0	0	0	0	0	0	0	0
	1978	0	—	0	0	0	0	0	0	1±0.4	0
GRASS	1976	95±5.3	—	79±7.7	94±2.8	92±3.1	92±3.1	92±3.1	98±0.0	90±5.2	97±1.8
	1977	19±4.4	98±0.0	24±5.4	57±13.4	33±8.7	24±5.4	19±4.4	19±4.4	52±6.1	28±5.4
	1978	80±4.5	—	42±5.0	48±12.0	48±15.8	71±13.8	64±16.4	76±9.5	90±3.1	74±10.6
FORB	1976	52±7.5	—	72±10.6	12±2.6	77±8.0	9±5.3	75±6.3	4±5.2	23±13.0	0
	1977	90±3.2	15±0.0	93±3.2	88±2.6	83±5.8	85±0.0	93±3.2	90±3.2	62±7.6	76±5.6
	1978	43±8.3	—	85±0.0	76±5.5	62±10.6	38±14.8	30±7.5	24±5.5	20±11.1	48±12.0
WOODY	1976	tr	—	0	0	tr	0	0	0	0	0
	1977	1±0.5	0	tr	0	0	0	0	0	0	0
	1978	1±0.5	—	3±3.0	0	0	0	0	0	0	0
OPEN	1976	2±0.3	—	4±2.7	3±1.9	1±0.5	5±2.4	1±0.5	2±0.4	6±3.0	6±2.9
	1977	0	0	1±0.5	tr	1±0.5	1±0.5	tr	0	2±0.0	tr
	1978	0	—	1±0.6	2±0.5	2±0.6	2±0.6	2±0.6	2±0.0	1±0.5	2±0.6

[1]CheAlb = lamb's quarters (*Chenopodium album* L.), ConCan = horse-weed [*Conyza canadensis* (L.) Cronq.], PolPen = Pennsylvania smartweed (*Polygonum pensylvanicum* L.), SetFab = Chinese foxtail (*Setaria faberi* Herrm.) (Great Plains Flora Association 1986).

Effects on Individual Species

While neither 2,4-D nor atrazine were the most successful method in forb diversity establishment, various species-specific results were observed that may be useful in those instances where herbicide application is deemed necessary. Such a need is likely to be determined for locations, such as the lowland of the present study, where the potential exists for substantial accumulations of undesirable plant biomass.

Effects on seeded species: upland (low biomass) site.

Data for 1978 were collected only from the upland site due to the inadvertent mowing of the lowland site prior to evaluation. These data, however, reflect the net effect of reestablishment efforts and thus are particularly relevant to the principal objective of this study. It was also only on the upland that forbs were successfully seeded in any other than the mowed plot (Figure 1, Tables 2 and 3).

While individual forb species differed, 1978 data generally indicate that 2,4-D applied once and at concentrations varying from 1.1-2.2 kg/ha significantly increased the canopy cover of Maximilian sunflower (*Helianthus maximilianii* Schrad.) and false sunflower [*Heliopsis helianthoides* (L.) Sweet var. *scabra* (Dun.) Fern.]. These species declined either with atrazine or with any retreatment. Grayhead prairie coneflower [*Ratibida pinnata* (Vent.) Barnh.] was increased by single treatments of both 2,4-D and atrazine although it, too, declined with retreatment. For grass establishment, high concentrations of atrazine for little bluestem and 2,4-D for blue grama were more successful than the control (Table 3). As with switchgrass in the lowland, little bluestem was one of three grass species to show a consistent increase following treatment with atrazine.

Of the seeded forbs, only white prairie clover (*Dalea candida* Michx. *ex* Willd.) increased with retreatment. Little bluestem responded similarly. By 1978, blue grama cover was higher with a single treatment of 2,4-D than in the control, although its cover was substantially lower with atrazine. Other seeded species were too infrequent to provide reliable information on the effect of treatments. The upland mowed site could not be evaluated in 1978, but data from previous years indicate that mowing enhanced the establishment of many seeded species.

These results suggest that, where standing crop biomass is low, perhaps around 0.5 kg/m^2, a diverse forb and grass stand can be obtained without applying herbicides. Should herbicides be deemed necessary, however, a single application of 2,4-D is more likely to result in the desired diversity than is the use of atrazine or the use of any second-year retreatment.

Effects on undesirable species: lowland (high biomass) site.

Giant ragweed (*Ambrosia trifida* L.), annual sunflower (*Helianthus annuus* L.), Pennsylvania smartweed (*Polygonum pensylvanicum* L.), and Chinese foxtail (*Setaria faberi* Herrm.) were the dominant undesirable species of the lowland site, although a total of 22 such species was recorded during the study. The effect

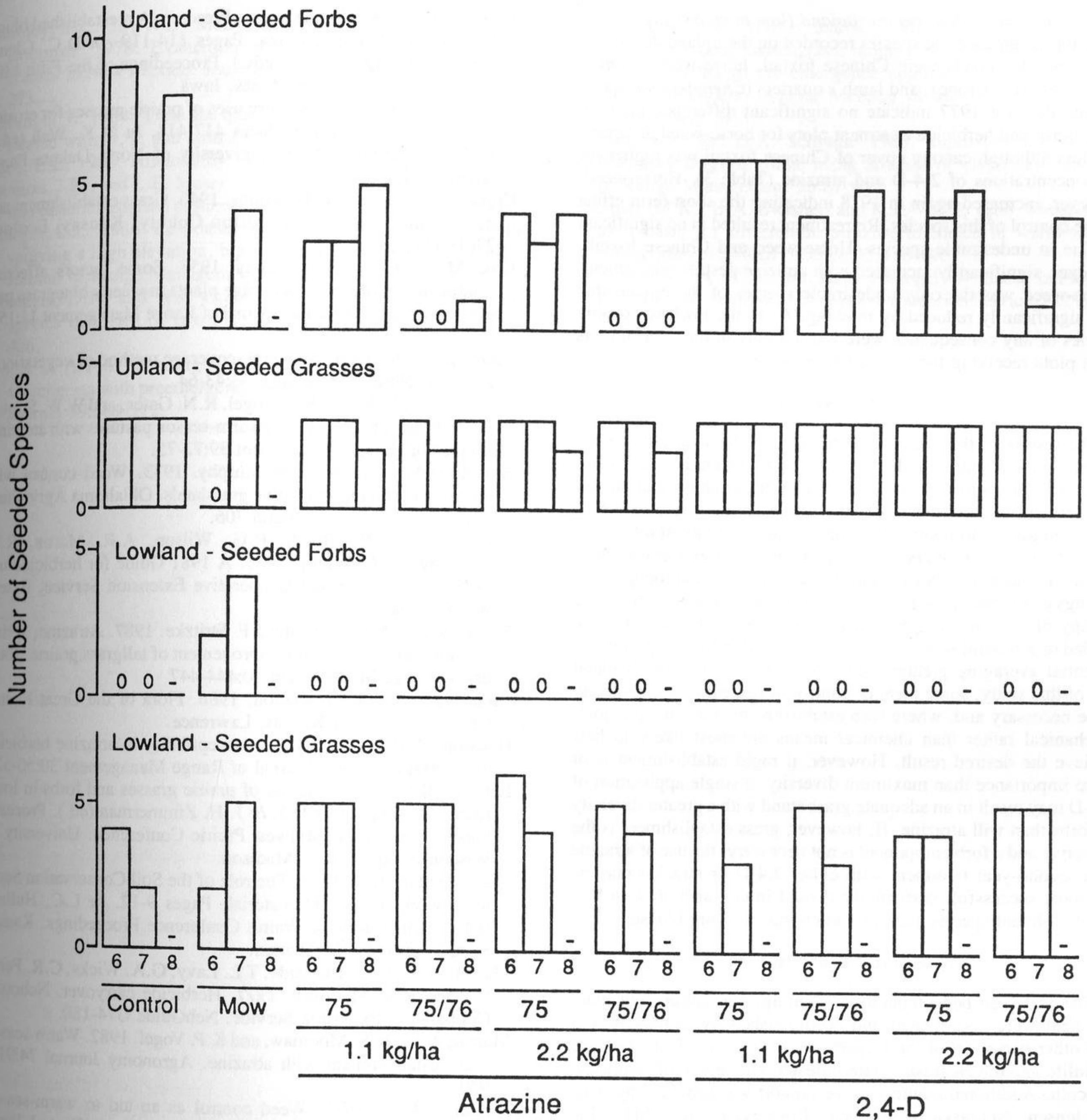


FIG. 2. Number of seeded species located within 1.1 and 2.2 kg/ ha herbicide treatment plots for 1976-78. 75 = treated in 1975, 75/76 = treated in both 1975 and 1976, 6 = 1976 data, 7 = 1977 data, 8 = 1989 date, 0 = none, - = not evaluated.

of a single application of 2,4-D or atrazine was assessed by comparing means and standard errors from the control plot with each treated plot using data from 1977, two growing seasons following herbicide retreatment. This date was selected since it was the last year during which both upland and lowland sites were evaluated. For both 2,4-D and atrazine, declines were noted for giant ragweed at all concentrations and Chinese foxtail at high concentrations (Table 2). Chinese foxtail, as well as annual sunflower, were two of only a few species that showed a consistent decline as application of atrazine increased from 0.6 to 2.2 kg/ha. Areas treated with low concentrations of 2,4-D, however, contained high annual sunflower cover. Similarly, low concentrations of atrazine did not adversely affect Pennsylvania smartweed, although all concentrations of 2,4-D and high concentrations of atrazine resulted in significant increases in this species.

Retreatment with 2,4-D or atrazine was assessed by comparing mean and standard errors from single-year treatment plots to those from two-year treatment plots for 1977 data. For lowland 2,4-D retreatments, annual sunflower declined at low concentrations, and giant ragweed declined at high concentrations (Table 2). Chinese foxtail, however, increased following retreatment at 2.2 kg/ha 2,4-D. With atrazine, however, giant ragweed, annual sunflower, and Pennsylvania smartweed all declined at all concentrations in plots treated the previous year. At least in part, these responses are likely to reflect the effect of an increasingly greater canopy cover of switchgrass occasioned by atrazine treatments. Perennial grasses, such as switchgrass, with established root systems would be expected to have a long-term competitive advantage over annuals.

Mowing in the lowland resulted in significant declines in giant ragweed but an increase in Pennsylvania smartweed (Table 2). Woody species of any consequence were located only in the control plots or in plots receiving the lowest herbicide rate.

Effects on undesirable species: upland (low biomass) site.

Of the 18 undesirable species recorded on the upland during the study, the dominants were Chinese foxtail, horse-weed [*Conyza canadensis* (L.) Cronq], and lamb's quarters (*Chenopodium* spp.). Upland data for 1977 indicate no significant difference between the control and herbicide treatment plots for horse-weed or lamb's quarters although canopy cover of Chinese foxtail was higher for all concentrations of 2,4-D and atrazine (Table 3). Horse-weed, however, increased again in 1978 indicating the short-term effect on the control of this species. Retreatment resulted in no significant decline in undesirable species. Horse-weed and Chinese foxtail, however, significantly increased with atrazine despite retreatment. Horse-weed was the only undesirable species of the upland that was significantly reduced by mowing. As in the lowland, woody species of any consequence were located only in the control plots or in plots receiving the lowest herbicide rate.

CONCLUSIONS

The results of this study need to be considered in light of the absence of replication and, thus, should be taken as preliminary in nature. The study, however, presents information that should be useful in making decisions until more studies are conducted. Based on this preliminary study, one of the most important factors in reestablishing a diverse native perennial forb and grass stand, at least in eastern Nebraska and in the soil types and topographic settings evaluated, appears be the prevention of a dense vegetative canopy of any one species, whether that species be one of those seeded or a ruderal species. For sites with a standing crop biomass potential averaging greater than 0.5 kg/m^2, such as the lowland site of this study, some form of control of ruderal species is likely to be necessary and, where forb establishment is a principal goal, mechanical rather than chemical means are most likely to best achieve the desired result. However, if rapid establishment is of more importance than maximum diversity, a single application of 2,4-D may result in an adequate grass stand with a greater diversity of forbs than will atrazine. If, however, grass establishment is the objective and a forb component is not necessary, the use of atrazine or a second-year treatment with either 2,4-D or atrazine may be the most successful, particularly if used in conjunction with herbicide-tolerant species such as switchgrass and big bluestem.

ACKNOWLEDGEMENTS

Site and seed-bed preparation, seeding, and subsequent management were coordinated and accomplished by Dennis Adams and other personnel of the Department of Forestry, Fisheries, and Wildlife and the Nebraska State Forester, University of Nebraska, Lincoln. Additional administrative support was provided by Peter N. Jensen, Nebraska State Range Conservationist, USDA Soil Conservation Service.

LITERATURE CITED

Bahler, C.C., K.P. Vogel, and L.E. Moser. 1984. Atrazine tolerance in warm-season grass seedlings. Agronomy Journal 76:891-895.

Baker, R.L., and J. Powell. 1978. Oklahoma tallgrass prairie response to natrazine with 2,4-D and fertilizer. Pages 681-683. *In* D.N. Hyder (ed.). Proceedings of the First International Rangeland Congress, Denver.

Bartlett, P.A. 1975. Soil survey of Douglas and Sarpy counties, Nebraska. USDA Soil Conservation Service and University of Nebraska Conservation and Survey Division, Lincoln.

Bland, M.K. 1970. Prairie establishment at the Michigan Botanical Gardens. Pages 46-47. *In* P. Schramm (ed.). Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College Biological Field Station Special Publication Number 3. Galesburg, Illinois.

Bragg, T.B. 1978. Allwine Prairie Preserve: A reestablished bluestem grassland research area. Pages 114-119. *In* D.C. Glenn-Lewin and R.Q. Landers (eds.). Proceedings of the Fifth Midwest Prairie Conference, Ames, Iowa.

Brakeman, W.G. 1975. Industry uses of prairie grasses for erosion control and landscaping. Pages 417-418. *In* M.K. Wali (ed.). Prairie: A Multiple View. University of North Dakota Press, Grand Forks.

Cornelius, D.R., and M.D. Atkins. 1946. Grass establishment and development studies in Morton County, Kansas. Ecology 27(4):3342-353.

Cox, M.L., and M.K. McCarty. 1958. Some factors affecting establishment of desirable forage plants in weedy bluegrass pastures of eastern Nebraska. Journal of Range Management 11:159-164.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43-64.

Dill, T.O., S.S. Waller, K.P. Vogel, R.N. Gates, and W.W. Stroup. 1986. Renovation of seeded warm-season pastures with atrazine. Journal of Range Management 39:72-75.

Elwell, H.M., and W.E. McMurphy. 1973. Weed control with phenoxy herbicides on native grasslands. Oklahoma Agriculture Experiment Station, Bulletin 706.

Furrer, J.D., F.W. Roeth, R.G. Wilson, A.R. Martin, R.S. Moomaw, G.A. Wicks. 1981. A 1981 Guide for herbicide use in Nebraska. Nebraska Cooperative Extension Service, Extension Circular 81-130.

Gillen, R.L., D. Rollins, and J.F. Stritzke. 1987. Atrazine, spring burning, and nitrogen for improvement of tallgrass prairie. Journal of Range Management 40:444-447

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Houston, W.R. 1977. Species susceptibility to atrazine herbicide on shortgrass range. Journal of Range Management 30:50-52.

Landers, R.Q. 1972. The use of prairie grasses and forbs in Iowa roadsides. Pages 180-183. *In* J. H. Zimmerman (ed.). Proceedings of the Second Midwest Prairie Conference. University of Wisconsin Arboretum, Madison.

MacLauchlan, R.S. 1973. The role of the Soil Conservation Service's work with plant material. Pages 9-12. *In* L.C. Hulbert (ed.). Third Midwest Prairie Conference Proceedings. Kansas State University, Manhattan.

Martin, A.R., O.C. Burnside, T.L. Lavy, G.A. Wicks, C.R. Fenster, and R.S. Moomaw. 1977. Herbicide carryover. Nebraska Cooperative Extension Service, NebGuide G74-180.

Martin, A.R., R.S. Moomaw, and K.P. Vogel. 1982. Warm-season grass establishment with atrazine. Agronomy Journal 74:916-920.

McCarty, M.K. 1976. Weed control as an aid to warm-season grass establishment. Proceedings of the North Central Weed Control Conference 31:99-102.

McCarty, M.K., M.L. Cox, and D.L. Linscott. 1974. The Effect of 2,4-D, grazing management and nitrogen fertilizer on pasture production. Nebraska Agricultural Experiment Station, Research Bulletin 260.

Morrow, L.A., C.R. Fenster, and M.K. McCarty. 1977. Control of downy brome on Nebraska rangeland. Journal of Range Management 30:293-296.

Morrow, L.A., and M.K. McCarty. 1975. Control of green sagewort in the Nebraska Sandhills. Weed Science 23:465-469.

Morrow, L.A., and M.K. McCarty. 1976. Selectivity and soil persistence of certain herbicides used on perennial forage grasses. Journal of Environmental Quality 5:462-465.

Plumb G. 1988. Atrazine of little value on a native grassland reseeding (South Dakota). Restoration & Management Notes 6:90-91.

Quimby, P.C. Jr., R.L. McDonald, R.G. Lohmiller, and R.L. Brammer. 1978. Evaluation of herbicides for roadside weed control in New Mexico. Journal of Range Management 31:270-273.

Rehm, G.W. 1984. Yield and quality of warm-season grass mixture treated with N, P, and atrazine. Agronomy Journal 76:731-733.

Rice, E.L. 1984. Allelopathy. Academic Press, San Francisco.

Samson, J.R., and L.E. Moser. 1982. Sod-seeding perennial grasses into eastern Nebraska pastures. Agronomy Journal 74:1055-1060.

Sturges, D.L. 1986. Responses of vegetation and ground cover to spraying a high elevation, big sagebrush watershed with 2,4-D. Journal of Range Management 39:141-146.

Tomkins, D.J., and W.F. Grant. 1977. Effects of herbicides on species diversity of two plant communities. Ecology 58:398-406.

Vogel, K.P. 1987. Seeding rates for establishing big bluestem and switchgrass with preemergence atrazine applications. Agronomy Journal 79:509-512.

Vogel, K.P., A.R. Martin, and R.S. Moomaw. 1981. Tolerance of big bluestem, switchgrass, indiangrass, sideoats grama, and sand lovegrass to pre-emergence application of atrazine. Abstracts of Papers, Annual Meeting of the Society for Range Management 34:31.

Waller, S.S., and D.K. Schmidt. 1983. Improvement of eastern Nebraska tallgrass range using atrazine or glyphosate. Journal of Range Management 36:87-90.

Weimer, M.R., B.A. Swisher, and K.P. Vogel. 1988. Metabolism as a basis for differential atrazine tolerance in warm-season forage grasses. Weed Science 35:436-440.

Wilson, R.G. Jr., A. Martin, and J. Furrer. 1984. Brush and woody plant control. Nebraska Cooperative Extension Service, NebGuide G84-704.

FORAGE VALUE OF WEED SPECIES IN A GRASS SEEDING

B. K. Lawrence, S. S. Waller, L. E. Moser, B. E. Anderson, Department of Agronomy

and

L.L. Larson

Animal Science Department, University of Nebraska, Lincoln, Nebraska 68583

Abstract. Weeds are a major problem in seeding rangeland and cropland to native grasses. However, many immature weedy forbs and grasses are palatable to cattle. Research was conducted using yearling cattle for weed control in big bluestem (*Andropogon gerardii* var. *gerardii* Vitman) seedings (1987, 1988) at Mead, Nebraska on a Sharpsburg silty clay loam (fine, montmorillonitic, mesic Typic Argiudoll) soil. Prominent volunteer species were annual foxtails (*Setaria* spp. Beauv.), redroot pigweed (*Amaranthus retroflexus* SSL.), velvetleaf (*Abutilon theophrasti* Medic.), and common ragweed (*Ambrosia artemisiifolia* L.). Cattle consumed annual foxtails and redroot pigweed, but did not consume velvetleaf or common ragweed. Annual foxtails were grazed completely while heifers mainly stripped leaves and defoliated the tops of redroot pigweed. Redroot pigweed and annual foxtails were randomly collected within blocks during both grazing seasons to quantify forage value. Foliage (upper stem and leaves) was analyzed for crude protein (CP), neutral detergent fiber (NDF), acid detergent fiber (ADF), and *in vitro* dry matter disappearance (IVDMD). Redroot pigweed foliage and leaves were analyzed for nitrate (NO_3). Crude protein levels of annual foxtails and redroot pigweed were never below nutritional requirements for heifers. Fiber (NDF and ADF) and IVDMD values were similar to early-vegetative smooth brome (*Bromus inermis* Leyss.) and early-bloom alfalfa (*Medicago sativa* L.). Nitrate concentration reached toxic levels (10,000 ppm NO_3) in redroot pigweed by mid-July, 1987. In 1988 nitrate levels exceeded the toxic level at the beginning of the grazing season. An abundance of forage nitrate accumulators in weedy vegetation limits grazing as a weed control practice. However, grazing may be an adequate weed control practice when the prominent weeds are annual grasses.

Key Words. redroot pigweed, *Amaranthus retroflexus*, annual foxtails, *Setaria* spp., forage value, nitrates, seeding, Nebraska

INTRODUCTION

Weed competition is the primary reason for seeding failures (Anderson 1981, King 1987). However, weeds are often palatable and nutritious before reaching maturity and can be used as a forage resource in many circumstances. Launchbaugh and Owensby (1978) suggested using the weed crop in first-year grass seedings as a grazing resource. Big bluestem (*Andropogon gerardii* var. *gerardii* Vitman) seedings grazed or mowed regularly (twice weekly from late April to mid August), or treated (0.75 kg/ha) with 2,4-D [(2,4-dichlorophenoxy)acetic acid] on 15 June produced comparable results (Launchbaugh and Owensby 1978). Anderson (1986) listed flash grazing as an effective weed control method.

Redroot pigweed (*Amaranthus retroflexus* L.) is a nitrate accumulator (Osweiler *et al*. 1985). Potential toxic level is 10,000 ppm NO_3 (Bradley *et al*., Osweiler *et al*. 1985). Others reported lower concentrations for potential toxic levels (Lawrence *et al*. 1981, Rasby *et al*. 1988). Nitrate accumulation in plants is affected by several factors: plant species, content and form of soil nitrogen, soil conditions, drought conditions, light intensity, and herbicide treatment. Nitrate concentration is higher in the lower stem than in other plant parts (Osweiler *et al*. 1985). Pigweed species (*Amaranthus* spp. L.), are excellent sources of protein (Cheeke *et al*., Rawate 1983, Bressani 1983). The objective of this study was to quantify the forage quality of available weed species occurring in a big bluestem seeding in eastern Nebraska.

METHODS

The study area had been a weedy smooth brome (*Bromus inermis* Leyss.) pasture located at the Agricultural Research and Development Center near Mead, Nebraska on a Sharpsburg silty clay loam (fine, montmorillonitic, mesic Typic Argiudoll) soil. The pasture was tilled and planted to corn (*Zea mays* L.) in 1985 and 1986. 'Pawnee' big bluestem was seeded (220 PLS/m²) on May 8, 1987 on one-half of the area following a double disking of the corn residue. The remainder was seeded to corn. On 25 April 1988 the remaining half was seeded with Pawnee big bluestem.

Three weed control practices (herbicide, flash grazing, and continuous grazing) were applied to paddocks in a randomized complete block design with four replications. Atrazine [2-chloro-4-(ethylamino)-6-(isopropylamino)-s-triazine] was applied (2.2 kg/ha) on 14 May 1987 and 6 May 1988. Flash grazing (10-28 yearlings/0.05 ha) of paddocks was accomplished in less than 24 hr/occupation four times during 1987 and twice in 1988. Paddocks were grazed when redroot pigweed was 30-60 cm tall. Continuous grazing (5 yearlings/0.20 ha) occurred from 10 June to 22 July 1987. Cattle were removed from plots during wet conditions. Adequate water was provided in each paddock and hay was fed as needed in the continuously grazed paddocks. Continuous grazing was not attempted in 1988 due to high nitrate levels.

Redroot pigweed and annual foxtails (*Setaria* spp. Beauv.) were clipped at ground level and separated into foliage (upper stem and leaves) and stems. Giant foxtail (*Setaria faberii* Herm.), yellow foxtail [*Setaria glauca* (L.) Beauv.], bristly foxtail [*Setaria verticillata* (L.) Beauv.], and green foxtail [*Setaria viridis* (L.) Beauv.] were included as annual foxtails. Lower stems and leaves were excluded due to little or no consumption by grazing livestock. Annual foxtail foliage included all plant material except the lower 10 cm of the plant. Redroot pigweed foliage was all plant material except the lower 15 cm. Plant material (500 g) representative of available forage and independent of grazing treatment was randomly collected and composited from a selected replication(s) at each sample date. Samples were weighed, dried at 60 C, and ground to pass a 1 mm screen. Multiple replications were sampled when stage of growth was variable among blocks. Samples were collected 6 times in 1987 and 3 times in 1988.

Crude protein (CP) was determined by Kjeldahl nitrogen. The Van Soest method was used for neutral detergent fiber (NDF) and acid detergent fiber (ADF) (Goering and Van Soest 1970). Duplicate samples were run for NDF and ADF analysis. Values not within 2% were reanalyzed. The sample value is a mean of duplicates when one block was sampled or a mean of block values when multiple blocks were sampled to characterize the vegetation. *In vitro* dry matter disappearance (IVDMD) was determined using the method described by Marten and Barnes (1981).

Nitrate (NO_3) was determined using a flow injection system, similar to the method described by Carlson and Paul (1969). Values are the mean of all samples collected for the date to give a general characterization. In 1988 a second category of leaves only was also sampled.

RESULTS AND DISCUSSION

Velvetleaf (*Abutilon theophrasti* Medic.), common ragweed (*Ambrosia artemisiifolia* L.), redroot pigweed, and annual foxtails comprised the majority of the weed population in 1987. Livestock avoided velvetleaf and common ragweed. Consumption of redroot pigweed and annual foxtails appeared similar when both were relatively abundant. In 1988, velvetleaf and common ragweed were not as abundant, and the annual foxtails were also reduced. The majority of the weedy vegetation was redroot pigweed.

Crude Protein

Crude protein concentration in redroot pigweed and annual foxtails generally declined through the sampling period during 1987 except for the July 16 sampling date (Table 1). Both species had initiated seed production by 23 June 1987. Redroot pigweed usually was higher than annual foxtails in crude protein. General trends in crude protein values reflected advancing maturity of the plant material. Data for 16 July 1987 were an exception due to a high proportion of regrowth plant material following grazing and timely rain. Redroot pigweed appeared to be a valuable protein source and annual foxtails never were lower than about 12% crude protein. Similar trends were recorded for 1988 (Table 2). Redroot pigweed and annual foxtails contained crude protein levels similar to early-vegetative smooth brome and early-bloom alfalfa (*Medicago sativa* L.). Crude protein, NDF, and ADF values for comparison forages are from Church (1984). Values of IVDMD are typical of these species in eastern Nebraska (Dr. B.E. Anderson, University of Nebraska-Lincoln, personal communication).

Neutral Detergent Fiber

Neutral detergent fiber estimates cell wall components and is inversely related to voluntary intake. Redroot pigweed and annual foxtails NDF values generally increased through the sampling pe-

Table 1. Forage quality of redroot pigweed (AMRE) and annual foxtails (SESP) foliage collected in 1987 from grazed paddocks of a new big bluestem seeding at Mead, Nebraska.

	CP[1]		*NDF*[2]		*ADF*[3]		*IVDMD*[4]	
Date	*AMRE*	*SESP*	*AMRE*	*SESP*	*AMRE*	*SESP*	*AMRE*	*SESP*
	%							
June 11	23.0	17.7	25.9	45.1	15.9	23.6	71.9	73.0
June 16	20.5	16.0	27.1	43.1	14.8	22.4	76.3	70.9
June 23	19.1	15.7	28.8	47.6	15.4	24.5	77.8	71.1
July 6	17.5	14.2	29.9	50.8	15.9	24.0	75.9	74.2
July 16	18.1	19.0	40.7	42.8	23.7	20.6	75.7	73.3
July 22	15.5	12.3	40.8	53.1	24.5	26.9	72.0	68.6
	Forage Comparisons[5]							
Smooth brome (early vegetative)	23.0		48.0		27.0		70.0	
Alfalfa hay (early bloom)	17.0		48.0		38.0		60.0	

[1]Crude protein
[2]Neutral detergent fiber
[3]Acid detergent fiber
[4]In vitro dry matter disappearance
[5]CP, NDF, and ADF from Church (1984), IVDMD from Dr. B.E. Anderson, University of Nebraska-Lincoln, (personal communication)

Table 2. Forage quality of redroot pigweed (AMRE) and annual foxtails (SESP) foliage collected in 1988 from grazed paddocks of a new big bluestem seeding at Mead, Nebraska.

	CP[1]		*NDF*[2]		*ADF*[3]		*IVDMD*[4]	
Date	*AMRE*	*SESP*	*AMRE*	*SESP*	*AMRE*	*SESP*	*AMRE*	*SESP*
	%							
June 14	22.3	17.5	29.7	48.8	16.9	26.1	71.7	74.9
June 20	19.8	18.2	32.3	54.5	22.3	31.8	72.7	74.2
June 28	17.9	16.3	37.2	51.5	27.9	25.6	73.0	74.7
	Forage Comparisons[5]							
Smooth brome (early vegetative)	23.0		48.0		27.0		70.0	
Alfalfa hay (early bloom)	17.0		48.0		38.0		60.0	

[1]Crude protein
[2]Neutral detergent fiber
[3]Acid detergent fiber
[4]In vitro dry matter disappearance
[5]CP, NDF, and ADF from Church (1984), IVDMD from Dr. B.E. Anderson, University of Nebraska-Lincoln, (personal communication)

riod as plant maturity advanced (Tables 1 and 2). Redroot pigweed had a continual increase in NDF concentration while annual foxtails were relatively high early in the season and changed very little through the remainder of the sampling period. Redroot pigweed had less NDF than smooth brome, alfalfa, or annual foxtails. Redroot pigweed should have a higher voluntary intake, based on NDF values, than smooth brome or alfalfa while intake of annual foxtails should be similar to these forages.

Acid Detergent Fiber

Acid detergent fiber estimates cellulose and lignin and is negatively related to digestibility. Like NDF, ADF values in redroot pigweed increased and in annual foxtails remained nearly constant during the sampling period (Tables 1 and 2). Redroot pigweed had lower percentage ADF than annual foxtails early in the growing season. Both weed species had lower ADF values than early-bloom alfalfa. Averaging across dates, annual foxtails had similar ADF levels as smooth brome, and redroot pigweed was generally lower in ADF than smooth brome.

In Vitro Dry Matter Disappearance

Changes in percent IVDMD were slight through the grazing season. Redroot pigweed and annual foxtails were similar both years (Tables 1 and 2). The IVDMD of weed species was similar to early-vegetative smooth brome, and higher than in early-bloom alfalfa.

Nitrate

Amaranthus spp. are known to accumulate nitrate (Osweiler *et al.* 1985). Although concentrations were above the potentially toxic level (10,000 ppm NO_3), acute nitrate poisoning did not occur in 1987 (Table 3). Species composition of paddocks was primarily redroot pigweed and annual foxtails. Cattle did not exhibit preference for either redroot pigweed or annual foxtails when placed onto experimental paddocks. Ruminants have been shown to tolerate higher levels of nitrates when dosage is spread throughout the feeding period or mixed with the total diet (Osweiler *et al.* 1985). Dietary nitrates from pigweed may have been diluted by annual foxtails to reduce nitrate poisoning potential.

Table 3. Nitrate concentration (ppm NO_3) of redroot pigweed foliage and leaf samples collected in 1987 and 1988 from grazed paddocks of a new big bluestem seeding at Mead, Nebraska.

1987		*1988*		
Date	*Foliage*	*Date*	*Leaf*	*Foliage*
	ppm NO_3		---------- ppm NO_3 ----------	
June 11	16,677	June 14	—[1]	55,626
June 16	15,850	June 20	32,040	50,554
June 23	10,735	June 28	23,418	47,342
July 6	8,674		—	
July 16	11,367		—	
July 22	18,402		—	

[1]No data collected

Nitrate was higher in 1988 (Table 3) than in 1987. The growing season of 1988 was characterized by dry conditions, which often enhance nitrate accumulation (Osweiler *et al.* 1985). Species composition was primarily redroot pigweed, and plant densities were greater than in 1987. Consequently, continuous grazing was not attempted in 1988.

Management of the flash grazing plots was altered due to the extremely high levels of nitrate encountered in 1988. Since Osweiler *et al.* (1985) indicated that nitrates were generally greater in the stalk compared to the leaf, a grazing strategy was designed to minimize stalk grazing. High plant density and low to moderate stocking densities for short periods of time resulted in leaf consumption. Stems on the upper part of the plant were not grazed until forage supplies were low. Nitrate concentration in the leaves (Table 3) was much lower than foliage samples. However, nitrates in the leaves were still higher than the potentially toxic level for nitrate poisoning.

CONCLUSIONS

Redroot pigweed and annual foxtails have good potential as forage resources when grazing is used as a method to control weeds in grass seedings. Their crude protein, fiber, and IVDMD levels compared favorably to early-vegetative smooth brome or early-bloom alfalfa. However, redroot pigweed is a nitrate accumulator and can present a safety problem when nitrate levels are excessive, and it is the predominant vegetation. Continuous grazing under these conditions is not advised and flash grazing must be monitored carefully.

Grazing is not likely to control unpalatable species like velvetleaf or ragweed if they are present in large amounts. Also, grazing is not likely to be effective when weed densities are so high that cattle cannot control weed growth. However, grazing may be an effective management practice for weed control when the predominant weeds are annual grasses.

LITERATURE CITED

Anderson, B. 1981. Establishing dryland forage grasses. Nebraska Cooperative Extension Service, G81-543.

Anderson, B. 1986. Warm-season grasses: facts and fantasy. Pages 11-20. *In* B. Anderson, G. Garner, S. Barnhart, and P. Ohlenbusch (eds.). Proceedings of the four state grassland management workshop. Northwest Missouri State University. Maryville.

Bradley, W.B., H.F. Epson, and O.A. Beath. 1940. Livestock poisoning by oat hay and other plants containing nitrate. Wyoming Agricultural Experiment Station Bulletin 241.

Bressani, R. 1983. World needs for improved nutrition and the role of vegetables and legumes. Asian Vegetable Research and Development Center, Tenth Anniversary Monograph Series. Shanhua, Taiwan, Republic of China.

Carlson, R.M., and J.L. Paul. 1969. Nitrate determination of plant extracts by the nitrate electrode. Journal of Agricultural and Food Chemistry 16:766.

Cheeke, P.R., R. Carlsson, and G.O. Kohler. 1981. Nutritive value of leaf protein concentrates prepared from *Amaranth* species. Canadian Journal of Animal Science 61:199-204.

Church, D.C. 1984. Livestock feeds and feeding. O & B Books, Incorporated, Corvallis, Oregon.

Goering, K. and P. Van Soest. 1970. Forage fiber analysis (apparatus, reagents, procedures and some applications). Agricultural Research Service, United States Department Agriculture Handbook 379.

King, M.A. 1987. Establishment of forage grasses on abandoned Sandhills B, Bcropland. Master of Science Thesis. University of Nebraska, Lincoln.

Launchbaugh, J.L., and C.E. Owensby. 1978. Kansas rangelands—their management based on a half century of research. Kansas Agricultural Experiment Station Bulletin 622.

Lawrence, T., G.E. Winkleman, and F.G. Warder. 1981. Nitrate accumulation in Altai wild ryegrass (*Elymus angustus*), Russian wild ryegrass (*E. junceus*), and crested wheatgrass (*Agropyron desertorum*). Canadian Journal of Plant Science 61:735-740.

Marten, G.C., and R.F. Barnes. 1981. Prediction of energy digestibility of forages with *in vitro* rumen fermentation and fungal enzyme systems. Pages 61-71. *In* W.J. Pigden, C.C. Balch, and M. Graham (eds.). Standardization of Analytical Methodology for Feeds. Unipuls, New York.

Osweiler, G.D., T.L. Carson, W.B. Buck, and G.A. Van Gelder. 1985. Clinical and diagnostic veterinary toxicology. Kendall/Hunt Publishing Company, Dubuque, Iowa.
Rasby, R., R. Stock, B. Anderson, and N. Schneider. 1988. Nitrates in livestock feeding. Nebraska Cooperative Extension Service, G74-170.
Rawate, P.D. 1983. *Amaranth* (pigweed): A crop to help solve the world protein shortage. Pages 287-298. *In* W. Lockeretz (ed.). Environmentally Sound Agriculture. Praeger Publishers. New York, New York.

PRAIRIE ESTABLISHMENT IN SOUTHWESTERN OHIO

Kimberly A. Lutz
468 Bryn Mawr Drive, San Antonio, Texas 78209

Abstract. In 1979 a tallgrass prairie was established in southwestern Ohio; a second prairie, adjacent to the first, was established in 1983 (4-year and 8-year sites). These sites differed in time since establishment, seed source, extent of burning, and extent of soil preparation. Six remnant prairies were also selected for comparison with the established sites. The 8-year site was dominated by switchgrass (*Panicum virgatum* L.) and indiangrass [*Sorghastrum nutans* (L.) Nash.], components of the original seed mix, while the 4-year site was dominated by old-field species and big bluestem (*Andropogon gerardii* Vitman). Both 4-year and 8-year sites were equally similar to native Ohio prairies in terms of species presence, but not in terms of species abundance. Most of the vegetational differences between the established sites were attributed to the source of the seed used in prairie establishment. The seed source also accounted for differences between the study sites and native Ohio sites.

Key Words. establishment methods, reconstruction, remnants, tallgrass prairie, Ohio

INTRODUCTION

A peninsula of tallgrass prairie once extended across the midwest covering approximately 1 million square kilometers (Barbour *et al.* 1980). The easternmost extension of this vegetational unit consisted of isolated prairie patches occurring in the state of Ohio (Gleason 1922, Transeau 1935, Wistendahl 1975). Today, 55 of Ohio's 88 counties support remnants of this once vast ecosystem (Gordon 1960, Cusick and Troutman 1978). As in other portions of the midwest, Ohio's prairies have been extensively modified or eliminated through cultivation, overgrazing of domestic stock and fire suppression policies. As the number of native prairies has decreased, interest in reconstruction of tallgrass prairies has increased.

In 1979, a tallgrass prairie was established in southwestern Ohio by the Hamilton County Park District. A second prairie, adjacent to the first, was established in 1983, hereafter these sites will be referred to as the 4-year and 8-year sites. While the sites selected did not presently harbor prairie remnants, there was historical precedence for prairie establishment in southwestern Ohio, as there are many prairie species (Braun 1916 and 1921) and several prairie remnants know from the Cincinnati region (Bryant 1981, Irwin 1929).

The research objectives were to answer the following questions regarding the two established sites: 1) how did differences in establishment techniques affect the vegetational composition of two reconstructed prairies in southwestern Ohio and 2) which reconstruction was most similar in vegetational composition to native Ohio prairies? Answers to these questions were investigated by: a) determining species composition of the 4-year and 8-year established sites and b) comparing established sites with native relic prairies.

METHODS

Study Site

The study site was composed of two adjacent, established prairies in southwestern Ohio (Figure 1). These sites differed in time since establishment, seed course, extent of burning, and extent of soil preparation (Table 1).

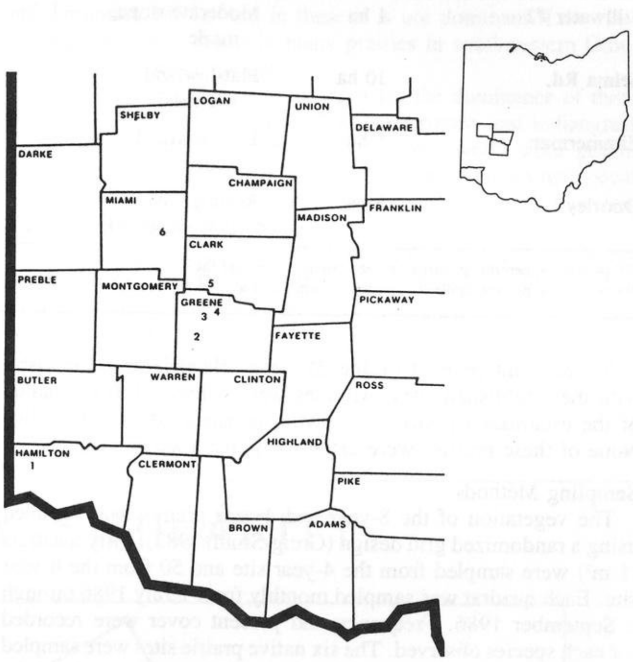


FIG. 1. Location of established sites and remnant prairies.

Table 1. Comparison of two established prairies in southwestern Ohio.

	8-year site	*4-year site*
Date of establishment	1979	1983
Soil composition (in ppm)	N = 6, P = 3, K = 113, pH = 4.7	N = 7, P = 3, K = 131, pH = 4.7
Original vegetation	Old field species including sasafrass, goldenrod, and blackberry	Old field species including sasafrass, goldenrod and blackberry
Seed source	Sharp Bros., Healy, Kansas equal amounts of big bluestem, little bluestem, indiangrass, and switchgrass. 6.8 PLS kg per ha native seed added in 1983.	Collected from native prairies within a 160 km radius of the established site. 2.3-3.2 kg seed and chaff per ha.
Fire management	1983, 95% burn	1983, prior to planting
Soil preparation	Disc harrowed prior to planting.	Shallow plowing

Table 2. Summary of community comparisons.

Prairie	Size	Aspect	PS (4-yr)[1]	PS (8-yr)[2]	Dominants
4-year site	1.5 ha	Flat, mesic	——	49.71	goldenrod, big bluestem broomsedge
8-year site	1.5 ha	Flat, mesic	49.71	——	switchgrass, indiangrass
Herr Rd.	4 ha	Hillside, xeric	30.24	29.43	little bluestem, goldenrod
Stillwater #1	4 ha	Moderate slope, mesic	27.05	30.05	little bluestem, big bluestem, asters
Stillwater #2	1 ha	Moderate slope, mesic	16.69	31.49	goldenrod, Queen Anne's lace, grey-headed coneflower
Selma Rd.	10 ha	Flat-lowland, wet mesic	28.45	28.06	big bluestem, indiangrass, grey-headed coneflower
Zimmerman	5 ha	Flat, lowland, hydric	12.03	20.79	prairie dock, Queen Anne's lace, Virginia mountain mint
Doorley	3 ha	Rolling, river-bottom, hydric	17.22	17.28	big bluestem, orange coneflower, marsh bedstraw

[1]PS (4-year) = percent similarity between remnant sites and the 4-year site.
[2]PS (8-year) = percent similarity between remnant sites and the 8-year site.

Six remnant prairies (Table 2) were selected for comparison with the established sites. All sites were within a 160 km radius of the established prairies, occurring in glaciated western Ohio. None of these prairies were extensively disturbed or managed.

Sampling Methods

The vegetation of the 8-year and 4-year prairies was sampled using a randomized grid design (Greig-Smith 1983). Fifty quadrats (1 m^2) were sampled from the 4-year site and 50 from the 8-year site. Each quadrat was sampled monthly from 1 July 1986 through 6 September 1986. Frequency and percent cover were recorded for each species observed. The six native prairie sites were sampled during the month of August 1986. Sampling was completed for each of the two established sites. The number of samples taken per site varied, however, all were in excess of 25 quadrats.

RESULTS

Vegetational Composition of Established Sites

A total of 121 species of vascular plants belonging to 41 families were identified at the study site. Nineteen species were unique to the 8-year site, and 35 were unique to the 4-year site. Sixty-five species were common to both sites. The Compositae comprised 28% of the flora followed in decreasing order by the Gramineae (14%), the Fabaceae (8%), and the Rosaceae (5%) on both the 4- and 8-year sites. These families, along with the Labiatae, were the dominant families of plants in native tallgrass prairies (Weaver 1968).

Composition of the 8-Year Site

Switchgrass (*Panicum virgatum* L.) and indiangrass [*Sorghastrum nutans* (L.) Nash] were found to have the highest values for percent frequency, percent cover, and importance values (percent frequency + percent cover/2) on the 8-year site. Little bluestem (*Andropogon scoparius* Michx.) and big bluestem (*Andropogon gerardii* Vitman) were among the ten species with the highest importance values, ranking fifth and seventh, respectively.

Many weedy species were also found to be dominant in the 8-year prairie community. Goldenrod (*Solidago* L. spp.) was frequently encountered and contributed greatly to overall cover. Bush clover (*Lespedeza procumbens* Michx.), Korean bush clover (*Lespedeza stipulacea* Maxim.), woolly panicgrass (*Panicum lanuginosum* Ell.), cinquefoil (*Potentilla reptans* L.) and blackberry (*Rubus allegheniensis* Porter) also had high frequencies but had lower percent cover.

Percent frequency, percent cover, and importance of values of prairie species increased gradually throughout the growing season while seasonal variation was observed among the weedy species. For example, Korean bush clover, a Eurasian perennial, peaked in August with an importance value of 4.01, followed by a decline (IV = 1.99) in September. Increasing importance values were noted for prairie grasses which gradually developed throughout the summer (e.g. indiangrass July IV = 12.8, August IV = 14.54, September IV = 19.04). The percent cover, across all species, remained constant throughout the sampling period. Mean percent cover for all species: July = 80.8, August = 76.9, September = 76.9. The average number of species per quadrat was 6.1.

Vegetational Composition of the 4-Year Site

The 4-year site was dominated by weedy vegetation. Goldenrods ranked first in all measures (average IV = 15.6). Other weedy dominants included ragweed (*Ambrosia artemisiifolia* L.), woolly panicgrass, blackberry, broom sedge (*Andropogon virginicus* L.) and cinquefoil. Only one prairie species, big bluestem, had a high importance value (maximum IV = 8.45).

Many species exhibited seasonal dominance. Purple milkwort (*Polygala sanguinea* L.) had an importance value of 3.80 for July dropping to 1.15 in August and 0.51 in September. Other seasonal changes were noted for green foxtail [*Setaria viridis* (L.) Beauv.] which peaked in June, tick trefoil [*Desmondium canadense* (L.) DC.] which peaked in mid-summer, and asters which peaked in September. Percent cover, across all species, remained relatively constant throughout the growing season. Mean percent cover for all species was as follows: July = 70.9, August = 65.4, September = 69.87. The average number of species per quadrat was 9.6.

The 4-year site had greater species richness with 98 total species, while the 8-year site had a total of only 84 species. The 4-year site also had greater diversity (H' = 1.49). Diversity for the 8-year site was H' = 1.31. The Shannon-Wiener Index was used to determine diversity (H'). The formula used was:

$$\text{Shannon-Wiener Index: } H' = \Sigma P_i \log P_i$$

where Σ = the number of species and P_i = the proportion belonging to the *i*th species.

Community Comparisons

The Percent Similarity Index (PS), weighted for percent frequency, was used to compare community samples (Mueller-Dombois and Ellenberg 1974).

$$\text{Community Coefficient: } CCj = 2(FC)/FA + FB + 2(FC)$$

FA = the % frequency of species unique to community A, FB = the % frequency of species unique to community B, FC = the % frequency of species in both community A and B.

Vegetation at the 4-year and 8-year sites was compared to the vegetation at each of the six remnant prairie communities (Figure 2). The 4- and 8-year sites were also compared. The adjacent established sites had greater similarity to each other than to the remnant prairies (PS = 49.7%). The 4-year and 8-year sites were equally similar to all remnant prairies with the exception of Stillwater Prairie #2 and Zimmerman Prairie. The 4-year site was considerably more similar to these prairie remnants since they were both dominated by forbs. The prairie most similar to the 8-year site was Herr Road Prairie (PS = 30.24). Both sites were dominated by little bluestem and lesser amounts of indiangrass with dicots such as goldenrod, cinquefoil, and poison ivy (*Toxicoderdron* P. Mill. sp.) prominent in the species composition. Stillwater Prairie #2 was found to be most similar to the 4-year site (PS = 31.5). Both sites are for dominated with an abundance of Queen Anne's lace (*Daucus carota* L.), goldenrod, and grey-headed coneflower [*Ratibida pinnata* (Vent.) Barnh.].

The communities were re-analyzed, separating prairie species from weedy vegetation (Figure 3). Determination of prairie species classification follows Cusick and Troutman (1978). The similarity of the 4- and 8-year sites to Herr Road, Stillwater #2, and Selma Road is primarily due to those weedy species these sites have in common. Zimmerman and Doorley's Prairie Fen increased dramatically in similarity to the 4- and 8-year sites when considering only prairie species.

DISCUSSION

Vegetational Data

The flora of the 8-year site was dominated by switchgrass and indiangrass with goldenrod, blackberry, and little bluestem as subdominants. The four grasses originally planted in the 8-year site are among those with the highest percent frequency, percent cover, and importance values. These grasses, however, were not typically found as dominants in Ohio prairies (Sears 1926, Jones 1944, Cusick and Troutman 1978, Nolan and Runkle 1985). Switchgrass was found primarily in the prairies of north-central Ohio (Cusick and Troutman 1978), and in these it is not dominant. Likewise, indiangrass, while found in many prairies in southwestern Ohio, is rarely a dominant species.

Several possible explanations exist for the dominance of these two species in the 8-year site. Both switchgrass and indiangrass produce tillers rapidly, within five to seven weeks after germination. Thus, germination and tillering of these species may occur several weeks in advance of such prairie grasses as big bluestem and little bluestem (Weaver 1954).

Most prairie grasses require aerated soils for optimum growth (Weaver 1954). Switchgrass and indiangrass, typically found in wetter lowlands with more poorly aerated soils, may indeed be better suited to the heavy clay soils characteristic of the 8-year site. Indiangrass is also known to invade open space more quickly

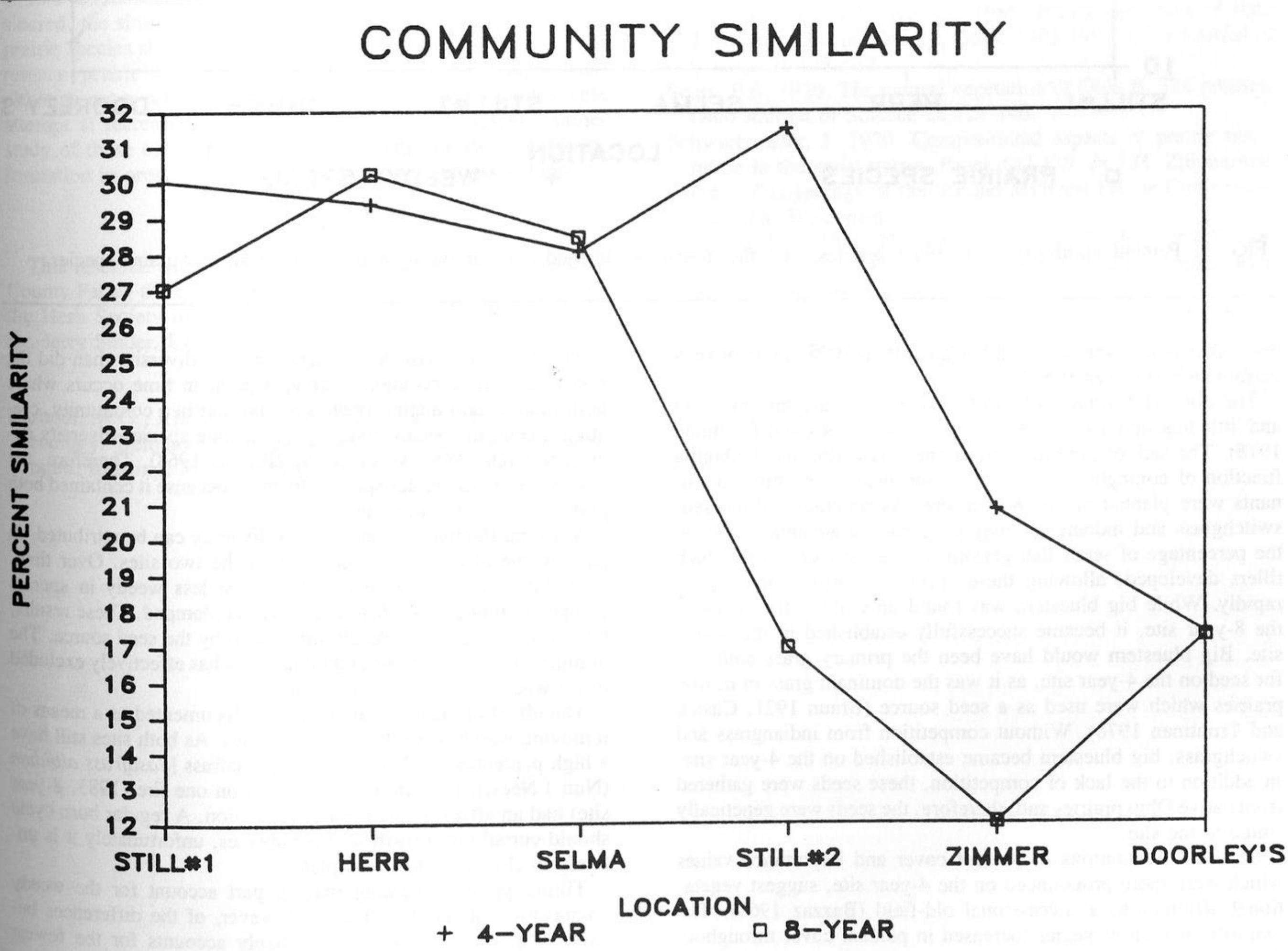


FIG. 2. Percent similarity of remnant prairies with the 4-year and 8-year established sites.

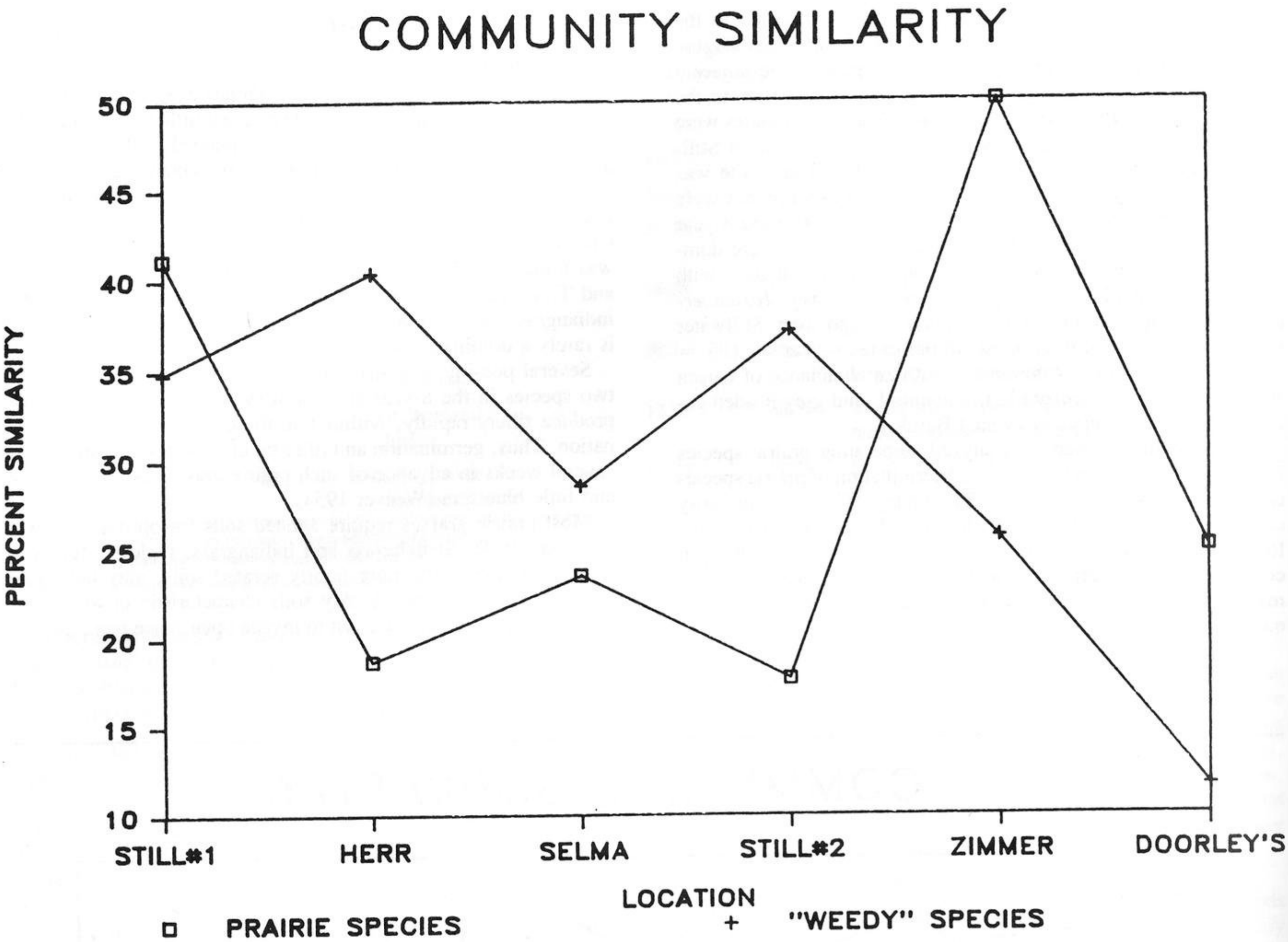


FIG. 3. Percent similarity of remnant prairies with the 8-year established site, comparing numbers of weedy and prairie species.

than other prairie species, as it has an extremely high rate of seed germination (Weaver 1954).

The dominant grasses of most Ohio prairies are big bluestem and little bluestem (Sears 1926, Jones 1944, Cusick and Troutman 1978). The lack of big bluestem on the 8-year site may be both a function of competition and time. Four aggressive prairie dominants were planted on the 8-year site. As previously discussed, switchgrass and indiangrass may have had an advantage both in the percentage of seeds that germinate and the speed with which tillers developed, allowing these species to invade open space rapidly. While big bluestem was found only along the edges of the 8-year site, it became successfully established in the 4-year site. Big bluestem would have been the primary grass collected for seed on the 4-year site, as it was the dominant grass in nearby prairies which were used as a seed source (Braun 1921, Cusick and Troutman 1978). Without competition from indiangrass and switchgrass, big bluestem became established on the 4-year site. In addition to the lack of competition, these seeds were gathered from native Ohio prairies and, therefore, the seeds were genetically suited to the site.

Seasonal fluctuations in percent cover and importance values which were more pronounced on the 4-year site, suggest vegetational affinities to a successional old-field (Bazzaz 1968). The majority of prairie species increased in percent cover throughout the growing season, while old-fields, populated by cool- and warm-season species, fluctuated throughout the year.

The 4-year site also has a higher species diversity than did the 8-year site. In successional seres, a point in time occurs where both pioneer and mature species are present in a community, creating a peak in species diversity. After time species diversity decreased slightly to a steady value (Bazzaz 1968). Therefore, the 4-year site had a greater species diversity because it contained both prairie and old-field species.

Seasonal fluctuations and species diversity can be attributed, in part, to the differences in the ages of the two sites. Over time, both the 4-year and 8-year will become less weedy in species composition and these differences will be damped. These results, however, are again ultimately influenced by the seed source. The dominance of switchgrass and indiangrass has effectively excluded many weedy species from this site.

The effect of burning has long been documented as a means of removing woody vegetation from prairies. As both sites still have a high percentage of blackberry and sasafrass [*Sasafrass albidum* (Nutt.) Nees.], it is unlikely the effect on one fire (1983, 8-year site) had an affect on the present vegetation. A regular burn cycle should curtail the growth of these species, unfortunately it is unlikely to eliminate them completely.

Tilling prior to planting may in part account for the weedy composition of the 4-year site. However, of the differences between the sites, this variable probably accounts for the fewest differences between sites.

Community Data

The 4-year and 8-year sites were equally similar to all remnant prairies with the exception of Stillwater Prairie #2 and Zimmerman Prairie. The 4-year site was considerably more similar to these prairie remnants since they were both dominated by forbs. The grasses made up less than 10% of the species composition of Stillwater Prairie #2 and Zimmerman. They were all dominated by goldenrod species, Queen Anne's lace, and cinquefoil.

Additional observations were made concerning the types of prairie species and weedy species the sites had in common. The remnant prairie sites had an equal number of prairie and weedy species in their flora. The same weedy species were invading natural and established prairies alike. This was also found by Cusick and Troutman (1978) in their survey of Ohio prairies, as well as by Cottam and Wilson (1966) on the Curtis Prairie. Schwartzmeier (1970) examined the possibilities of planting companion crops with prairie weeds to decrease the weedy vegetation that invades nearly established prairies. Similar weeds were found to invade this Wisconsin tallgrass prairie reconstruction as well. With the exception of Stillwater Prairie #1, none of the native sites surveyed had been maintained by fire, mowing, or other management techniques. Therefore, it would be expected that these prairies would have a high incidence of weedy species. These remnants of the prairie ecosystem have remained as they occur in places too steep, too rocky, or with soils too poor to support other vegetation. As a result these sites may not require fire as frequently as larger black soil prairies.

In terms of presence only, the established prairies resemble Ohio's remnant prairies. When abundances of species were considered, the similarities begin to disappear. If possible, additional prairie species should be added to established sites to approximate remnant prairie vegetation. The 4-year and 8-year reconstructions, although not a perfect reflection of native prairies, are a valuable attempt at recreating a once rich and varied ecosystem. Further study of these established communities will provide valuable information in preserving endangered ecosystems for the future.

ACKNOWLEDGEMENTS

This research was conducted with the support of the Hamilton County Parks, the University of Cincinnati Research Council, and the Herb Society of greater Cincinnati. A special thanks also to Dr. Jerry Snider, University of Cincinnati.

LITERATURE CITED

Barbour, M.G., J.H. Burk, and W.D. Pitts. 1980. Terrestrial plant ecology. Benjamin/Cummings Publishing Company Incorporated, Reading, Massachusetts.

Bazzaz, F.A. 1968. Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology 56:485-488.

Braun, E.L. 1916. The physiographic ecology of the Cincinnati Region. Ohio Biological Survey Bulletin Number 7.

Braun, E.L. 1921. Source flora of the Cincinnati Region. Ecology 2:162-178.

Bryant, W.S. 1981. Prairies on Kansan outwash deposits in northern Kentucky. Pages 89-91. *In* R.L. Stuckey and K.J. Reese (eds.). Proceedings of the Sixth North American Prairie Conference. Ohio Biological Survey, Columbus.

Cottan, G., and H.C. Wilson. 1966. Community dynamics on an artificial prairie. Ecology 47:88-96.

Cusick, A.W., and K.R. Troutman. 1978. The prairie survey project: A summary of data to date. Ohio Biological Survey Circular Number 10.

Gleason, H.A. 1922. The vegetational history of the middle west. Annals of the Association of Geographers 12:39-86.

Gordon, R.B. 1960. The natural vegetation of Ohio in pioneer days. Ohio Biological Survey Bulletin 3:1-109.

Greig-Smith, P. 1983. Quantitative plant ecology. Blackwell Scientific Publications, Oxford.

Irwin, N.M. 1929. The Cedar Cliffs Prairie opening of the Cincinnati Region. Proceedings of the Ohio Academy of Sciences. Special Paper 21:203-233.

Jones, C.H. 1944. Studies in Ohio floristics III. Vegetation of Ohio prairies. Bulletin of the Torrey Botanical Club 71:536-548.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetational ecology. John Wiley & Sons. New York.

Nolan, D.B, and J.R. Runkle. 1985. Prairies and fens of Bath Township, Greene County, Ohio: 1802-1984. Ohio Journal of Science 85:125-130.

Sears, P.B. 1926. The natural vegetation of Ohio II. The prairies. Ohio Journal of Science 26:128-146.

Schwartzmeier, J. 1970. Competitional aspects of prairie restoration in the early stages. Pages 122-139. *In* J.H. Zimmerman (ed.). Proceedings of the Second Midwest Prairie Conference. Madison, Wisconsin.

Transeau, E.A. 1935. The prairie peninsula. Ecology 16:423-448.

Weaver, J.E. 1954. The North American Prairie. Johnsen Publishing Company, Lincoln, Nebraska.

Weaver, J.E. 1968. Prairie plants and their environment. University of Nebraska Press, Lincoln.

Wistendahl, W.A. 1975. Buffalo Beats, a relict prairie within a southeastern Ohio forest. Bulletin of the Torrey Botanical Club 102:178-186.

EFFECT OF EASTERN RED CEDAR ON SEEDLING ESTABLISHMENT OF PRAIRIE PLANTS

Dan J. Stipe and Thomas B. Bragg
Department of Biology, University of Nebraska at Omaha,
Omaha, Nebraska 68182-0040

Abstract. To test the hypothesis that eastern red cedar (*Juniperus virginiana* L.) is allelopathic, seedling establishment of five herbaceous prairie species was evaluated by growing seeds in soil collected beneath and adjacent to a stand of this tree species. While four species showed no significant effect, the germination of one species, finger coreopsis (*Coreopsis palmata* Nutt.), was significantly reduced. Since eastern red cedar is an early invader of unburned prairie, such an allelopathic effect, even on only a few species, is of particular concern in that it has the potential to hasten degradation of invaded prairie sites.

Key Words. eastern red cedar, *Juniperus virginiana*, finger coreopsis, *Coreopsis palmata*, allelopathy, Nebraska

INTRODUCTION

Eastern red cedar (*Juniperus virginiana* L.) is purported to produce plant phytotoxins that adversely affect other plant species (Rice 1974, Gehring 1983), although evidence for this allelopathic effect does not appear to have been reported in the literature. As one of the early successional species of unburned tallgrass prairie (Bragg 1974), any allelopathic effect of eastern red cedar is of particular concern since it would have the potential to hasten the decline of prairie species that marginally persist under the canopy of invading trees. The purpose of this study, therefore, was to document whether such an effect occurs and, if so, to identify native prairie species that may be affected.

METHODS

In April 1986, two soil samples were collected at Allwine Prairie Preserve, a research site located 20 km northwest of Omaha, Nebraska. One sample was collected from beneath a grove of eastern red cedar trees (Tree Sample) and another was collected from a nearby grass-dominated area (Grassland Sample). The Grassland Sample was within 10 m of the edge of the trees but neither beneath nor down slope from them; the dominant grass species in this sample was smooth brome (*Bromus inermis* Leyss. ssp. *inermis*). No herbaceous vegetation was present under the cedar canopy. After removal of litter, soil samples were collected to a depth of 5 cm, thoroughly mixed, and each of the two samples placed in three flats (55 x 35 cm) to a depth of 4 cm. The six flats, three per sample, were placed side-by-side in a well-lighted portion of a greenhouse with Tree Sample and Grassland Sample flats alternated to reduce any effect of location. All flats were perforated at the bottom to provide drainage.

Seeds from five species of tallgrass prairie plants (Table 1) were collected in the Fall of 1985 and stored over winter at 4 C. Seeds were collected from Hover Prairie, a native grassland within 15 km of Omaha, Nebraska. Prior to planting, seed samples were visually inspected under a dissecting microscope, and those appearing unlikely to be viable were removed. On 6 April 1986, 25 seeds of each species were planted in separate rows in each of the replicate flats. The seeds were barely covered with soil. Flats were kept well watered throughout the study using the same tapwater source. Seedling establishment was the parameter measured to assess any potential allelopathic effect of eastern red cedar. Growth of the seedling to a height of at least 5 mm was considered to represent successful establishment. Establishment was recorded on 12 and 21 May and on 4 June 1986; mortality was also recorded on the latter of these dates.

Table 1. Establishment of five prairie species in soil collected beneath and adjacent to eastern red cedar trees. Species ordered from most to least negative response. Values represent mean percent germination ± Standard Error from each of three, 25-seed samples. Species nomenclature is from the Great Plains Flora Association (1986).

	Seedling establishment	
Species	*Grassland sample*	*Tree sample*
	% (± S.E.)	
Finger coreopsis (*Coreopsis palmata* Nutt.)	84 + 2.8[1]	0
Indiangrass [*Sorghastrum nutans* (L.) Nash]	21 + 2.4	13 + 0.9
Canada wild rye (*Elymus canadensis* L.)	35 + 1.7	28 + 1.6
Sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.]	17 + 1.2	13 + 1.2
Leadplant (*Amorpha canescens* Pursh)	1 + 0.5	1 + 0.5

[1]Significant difference at the 95% confidence limit.

RESULTS AND DISCUSSION

Of the five species evaluated, only finger coreopsis (*Coreopsis palmata* Nutt.) showed a significant difference between treatments (Table 1), as determined by t-tests at the 95% Confidence Interval. The response was even more noteworthy since total germination of this species was nearly 50% greater than any of the other species evaluated. While differences between treatments for other species were not significant, there was a consistently higher germination in the Grassland Samples for all other species except leadplant (*Amorpha canescens* Pursh) for which germination in both treatments was equally low. Mortality of germinated seeds generally was minimal and was not consistently related to any treatment; with one exception, all mortality occurred during the latter portion of the 2-month study.

This study supports the theory that eastern red cedar produces allelochemicals that affect establishment of at least some prairie species, although it is not clear whether the effect prevents germination or simply delays it. The implication from this conclusion is that eastern red cedar should be of particular concern in prairie management since it has the potential to increase the rate of degradation of prairie beyond the effects of shading of invading trees alone.

LITERATURE CITED

Bragg, T.B. 1974. Woody plant succession on various soils of unburned bluestem prairie in Kansas. Doctor of Philosophy Dissertation, Kansas State University, Manhattan.

Gehring, J.L. 1983. Vegetational changes under isolated *Juniperus virginiana* in an eastern Nebraska bluestem prairie. Master of Arts Thesis, University of Nebraska at Omaha.

Rice, E. 1974. Allelopathy. Academic Press, New York.

ESTABLISHMENT OF GRASSES ON SEWAGE SLUDGE-AMENDED STRIP MINE SPOILS

Cassandra S. Rodgers
Illinois Department of Transportation, District 2, 819 Depot Avenue, Dixon, Illinois 61021
and
Roger C. Anderson
Department of Biological Sciences, Illinois State University, Normal, Illinois 61761

Abstract. Usefulness of native prairie and domesticated grasses in revegetating strip mine spoil and producing biomass was examined on 30-year old, recontoured spoil banks located near Canton, Illinois. Grasses were planted in the spring and fall on strip mine spoil and spoil amended with 333 MT/ha of dry sewage sludge. By the end of the second growing season, indiangrass [*Sorghastrum nutans* (L.) Nash] produced more biomass than the other warm-season grasses, switchgrass (*Panicum virgatum* L.) and little bluestem [*Schizachyrium scoparium* (Michx.) Nash], on the unamended plots, and no warm-season grasses survived on the sludge amended plots. Warm-season grasses were able to compete with weedy species on unamended sites, but two cool-season grasses, reed canarygrass (*Phalaris arundinacea* L.) and Kentucky 31 tall fescue (*Festuca arundinacea* Schreb.), produced more biomass on amended sites than on unamended sites.

Key Words. strip mine spoils, prairie, sewage, sludge, grasses, biomass, Illinois

INTRODUCTION

Strip mining removes topsoil, subsoil, and bedrock material overlying coal seams. Mine spoils, produced prior to the Federal Surface Mining Control and Reclamation Act of 1977, were usually an uneven mixture of consolidated (bedrock) and unconsolidated (till and loess) overburden with no definite soil profile (Ashby *et al*. 1979). Thus, the resulting spoil surface was low in organic matter and essential nutrients, such as nitrogen, potassium, and phosphorous (Richardson and Evans 1986). Major problems associated with revegetating strip mined soils are 1) substrate pH that was often either excessively high (> 10.0) or low (< 4.0) for vegetation establishment (McGuire et al . 1983, Shuman 1986); 2) high soil temperature and low soil moisture during germination and seedling growth (Bell and Ungar 1981, Jastrow *et al*. 1984); and 3) high concentration of soluble salts in the spoil that inhibited revegetation (Jastrow *et al*. 1984, Stark and Redente 1985, Smith *et al*. 1986).

Sewage sludge has been shown to improve many physical and chemical properties of mine spoils. Sludge added essential nutrients for plant growth, increased the humus content and water holding capacity (Epstein 1975, Joost *et al*. 1987), improved the pH of spoils (Epstein 1975, McGuire *et al*. 1983), and generally enhanced plant growth (Anderson and Birkenholz 1983, Joost *et al*. 1987). However, sludge often contained heavy metals (Zn, Cu, Cr, Ni, Pb, and Cd) which could accumulate in soil or plant tissues (Pietz *et al*. 1983).

Native prairie grasses may be excellent plants for spoil reclamation, but their potential use in mine spoil reclamation has been analyzed by relatively few workers (Schramm and Kalvin 1978, Master and Taylor 1979, Anderson and Birkenholz 1983, Kuenstler *et al*. 1983, Jastrow *et al*. 1984, Bonfert *et al*. 1986). Roots of some prairie grasses penetrate the soil to a depth of 200 cm or more and increase soil friability (Hole and Nielsen 1970). Two-thirds of the prairie biomass is below ground (Risser *et al*. 1981), and as roots and other underground organs decay *in situ* they increase the organic matter content of the soil (Hole and Nielsen 1970). The aboveground parts of the plants also form a protective cover that retard runoff and conserve soil moisture, and they have the potential to yield large quantities of biomass (Old 1969, Risser *et al*. 1981, Anderson 1985).

Prairie grasses are usually planted in spring or early summer so the soil can be worked late in the spring to control cool-season weeds (Schramm 1970). Also, prairie grasses do not have vigorous growth until later in the growing season (Wilson 1970). Strip mine spoils often become dry by early summer making grass establishment difficult. Schramm and Kalvin (1978) and Anderson and Birkenholz (1983) suggested that seeds be planted in the late fall or early spring rather than late spring or early summer to avoid the severe summer drought effects which occur on strip mined land.

METHODS

Description of Study Site

Study plots were established on a strip mine spoil site (6,289 hectares) owned by the Metropolitan Sanitary District of Greater Chicago near Canton in west-central Illinois. The spoil banks were about 30-years old but were recontoured before the experimental work was started. Mean annual precipitation was about 96.5 cm. Dry sewage sludge was applied at a rate of about 333 MT/ha and worked into the top 15 cm of spoil by use of a disk on one-half of the research plots during the year (1979) before the fall planting. The seed beds were prepared by disking prior to planting.

Plant and Sampling of Biomass

Four planting treatments were established: unamended-fall, amended-fall, unamended-spring, and amended-spring. Five grass species: three native prairie, warm-season grasses, switchgrass (*Panicum virgatum* L.), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], and indiangrass [*Sorghastrum nutans* (L.) Nash]; and two cool-season, domestic grasses, reed canarygrass (*Phalaris arundinacea* L.) and Kentucky 31 tall fescue (*Festuca arundinacea* Schreb.), and a mix of the three prairie grasses were planted in separate subplots (13.5 x 30 m) within each treatment plot. There were four replicates of each treatment. Fall and spring planting occurred on 1 November 1980, and 1 and 2 June 1981, respectively. Seed, purchased from a commercial grower in Nebraska, was hand broadcasted at a rate of about 495 live seeds/m² (Table 1).

Table 1. Seeding rates (kg/ha) for the grass species in monoculture and mixed plantings of field study.

seeding rate	*Monoculture seeding rate*	*Mixed*
	kg/ha	
Kentucky 31 fescue	8.9	—
Reed canarygrass	7.1	—
Switchgrass	7.1	2.4
Indiangrass	11.2	3.7
Little bluestem	15.4	5.1

During the first growing season, planting success was monitored by counting seedlings of weeds and prairie grasses in 30 quadrats (25 x 25 cm) that were randomly located in each subplot. Aboveground biomass production was estimated using 5 clip quadrats (25 x 25 cm) harvested from each subplot once a month during the first (1981) and second (1982) growing seasons. Tissue samples were oven dried at 70-80 C for 48 hours and then sorted into planted grasses and weeds and weighed. During the first growing season, plots were mowed after each month's sampling to simulate biomass harvest and to also control weeds. During the second growing season, the plots were mowed only after the June sampling period, except one-half of the amended plots were not mowed at all during the second growing season. Only data from mowed plots are presented.

Soil Analyses

pH, organic matter, available P, K, Ca, and Mg, and total N.
At the end of each growing season (fall 1981 and 1982) and at the time of fall planting (1980), soil samples were obtained at two depths (0-15 cm and 15-30 cm) from each plot. Each treatment sample was a composite of two to three soil cores randomly collected from each subplot. Samples were air dried, ground, and analyzed by the Soil and Plant Analysis Laboratory of the University of Wisconsin for pH, organic matter, available P (Bray No. 1), K, Ca, and Mg, and total N (Liegel and Schulte 1977). Soil texture was determined by using the Bouyoucos Hydrometer Method (Bouyoucos 1951).

Electrical conductivity.
Soil samples were collected randomly at two depths (0-15 cm and 15-30 cm) from each plot for determination of electrical conductivity. Electrical conductance of soil solution extracts was measured according to the procedure for analyzing mine soils used by the U.S. Environmental Protection Agency (Sobek *et al.* 1978). The amount of dissolved salts in the extract was approximately proportional to the amount of electrical current conducted through the extract.

RESULTS

First Growing Season

A three-way ANOVA was used to compare seedling counts by season (spring *vs.* fall planting time), substrate (strip mine spoil *vs.* amended spoil), and species. The only significant difference in seedling counts was due to substrates. Significantly ($p < 0.05$) more seedlings were counted in the unamended strip mine spoil (mean ± s.d. for all species and seasons = 56.5 ± 33.4) than in the amended spoil (mean ± s.d. = 17.0 ± 13.5).

Biomass was sampled once a month during the first growing season (June through September 1981), but only the results from the end of the growing season (September) were used to illustrate these data. A three-way ANOVA by season, substrate, and species was performed on the planted species biomass data from the end of the first growing season. Significant effects on biomass production were attributable to species, but no other main effects, substrate or season, were significant. Significant two-way interactions occurred between season (planting time) and species. All other two-way interactions and the three-way interactions were not significant.

No significant differences occurred in mean biomass across substrate and season (mean ± s.d.) among the three warm-season grasses (indiangrass, 19.34 ± 32.19; switchgrass, 32.16 ± 55.47; and little bluestem, 23.85 ± 36.53), and the mixed plantings of these three species (45.61 ± 59.07). No significant differences occurred between the two cool-season species (fescue, 118.24 ± 94.08; and reed canarygrass, 80.21 ± 52.68), or between reed canarygrass and the mixed planting of warm-season grasses. However, mean biomass of fescue was significantly greater than that of the warm-season species and the mixed plantings of these species (Rodgers 1987).

A two-way ANOVA (planting season, substrate) was performed on the total biomass (planted species plus weedy species) at the end of the first growing season (September, 1981). There were significant main effects due to substrates, but not season. The two-way interactions were not significant. The treatments having strip mine spoil amended with sludge produced a significantly greater amount of total biomass than the unamended strip mine spoil (416.29 ± 254.28 *vs.* 210.32 ± 147.40 mean ± s.d.). However, on the amended sites a larger proportion of the total biomass (88%) was comprised of weeds than on the unamended sites (73%).

Second Growing Season

Planted species biomass (June).
Three-way ANOVA (season, substrate, species) indicated sig-

Table 2. Average biomass (mean ± s.d., g/m²) (of planted species and weedy species) at the beginning of the second growing season (June 1982) by species and treatment.

	Unamended				*Amended*			
	Spring		*Fall*		*Spring*		*Fall*	
Species	*Planted*	*Weeds*	*Planted*	*Weeds*	*Planted*	*Weeds*	*Planted*	*Weeds*
	gm/m² (s.d.)							
Indiangrass	71.36ab[1] (60.07)	61.44ABC (96.97)	72.48ab (92.28)	130.64CDEF (69.72)	0.48a (2.15)	190.56F (208.90)	2.08a (7.63)	171.84EF (85.26)
Switchgrass	107.09abc (112.96)	76.59ABCDE (143.08)	58.40a (45.04)	129.92CDEF (102.70)	10.16a (17.66)	155.04DEF (74.82)	3.44a (6.28)	204.88G (179.94)
Little bluestem	120.00abc (129.42)	59.20ABC (87.44)	72.72ab (64.17)	69.44ABCD (66.22)	7.68a (15.57)	182.80F (106.23)	5.36a (12.45)	195.52F (227.30)
Mixture	132.48abc (97.43)	68.08ABCD (131.72)	40.96a (39.14)	148.32CDEF (117.08)	25.44a (66.19)	174.88F (76.51)	6.16a (13.82)	213.76G (99.65)
Reed canary	252.91cd (92.74)	4.05A (15.70)	222.80bcd (247.58)	82.32ABCDE (135.63)	962.72e (455.18)	14.24A (34.89)	1660.56f (1008.11)	105.44BCDEF (463.66)
Fescue	313.12d (149.75)	20.96AB (34.81)	222.40bcd (139.76)	18.80AB (34.55)	624.80e (361.23)	28.56AB (68.90)	612.96e (245.57)	29.68AB (47.01)

[1]Values followed by the same letter are not significantly ($p < 0.05$) different for all means presented. This comparison was made separately for planted species and weeds as indicated by different case letters.

nificant differences in biomass production of planted species at the beginning of the second growing season (June 1982) due to the main effects of substrate and species, but not season. There was no significant difference in the biomass produced between spring and fall planted plots. All two-way interactions and the three-way interactions were significant.

Cool-season grasses produced significantly more biomass than the warm-season grasses and the mixture for fall-amended and spring-amended treatments. No significant differences occurred in biomass production for any treatment among the warm-season grasses, including the mixture. Reed canarygrass produced significantly more biomass than fescue on the fall-amended plots, but not on the spring-amended or unamended plots (Table 2).

When procedures were used to separate all means (Table 2), there were no significant differences in biomass production among warm-season grass species. This apparently occurs because of the wide range of biomass values (0.48 to 1660.56 g/m^2) that results when warm-season and cool-season grasses are considered together. Therefore, the warm-season grass species were compared separately. The unamended-spring treatments of the mixture, little bluestem, and switchgrass produced significantly more biomass than all other warm-season grass species regardless of treatment. Although the spring-amended treatment of indiangrass produced the smallest amount of biomass, it was not significantly different from all other amended treatments. Also, for little bluestem, switchgrass, and the mixture, spring unamended plantings produced significantly more biomass than fall unamended plantings.

Weed biomass (June).

A three-way ANOVA (season, substrate, species) of weedy species biomass in June 1982, revealed that there were significant effects due to substrate, season, and planted grass species with which the weeds were growing. There were no significant two-way or three-way interactions. There was significantly greater weed biomass produced on plots amended with sludge (mean ± s.d. for all species plots and seasons = 138.9 ± 190.2 g/m^2) than unamended plots (73.9 ± 102.6 g/m^2), and there was also significantly more weed biomass produced in plots planted in the fall (125.0 ± 183.1 g/m^2) than in the spring (88.4 ± 121.6 g/m^2).

No significant differences occurred in weed biomass production among warm-season grass plots for any of the unamended treatments. On amended plots, cool-season grass plots had significantly less weed biomass than the warm-season grass plots, except for the weed biomass on reed canarygrass fall-amended plots, which was not significantly different from the weed production on indiangrass or little bluestem fall-amended plots. On spring-unamended plots, however, there were no significant differences among species plots (Table 2).

Planted species biomass (September).

Three-way ANOVA (season of planting, substrate, and species) performed on the biomass data of the planted species from the end of the second growing season (September 1982) indicated that there were significant differences among treatments due to the main effects of substrate and species. There was no significant difference in the biomass produced on plots planted in spring or fall. Significant two-way interactions occurred between substrate and species. Three-way interactions were also significant.

No biomass was produced by warm-season grasses on amended plots (Table 3). When the biomass of each species was compared across treatments, two warm-season grasses, indiangrass and little bluestem, produced significantly more biomass on spring-unamended plots than on fall-unamended plots. Switchgrass produced more biomass on the fall-unamended plots than the spring-unamended plots and there was no difference between fall- and spring-unamended plots for the mixture of warm-season grasses. Spring plantings of indiangrass on unamended plots and reed canarygrass on fall-amended plots produced significantly more biomass than all other species plantings on amended and unamended plots.

Cool-season grasses produced more biomass on amended plots than unamended plots. Reed canarygrass fall-amended treatment plots produced significantly more biomass than the other plots of cool-season grasses. For fescue, no differences occurred between fall and spring plantings, but amended plots produced significantly more biomass than unamended plots.

Weed biomass (September).

Three-way ANOVA of the September 1982, data for the biomass of the weedy species growing in the species plots indicated there were significant effects on weed biomass production due to substrate, season, and species with which the weeds were growing. There were significant two-way interactions between substrate and season, substrate and species, and season and species, and significant three-way interactions.

Table 3. Average biomass (mean ± s.d., g/m²) (of planted species and weedy species) at the end of the second growing season (September 1982) by species and treatment.

	Unamended				*Amended*			
	Spring		*Fall*		*Spring*		*Fall*	
Species	*Planted*	*Weeds*	*Planted*	*Weeds*	*Planted*	*Weeds*	*Planted*	*Weeds*
	gm/m² (s.d.)							
Indiangrass	378.48h[1] (142.18)	109.36AB (102.70)	268.64g (189.84)	89.68A (71.57)	0.0a (0.0)	950.96G (374.13)	0.0a (0.0)	652.24F (250.79)
Switchgrass	142.19bcd (58.52)	39.79A (27.86)	185.92de (108.90)	46.48A (39.38)	0.0a (0.0)	505.20E (219.94)	0.0a (0.0)	905.92G (376.67)
Little bluestem	156.50cd (108.82)	91.76A (102.90)	83.76b (62.71)	70.32A (73.99)	0.0a (0.0)	484.96E (155.71)	0.0a (0.0)	953.44G (523.68)
Mixture	94.80bc (79.32)	76.88A (89.88)	111.36bc (61.15)	51.84A (52.32)	0.0a (0.0)	905.60G (339.12)	0.0a (0.0)	668.40F (192.59)
Reed canary	250.40efg (122.58)	19.84A (40.76)	192.96def (102.46)	31.68A (46.08)	254.24fg (147.21)	135.12ABC (80.94)	345.20h (185.02)	252.40CD (216.89)
Fescue	82.24b (57.97)	54.61A (105.31)	129.68bcd (66.34)	48.32A (86.39)	253.76fg (192.03)	228.72BCD (186.24)	230.32efg (229.32)	319.92D (163.75)

[1]Values followed by the same letter are not significantly ($p < 0.05$) different for all means presented. This comparison was made separately for planted species and weeds as indicated by different case letters.

For the spring-unamended and fall-unamended plots, no significant differences occurred in weedy biomass production among species plots, but for the amended treatments there were significant differences between species plots in weedy biomass production (Table 3). For the amended treatments, there was no significant difference in weedy biomass between fescue and reed canary plots, but there was significantly less weedy biomass on these plots than on the warm-season grass plots.

Soils

The strip mine spoils were composed of 16.0% sand, 28.6% silt, and 55.4% clay and are in the clay textural class. Addition of sewage sludge to the strip mine spoil decreased soil pH, and increased organic matter, total nitrogen, and available P, K, Ca, and Mg. Electrical conductivity of soil solution extracts was higher on amended sites at the 0-15 cm depth for two years following sludge amendment, however, it was about the same on amended and unamended sites during the third year (Rodgers 1987). Electrical conductivity was measured for only two years (1981 and 1982) at the 15-30 cm depth. Electrical conductivity was higher on the amended than the unamended site for the first year that measurements were taken at this depth but not the second. The electrical conductivities did not indicate that the field soils had excessively high levels of soluble salts. All of the soluble salt concentrations, except the 1980, amended, 0-15 cm sample and the 1981, amended, 15-30 cm sample, were less than 2 millimhos/cm. Salinity effects of soluble salt concentrations in this range were considered to be mostly negligible (Allison *et al.* 1969). The other two samples were in the 2-4 millimhos/cm range, which only affects yields of sensitive crops.

DISCUSSION

Comparison of Fall and Spring Plantings of Prairie Grasses

It was initially hypothesized that fall plantings of native prairie grass would be more successful than the late spring plantings on strip mine spoil. Fall plantings would become established in the early spring when soil moisture would be in good supply and before moisture supplies were reduced during summer, whereas spring plantings could be subjected to low moisture availability before they were well established. During the first growing season, seedling counts were used as a measure of establishment, but no significant differences occurred in seedling counts between fall and spring plantings. Similarly, analysis of biomass data obtained at the end of the first growing season showed no significant difference between plots planted at different times. The only significant difference between fall and spring planting times was for the weedy biomass produced during the second growing season which was greater on fall-planted plots than on spring-planted plots.

For the planted species, overall there was no significant effect on biomass production due to season of planting, but there were significant three-way interactions between species, planting times, and substrates. However, there was no consistent pattern between planting time (fall or spring) and success of the plantings. The two years of this study were unusually rainy and there was above normal summer precipitation. Based on data collected at Macomb, Illinois, 44 km to the west of the site, precipitation for 1981 was 133 cm (31 cm above normal), and for 1982 the precipitation was 122 cm, which was 20 cm above normal (National Oceanic and Atmospheric Administration 1981 and 1982). For the major portion of the growing season (May through September), precipitation was 21 cm above normal in 1981 and 15 cm above normal in 1982. Therefore, due to lack of normal summer precipitation, this study was not able to adequately test this hypothesis.

Comparison of Mixed and Single Species Plots on Strip Mine Spoils

After the first growing season, the mixture of warm-season grasses had a greater number of seedlings established than the single species plantings. Biomass production on mixed species plots was also greater than single species plots at the end of the first growing season and in June of the second growing season, but these differences were not significant. Strip mine spoils are composed of varied substrate conditions and are a heterogeneous mixture of environments. Therefore, the soil heterogeneity may have maintained species diversity allowing the different species to exploit different soil microhabitats (Fitter 1982) and increase seedling establishment on the mixed plots.

However, by September of the second growing season, some of the single species plots produced significantly more biomass than the mixed plots. This decrease in biomass production may have been caused by competition between the three plant species in the mixture (Harper 1977, Fitter 1982). By September, the warm-season grasses reached their peak in growth and production. Since these grasses attained different heights at maturity, there could be marked competition for light. The taller species may have shaded and thus reduced production of the shorter species (i.e. little bluestem), consequently, decreasing the total production of the mixed plantings.

Production of Planted Grass Species on Amended Sites *vs.* Unamended Sites

After the first growing season, substrate had no significant effect on biomass production of planted species. Amended treatments produced more total biomass than the unamended treatments, but a greater proportion of the total biomass produced on the amended sites was comprised of weeds than on the unamended sites. In contrast, for plant species harvested in June of the second growing season, there were significant differences between substrates. Amended plots produced more biomass than unamended plots when all planted species are considered. Examination of the data, however, shows that the majority of biomass in all treatments is being produced by the two cool-season species. These cool-season grasses produce more biomass on the amended plots than on the unamended plots. If the warm-season grasses are considered separately, more warm-season grass biomass is produced on the unamended plots than the amended plots. Also, more weed biomass was produced on the amended warm-season grass plots than on the unamended plots for the same species.

In September of the second growing season, unamended plots produced more planted species biomass than the plots amended with sewage sludge. This was largely the result of the absence of warm-season grass species on the amended plots. The weed biomass had increased on these plots and the warm-season grasses were unable to compete on the amended plots.

The results indicate that the warm-season, native prairie grasses were competitive with annual weeds on unamended sites. However, on amended sites, the abundance of inorganic nutrients encouraged weedy species such as giant ragweed (*Ambrosia trifida* L.), barnyard grass (*Echinochloa* sp. Beauv.), horseweed (*Erigeron canadensis* L.), common smartweed (*Polygonum pensylvanicum* L.) adapted to rich nutrient sites. They out-compete the native grasses. These same weed species are not as successful in competing with the cool-season grasses. The cool-season grasses maximized their growth earlier in the growing season than did the weeds. This apparently reduced the production of the weedy species on these plots compared to weed production on plots planted to warm-season grasses.

ACKNOWLEDGEMENTS

This project was funded in part by the following organizations: Metropolitan Sanitary District of Greater Chicago, U.S. Department of Agriculture, Phi Sigma-Beta Lambda Grant, and Illinois State University. We would like to acknowledge the Metropolitan Sanitary District of Greater Chicago for its cooperation and use of their property for this project. Special thanks goes to Dr. R. Michael Miller and Argonne National Laboratory for the use of their facilities and electrical conductivity equipment.

LITERATURE CITED

Allison, L.F., L. Bernstein, C.A. Bower, J.W. Brown, M. Fireman, J.T. Hatcher, H.E. Haywood, G.A. Pearson, R.C. Reeve, L.A. Richards, and L.W. Wilcox. 1969. Diagnosis and improvement of saline and alkali soils. U.S. Department of Agriculture Handbook 60.

Anderson, R.C. 1985. Aspects of the germination ecology and biomass production of eastern gamagrass (*Tripsacum dactyloides* L.). Botanical Gazette 146:353-364.

Anderson, R.C., and D. E. Birkenholz. 1983. Growth and establishment of prairie grasses and domestic forage on strip-mine soils. Pages 183-188. *In* C.L. Kucera (ed.). Proceedings of the Seventh North American Prairie Conference. Southwest Missouri State University, Springfield.

Ashby, W.C., W.C. Hood, and M.L. Guerke. 1979. Geochemical factors affecting plant growth in reclamation. Weeds, Trees, and Turf 18:28-33.

Bell, T.J., and I.A. Ungar. 1981. Factors affecting the establishment of natural vegetation on a coal strip mine spoil bank in southeastern Ohio. The American Midland Naturalist 105:19-31.

Bonfert, G.A., S.J. Josiah, and W.C. Ashby. 1986. Reclamation techniques and combustion technologies. Pages 185-190. *In* R.W. DeVore (ed.). Proceedings 1986 National Symposium on Mining, Hydrology, Sedimentology, and Reclamation. University of Kentucky, Lexington.

Bouyoucos, C.J. 1951. A recalibration of the hydrometer method for making mechanical analysis of soils. Agronomy Journal 43:434-438.

Epstein, E. 1975. Effect of sewage sludge on some soil physical properties. Journal of Environmental Quality 4:139-142.

Fitter, A.H. 1982. Influence of soil heterogeneity on the coexistence of grassland species. Journal of Ecology 70:139-148.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York.

Hole, F.D., and G.A. Nielsen. 1970. Soil genesis under prairie. Pages 28-34. *In* P. Schramm (ed.). Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College, Galesburg, Illinois.

Jastrow, J.D., J P. Schubert, W.S. Vinikour, A.A. Sobek, P.J. Sullivan, W.A. Master, E.D. Pentecost, and S.D. Zellmer. 1984. Amelioration of acidic waste materials resulting from energy mineral extraction. Pages 4-1 to 4-67. *In* A.J. Dvorak (ed.). Ecological Studies of Disturbed Landscapes: A Compendium of the Results of Five Years of Research Aimed at the Restoration of Disturbed Ecosystems. National Technical Information Service, United States Department of Commerce, Springfield, Virginia.

Joost, R.E., F.J. Olsen, and J.H. Jones. 1987. Revegetation and minesoil development of coal refuse amended with sewage sludge and limestone. Journal of Environmental Quality 16:65-68.

Kuenstler, W.F., D.S. Henry, and S.A. Sanders. 1983. Using prairie grasses for forage production on mine spoil. Pages 215-218. *In* C.L. Kucera (ed.) Proceedings of the seventh North American Prairie Conference. Southwest Missouri State University, Springfield.

Liegel, E.A., and E.E. Schulte (editors). 1977. Wisconsin soil testing plant analysis and feed and forage analysis procedures. Department of Soil Science, University of Wisconsin, Madison.

Master, W.A., and J.D. Taylor. 1979. Grundy County reclamation demonstration project phase II: progress report for 1977-78. ANL/LRP-TM-16. Argonne National Laboratory, Argonne, Illinois.

McGuire, P.E., M.R. Spivey, and R.H. Mason. 1983. The palzo project—water quality trends within a sludge-amended strip mine site. Pages 57-66. *In* D.H. Graves (ed.). Proceedings Symposium on Surface Mining, Hydrology, Sedimentology and Reclamation. University of Kentucky, Lexington.

National Oceanic and Atmospheric Administration. 1981. Climatological data, Illinois. 86:4. Environmental Data and Information Service, National Climatic Center, Asheville, North Carolina.

National Oceanic and Atmospheric Administration. 1982. Climatological data, Illinois. 87:4-5. Environmental Data and Information Service, National Climatic Center, Asheville, North Carolina.

Old, S.M. 1969. Microclimate, fire, and plant production in an Illinois prairie. Ecological Monographs 39:355-383.

Pietz, R.I., J.R. Peterson, T.D. Hinesly, E.L. Ziegler, K.E. Redborg, and C. Lue-Hing. 1983. Sewage sludge application to calcareous strip-mine spoil: II. Effect on spoil and corn cadmium, copper, nickel, and zinc. Journal of Environmental Quality 12:463-467.

Richardson, J.A., and M.E. Evans. 1986. Restoration of grassland after magnesian limestone quarrying. Journal of Applied Ecology 23:317-332.

Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton, and J.A. Wiens. 1981. The true prairie ecosystem. Hutchinson Ross Publishing Company, Stroudsburg, Pennsylvania.

Rodgers, C.S. 1987. Establishment of prairie grasses on strip mine spoils. Doctor of Philosophy Dissertation, Illinois State University, Normal.

Schramm, P. 1970. A practical restoration method for tallgrass prairie. Pages 63-65. *In* P. Schramm (ed.). Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College, Galesburg, Illinois.

Schramm, P., and R.L. Kalvin. 1978. The use of prairie in strip mine reclamation. Pages 151-153. *In* D.C. Glenn-Lewin and R.Q. Landers, Jr. (eds.). Proceedings of the Fifth Midwest Prairie Conference. Iowa State University, Ames.

Shuman, L.M. 1986. Effect of liming on the distribution of manganese, copper, iron, and zinc among soil fractions. Soil Science Society of America Journal 50:1236-1240.

Smith, J.A., E.J. DePuit, and G.E. Schuman. 1986. Wood residue and fertilizer amendment on bentonite mine spoils: II. Plant species responses. Journal of Environmental Quality 15:427-535.

Sobek, A.A., W.A. Schuller, J.R. Freeman, and R.M. Smith. 1978. Field and laboratory methods applicable to overburdens and minesoils. EPA-600/2-78-054, Industrial Environmental Research Laboratory, Cincinnati, Ohio.

Stark, J.M., and E.F. Redente. 1985. Soil-plant diversity relationships on a disturbed site in northwestern Colorado. Soil Science Society of America Journal 49:1028-1033.

Wilson, J. 1970. How to get a good stand of native prairie grass in Nebraska. Pages 61-63. *In* P. Schramm (ed.). Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College, Galesburg, Illinois.

GERMPLASM RESOURCES INFORMATION NETWORK AND *EX SITU* CONSERVATION OF GERMPLASM

Mark P. Widrlechner
Agricultural Research Service, U.S. Department of Agriculture, North Central Regional Plant Introduction Station, Iowa State University, Ames, Iowa 50011

Absract. The Germplasm Resources Information Network (GRIN), the master database of the National Plant Germplasm System, was queried to measure the usefulness and limitations of *ex situ* germplasm collections for prairie research. A list of 862 taxa of grasses and forbs native to the prairies of the midwestern United States was checked in a stepwise fashion against recognized names in the GRIN database. Each species was checked against recognized names in the taxonomy area of the database. For each recognized species, the accessions area was queried to see if any populations were entered in the database. The inventory area was then searched to learn if samples of these populations were available for free distribution to researchers and to determine which site is responsible for the maintenance of each available population. Populations of 146 taxa of prairie plants were represented in the GRIN database. Another major *ex situ* source of prairie plant germplasm was not accessible through the GRIN database. The USDA Soil Conservation Service Plant Materials Centers evaluate native species for their potential use in conservation and windbreak plantings. The holdings of the Plant Materials Centers and other institutions not yet part of the GRIN database are briefly discussed.

Key Words. germplasm, genetic diversity, database, seed sources, National Plant Germplasm System, species introduction

INTRODUCTION

The Agricultural Research Service of the U. S. Department of Agriculture coordinates a national network to maintain germplasm of agronomic and horticultural crop plants and their relatives. This system, also known as the National Plant Germplasm System (NPGS), preserves hundreds of thousands of seed and vegetative samples of a wide range of genera at sites throughout the United States (Council for Agricultural Science and Technology 1985). These germplasm collections are used by plant breeders, pathologists, entomologists, botanists, anthropologists, and other researchers in many nations. Samples are provided by the NPGS for scientific research at no cost to the user.

However, the collections in the NPGS have not been widely used by prairie researchers or others studying North American plant communities. This may be due to a lack of pertinent information about the system. Now that most of the holdings of the NPGS can be searched, both by sites within the system and by the public, by using the Germplasm Resources Information Network (GRIN) database (Perry *et al*. 1988), a database search was initiated to determine the extent of the prairie plant germplasm held by the NPGS. This report summarizes the results of a database search conducted during the spring of 1988 and provides information that may be helpful for potential users of the NPGS.

METHODS

During the spring of 1988, a list of species native to the prairies of the midwestern United States was compiled by checking habitats of all species described in the Flora of the Great Plains (Great Plains Flora Association 1986). To create a more complete listing, the initial compilation was supplemented by lists obtained from publications by Betz (1965) for Illinois, Morley (1969) for Minnesota, and Steyermark (1962) for Missouri. From these four sources, 862 taxa were identified that could be considered as native to the midwestern prairies.

These 862 taxa were then checked against the taxonomy area of the GRIN database. The taxa listed as valid names in the GRIN database were then checked for accession and inventory records. A hard copy of accession and inventory records was made from the database. Notes were taken on the availability of the accessions, the origins of the accessions, and the location of the site within the NPGS maintaining each accession.

RESULTS

Of the 862 taxa identified from a search of midwestern floras, 295 were found in the GRIN database. Of these 295 taxa, 275 were found to be valid names, whereas the other 20 were listed as synonyms. That only about a third of the taxa were listed may reflect a natural bias in the NPGS to emphasize crop plants and their relatives.

The 275 valid taxa, plus the GRIN-recognized names for the 20 synonyms, were then checked against the accession and inventory areas of the database to see if any populations of these species were being maintained in the NPGS. Only 146 taxa, of the original 862, were represented in the GRIN database with populations of U.S. or Canadian origin. These 146 taxa are listed in Table 1, along with the number of accessions that have inventory which is actually available for distribution. The site within the NPGS from which they can be obtained is also shown. Table 2 lists addresses for sites within the NPGS that maintain populations of prairie plant germplasm as indicated in the GRIN database search.

DISCUSSION

The sample of prairie plant germplasm represented in Table 1 is not extensive, but it does include some important collections. Many of the populations of big bluestem (*Andropogon gerardii* Vitman) and switchgrass (*Panicum virgatum* L.) held at the National Seed Storage Laboratory serve as reserve collections for a large nursery of native grasses established in the 1970's (Ross 1973 and 1974). This nursery is presently maintained by Dr. Arvid Boe, Department of Plant Science, South Dakota State University, Brookings, South Dakota 57707. Another important holding is the wild sunflower (*Helianthus spp.*) nursery at the Plant Introduction Station in Ames, Iowa. Sunflower is one of only a few important crops domesticated from germplasm native to North American prairies (Heiser 1978). In addition, a good cross section of western range grasses and legumes can be found at the Plant Introduction Station in Pullman, Washington.

The lack of good representation of many of the other prairie genera should not be too surprising, as the core of the NPGS includes the working collections of the four Regional Plant Introduction Stations. These introduction stations were originally established primarily to handle the maintenance of foreign germplasm of major crops (Wilson *et al*. 1985). As researchers consider more carefully the economic value of native species, representation of native species in the NPGS should increase.

Another branch of the United States Department of Agriculture works with native germplasm outside of the NPGS. Soil Conser-

Table 1. Prairie plant germplasm in the National Plant Germplasm System.

Taxon	Site[1]	Total number accessions	Number available
Acacia angustissima (P. Mill.) Kuntze	KPMC	8	8
Achillea millefolium L.	W-6	2	2
Allium cernuum Roth	W-6	1	0
Amelanchier alnifolia (Nutt.) Nutt	CCOR	20	20
	NC-7	5	3
	CPMC	1	0
Ammoselinum popei Torr. & Gray	NSSL	1	—[2]
Amorpha canescens Pursh	NC-7	9	0
	KPMC	1	1
Amorpha nana Nutt.	NPMC	1	0
Andropogon gerardii Vitman	NSSL	1063	—[2]
	S-9	19	14
	CPMC	1	0
	KPMC	2	1
Andropogon hallii Hack.	NSSL	3	—[2]
	S-9	5	1
	KPMC	4	1
Andropogon ternarius Michx.	S-9	1	1
Anemone cylindrica Gray	NSSL	1	2
Asclepias tuberosa L.	NPMC	18	10
Aster ericoides L.	KPMC	33	2
Aster novae-angliae L.	NPMC	50	16
Astragalus aboriginum Richards.	W-6	1	1
Astragalus adsurgens var. *robustior* Hook.	W-6	2	2
Astragalus agrestis Dougl. *ex* D. Don	W-6	1	0
Astragalus bisulcatus (Hook.) Gray	W-6	2	2
Astragalus canadensis L.	W-6	5	5
Astragalus crassicarpus Nutt.	W-6	2	1
Astragalus drummondii Dougl. *ex* Hook.	W-6	1	1
Astragalus flexuosus (Hook.) G. Don.	W-6	2	2
Astragalus lindheimeri Engelm. *ex* Gray	W-6	1	1
Astragalus missouriensis Nutt.	W-6	2	2
Astragalus racemosus Pursh	W-6	1	1
Atriplex heterosperma Bunge	W-6	1	0
Baptisia australis (L.) R. Br.	BPMC	1	1
	KPMC	3	2
Buchloe dactyloides (Nutt.) Engelm.	W-6	1	1
Calamovilfa longifolia (Hook.) Scribn.	CPMC	1	0
	NC-7	3	0
Calylophus serrulatus (Nutt.) Raven	NPMC	1	0
Carex lasiocarpa var. *latifolia* (Boeckl.) Gilly	W-6	1	0
Carex praegracilis W. Boott	W-6	1	0
Ceanothus americanus L.	NPMC	2	0
Ceanothus herbaceus var. *pubescens* (Torr. & Gray) Shinners	NC-7	1	0
Cephalanthus occidentalis L.	NPMC	1	0
Chamaecrista nictitans (L.) Moench	NSSL	1	—[2]
Crataegus crus-galli L.	CCOR	3	3
Crataegus succulenta Schrad. *ex* Link	CCOR	1	1
Croton capitatus Michx.	KPMC	2	2

Table 1. Continued

Taxon	*Site*[2]	*Total number accessions*	*Number available*
Dalea aurea Nutt. *ex* Pursh	KPMC	2	2
Dalea candida Michx. *ex* Willd.	NPMC	3	0
	NC-7	1	0
Dalea enneandra Nutt.	NC-7	4	0
Dalea multiflora (Nutt.) Shinners	NPMC	1	0
Dalea purpurea Vent.	NSSL	1	—[2]
	NPMC	2	0
Daucus pusillus Michx.	NC-7	3	0
	NSSL	1	—[2]
Deschampsia caespitosa (L.) Beauv.	W-6	9	8
Desmanthus illinoensis (Michx.) MacM. *ex.* B.L. Robins & Fern.	KPMC	21	8
	CPMC	1	1
	S-9	2	1
	NSSL	1	—[2]
Distichlis spicata (L.) Greene	CPMC	7	0
Distichlis stricta (Torr.) Rydb.	CPMC	7	0
Echinacea pallida var. *angustifolia* (DC.) Cronq.	NC-7	1	1
	KPMC	1	1
Elymus canadensis L.	NSSL	2	—[2]
	W-6	27	27
	KPMC	15	8
Elymus virginicus L.	W-6	31	31
	KPMC	4	1
Elytrigia dasystachya (Hook.) Love & Love	NSSL	3	—[2]
	W-6	7	7
Eragrostis secundiflora Presl.	W-6	1	1
Eragrostis trichodes (Nutt.) Wood	NSSL	4	—[2]
	W-6	3	3
Festuca ovina L.	W-6	8	8
Festuca scabrella Torr. *ex* Hook.	W-6	6	5
Fragaria vesca L.	CCOR	25	20
Fragaria vesca ssp. *bracteata* (Heller) Staudt.	CCOR	2	2
Fragaria virginiana Duchn.	CCOR	34	27
Fragaria virginiana ssp. *glauca* (S. Wats.) Staudt.	CCOR	23	21
Fraxinus pennsylvanica Marsh.	NSSL	1	—[2]
	KPMC	1	1
	NC-7	3	0
Glycyrrhiza lepidota Pursh	W-6	6	0
Hedysarum boreale ssp. *mackenzii* (Richards.) Welsh	NE-9	1	0
Helianthus grosseserratus Martens	NC-7	34	1
Helianthus maximilianii Schrad.	NC-7	57	0
	NPMC	3	2
	NSSL	1	—[2]
Helianthus mollis Lam.	NC-7	29	0
	KPMC	1	1
	CPMC	3	0
Helianthus occidentalis Riddell	NC-7	6	0
Helianthus occidentalis ssp. *plantagineus* (Torr. & Gray) Heiser	NC-7	11	0
Helianthus rigidus (Cass.) Desf.	NC-7	22	3
Helianthus rigidus spp. *subrhomboides* (Rydb.) Heiser	NC-7	12	0

Table 1. Continued

Taxon	*Site*[1]	*Total number accessions*	*Number available*
Helianthus salicifolius A. Dietr.	NC-7	5	0
	CPMC	1	0
Hilaria jamesii (Torr.) Benth.	S-9	1	0
	NSSL	1	—[2]
	NPMC	1	0
Indigofera miniata var. *leptosepala* (Nutt.) B.L. Turner	S-9	2	0
Iris missouriensis Nutt.	W-6	1	0
Koeleria cristata (L.) Pers.	W-6	2	2
	NSSL	1	—[2]
Lathyrus polymorphus Nutt.	W-6	2	1
Lespedeza capitata Michx.	S-9	23	0
	NSSL	15	—[2]
	NPMC	17	0
	KPMC	1	1
Lespedeza stuevei Nutt.	KPMC	2	1
Lesquerella auriculata (Engelm. & Gray) S. Wats.	W-6	1	0
Lesquerella gracilis (Hook.) S. Wats.	W-6	2	0
Leymus cinereus (Scribn. & Merr.) Love	NSSL	1	—[2]
	W-6	10	8
Leymus innovatus (Beal) Pilger	W-6	9	9
Liatris punctata Hook.	W-6	5	0
	KPMC	2	1
Liatris pycnostachya Michx.	NSSL	1	—[2]
Liatris spicata (L.) Willd.	NPMC	1	0
Lotus purshianus (Benth.) Clem. & Clem.	NE-9	3	3
Lupinus argenteus Pursh	W-6	9	5
Lupinus argenteus var. *tenellus* (Dougl. *ex* G. Don) D. Dunn	W-6	14	10
Lupinus caudatus Kellogg	W-6	4	4
Lupinus pusillus Pursh	W-6	1	1
Lupinus sericeus Pursh	W-6	28	24
Lupinus sericeus var. *egglestonianus* C.P. Sm.	W-6	4	2
Lupinus sericeus var. *flexuosus* (Lindl. *ex* J.G. Agardh) C.P. Sm.	W-6	20	16
Lupinus sericeus var. *maximus* C.P. Sm. *ex* Fleak & D. Dunn	W-6	2	2
Monarda citriodora Cerv. *ex* Lag.	NC-7	1	0
Monarda fistulosa L.	NC-7	16	0
Monarda pectinata Nutt.	NC-7	1	0
Monarda punctata L.	NC-7	2	1
Oenothera macrocarpa Nutt.	NSSL	3	—[2]
Oenothera speciosa Nutt.	KPMC	1	1
Oenothera villosa Thunb.	NSSL	42	—[2]
Oxytropis campestris var. *gracilis* (A. Nels.) Barneby	W-6	1	1
Oxytropis deflexa (Pallas) DC.	W-6	4	3
Oxytropis lambertii Pursh	W-6	1	1
Oxytropis sericea Nutt. *ex* Torr. & Gray	W-6	2	2
Panicum obtusum H.B.K.	S-9	2	0
	KPMC	3	1
	NPMC	1	1
Panicum virgatum L.	NSSL	141	—[2]
	S-9	23	20
	BPMC	4	1
	CPMC	6	1
	KPMC	1	1
	QPMC	1	1

Table 1. Continued

Taxon	*Site*[1]	*Total number accessions*	*Number available*
Pediomelum cuspidatum (Pursh) Rydb.	NPMC	3	0
Penstemon albidus Nutt.	NC-7	1	0
Penstemon secundiflorus Benth	NC-7	1	0
Phalaris caroliniana Walt.	NPMC	1	0
Phyla cuneifolia (Torr.) Greene	NC-7	1	0
Poa arida Vasey	CPMC	3	0
	NSSL	1	—[2]
Poa canbyi (Scribn.) Piper	W-6	6	6
Poa interior Rydb.	W-6	4	4
Psoralidium tenuiflorum (Pursh) Rydb.	KPMC	9	2
Pycnanthemum tenuifolium Schrad.	NC-7	7	0
Pycnanthemum virginianum (L.) Durand & Jackson	NC-7	8	0
Rhus aromatica var. *serotina* (Greene) Rehd.	NC-7	1	1
Rhus copallina L.	NC-7	18	10
	KPMC	1	1
Rosa setigera Michx.	NC-7	3	3
Rosa woodsii Lindl.	NC-7	4	4
Rubus allegheniensis Porter	CCOR	5	5
Rubus flagellaris Willd.	CCOR	3	3
Rudbeckia hirta L.	BPMC	1	1
	NPMC	3	4
Salix humilis var. *tristis* (Ait.) Griggs	CPMC	1	0
Salvia azurea var. *grandiflora* Benth.	NC-7	11	0
	NSSL	1	—[2]
Schedonnardus paniculatus (Nutt.) Trel.	NC-7	1	0
Schizachyrium scoparium (Michx.) Nash	NSSL	6	—[2]
	S-9	26	22
	CPMC	1	1
	KPMC	8	2
	NPMC	2	1
	W-6	2	2
Schrankia nuttallii (DC. *ex* Britt. & Rose) Standl.	W-6	2	0
Shepherdia argentea (Pursh) Nutt.	NC-7	1	1
Silphium laciniatum L.	W-6	2	0
Sorghastrum nutans (L.) Nash	NSSL	12	—[2]
	S-9	12	7
	CPMC	20	8
	KPMC	3	2
Spartina pectinata Link	NPMC	13	1
	W-6	2	2
Stachys palustris L.	NC-7	1	0
Stachys tenuifolia Willd.	NC-7	1	0
Stipa comata Trin. & Rupr.	W-6	2	2
Stipa spartea Trin.	W-6	1	1
Stipa viridula Trin.	NSSL	2	—[2]
	W-6	6	6
Strophostyles helvola (L.) Ell.	CPMC	2	2
Tephrosia virginiana (L.) Pers.	KPMC	2	2
Tridens muticus (Torr.) Nash	NC-7	1	1
	KPMC	2	2
Verbena halei Small	NC-7	1	0
Vicia americana Muhl. *ex* Willd.	S-9	1	0
Yucca glauca Nutt. *ex* Fraser	NC-7	4	0

[1]For explanation of site abbreviations see Table 2.
[2]The National Seed Storage Laboratory (NSSL) will only provide samples to researchers if there is no other source of the material, either within the NPGS or through commercial sources.

Table 2. Addresses for National Plant Germplasm System Sites with available prairie plant germplasm.

Plant Introduction Stations and Addresses:	
NC-7	- North Central Regional Plant Introduction Station Iowa State University Ames, Iowa 50011
NE-9	- Northeastern Regional Plant Introduction Station New York State Agricultural Experiment Station Geneva, New York 14456
S-9	- Southern Regional Plant Introduction Station 1109 Experiment Griffin, Georgia 30223-1797
W-6	- Western Regional Plant Introduction Station Washington State University 59 Johnson Hall Pullman, Washington 99164-6402
Plant Materials Centers and Addresses:	
BPMC	- Big Flats Plant Materials Center RD #1, Box 360A Corning, New York 14830
CPMC	- Coffeeville Plant Materials Center Route 3, Box 215A Coffeeville, Mississippi 38922
KPMC	- Knox City Plant Materials Center Route 1, Box 155 Knox City, Texas 79529
NPMC	- National Plant Materials Center BARC-East, Building 509 Beltsville, Maryland 20705
QPMC	- Quicksand Plant Materials Center Quicksand, Kentucky 41363
Other Sites and Addresses:	
CCOR	- National Clonal Germplasm Repository 33447 SE Peoria Road Corvallis, Oregon 97333
NSSL	- National Seed Storage Laboratory Colorado State University Fort Collins, Colorado 80523

vation Service Plant Materials Centers evaluate populations of a broad range of native species for their potential as windbreak and conservation plants (Soil Conservation Service 1979). A few of the populations held by the Plant Materials Centers are listed in the GRIN database, but more comprehensive lists can be obtained from the National Plant Materials Center (BARC-East, Building 509, Beltsville, Maryland 20705). Plant Materials Centers known for their collections of prairie plants include those at Manhattan, Kansas; Bismarck, North Dakota; Elsberry, Missouri; and Knox City, Texas.

Although the prairie plant germplasm held in the NPGS may be limited in scope, scientists may still find it useful for a number of purposes. Most NPGS collections are well documented geographically and taxonomically, and they may be useful for comparative studies or even for particular problems in prairie establishment or restoration. Obtaining documented seed samples from native stands can be a tedious process, which depends greatly upon proper timing and the right environmental conditions for seed production. Sites in the NPGS can provide specific documentation about collections and actual seed samples at no charge to *bona fide* researchers. If inventory is available, samples can usually be sent in a matter of weeks. When inventory is not available, arrangements can often be made to expedite seed increases. Some germplasm collections may even represent populations that are no longer growing *in situ*.

As scientists who work with prairie plants learn more about the NPGS, personal connections may be made that will lead to greater use of this resource and allow for a larger number of accessions of prairie species to be brought into the NPGS for preservation and the benefit of all.

ACKNOWLEDGEMENTS

The author wishes to thank Arvid Boe, John Pleasants, and Calvin Sperling for their helpful reviews; Raymond Clark for his assistance in getting this manuscript to publication; and especially to Neil Senechal for his willingness to present this report at the conference in my absence. Journal Paper Number J-13216 and Project 1018 of the Iowa Agriculture and Home Economics Experiment Station, Ames.

LITERATURE CITED

Betz, R.F. 1965. Prairie plants of the Chicago Region. The Morton Arboretum, Lisle, Illinois.

Council for Agricultural Science and Technology. 1985. Plant germplasm preservation and utilization in U.S. agriculture. Council for Agricultural Science and Technology Report 106.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Heiser, C.B., Jr. 1978. Taxonomy of *Helianthus* and origin of domesticate sunflower. Pages 31-53. *In* J.F. Carter (ed.). Sunflower science and technology. American Society of Agronomy, Madison, Wisconsin.

Morley, T. 1969. Spring flora of Minnesota. University of Minnesota Press, Minneapolis.

Perry, M., A.K. Stoner, and J.D. Mowder. 1988. Plant germplasm information management system: germplasm resources information network. HortScience 23;57-60.

Ross, J.G. 1973. Domestication of warm season grasses native to South Dakota. Pages 23-24. *In* Proceedings of the 22nd Western Grass Breeders Work Planning Conference. Agriculture Canada Research Station, Swift Current, Saskatchewan.

Ross, J.G. 1974. Preservation of representative plants from relict colonies of tall warm season grasses in eastern South Dakota and southeastern North Dakota. Proceedings of the South Dakota Academy of Science 53:299.

Soil Conservation Service. 1979. Plant materials for conservation. U.S. Department of Agriculture, Soil Conservation Service, Washington, D.C.

Steyermark, J.A. 1962. Flora of Missouri. Iowa State University Press, Ames.

Wilson, R.L., R.L. Clark, and M.P. Widrlechner. 1985. A brief history of the North Central Regional Plant Introduction Station and a list of genera maintained. Proceedings of the Iowa Academy of Science 92:63-66.

HULBERT'S STUDY OF FACTORS EFFECTING BOTANICAL COMPOSITION OF TALLGRASS PRAIRIE

David J. Gibson
Department of Biology, University of West Florida, Pensacola, Florida 32514

Abstract. Lloyd Hulbert's death in May 1986 left a wealth of unfinished projects as well as the legacy of Konza Prairie Research Natural Area, Kansas. One of these was an incomplete manuscript on fire, mowing, and soil effects on the tallgrass prairie, in which canopy cover and frequency in 27 soil-treatment combinations from Konza Prairie were reported. Treatments included unburned and April burned at 1-, 2-, and 4-year intervals, annual burning during three seasons, and mowing during two seasons. Soils ranged from deep and non-rocky to shallow, rocky, silty clay loams. Late April burning favored tall C_4 grasses at the expense of most forbs, whereas autumn and March burning allowed many forbs to do well. More species occurred on shallow, rocky soils than on deep soils. Annuals and biennials succeeded in mowed areas but not in burned areas. Tables of partially summarized data are included with this report so that other researchers may make use of them.

Key Words. tallgrass prairie, fire, mowing, soil, plant communities, species richness, Kansas

INTRODUCTION

Burning frequency and soil type were major determinants of the plant species composition of tallgrass prairie (Abrams and Hulbert 1987, Gibson and Hulbert 1987, Gibson 1988). The season in the year that burning occurs also had an important impact on the prairie (Aldous 1934, Owensby and Anderson 1967, Adams *et al.* 1982, Towne and Owensby 1984). Fire removed accumulated litter (Knapp and Seastedt 1986), allowed the soil surface to become warmer during the early part of the growing season (Hulbert 1988), and may lead to a more productive (Abrams *et al.* 1986), lower diversity, structurally more uniform grassland. The importance of soil type upon the composition of the prairie lies, in part, in the differential texture and water-holding capacities of various soils (Barnes and Harrison 1982, Archer 1984). Mowing for hay and to control certain undesirable range plants is a common management practice in the prairie that also affects species composition in a manner similar to burning (Crockett 1966, Christiansen 1972, Zimmerman and Kucera 1977, Hover and Bragg 1981). Although several studies have been conducted on one or more aspects of the effects of fire, mowing, and soil type on tallgrass prairie species composition, none have considered the effects of all three factors at a single site.

In 1983, Lloyd C. Hulbert sampled the plant species composition in 27 soil treatment combinations on Konza Prairie Research Natural Area, Riley and Geary counties, Kansas. Treatments included unburned and April burned at 1-, 2-, and 4-year intervals, annual burning at 3 seasons, mowing at 3 seasons and 5 soil types (Table 1). Before his death in May 1986 (Platt 1988), Hulbert summarized these data in tabular form and started to write a manuscript. These data are presented in this report (Tables 2, 3 and 4). The dissemination of these data will hopefully provide a resource- and database for other workers in this area of prairie research.

Table 1. Summary of soil characteristics and 27 soil-treatment combinations sampled by Hulbert to determine the effects of fire, mowing and soil type in tallgrass prairie vegetation. Figures indicate the number of replicate sample sites per soil-treatment combination. Soil characteristics from Jantz *et al.* (1975).

Soil characteristics and Plot combinations	*Soil type*				
	Florence	*Sogn*	*Benfield*	*Irwin*	*Tully*
Depth (cm)	*25*	*23*	*15*	*28*	*25*
Topography	*upper rim of slopes*	*slopes*	*ridge tops*	*ridge tops*	*foot slopes*
Slope	*level*	*5-20%*	*level*	*4-8%*	*4-8%*
texture (all loams)	*cherty silt*	*silty clay*	*silty clay*	*silty clay*	*silty clay*
Treatment Combinations					
Annual burn: March	1				2
late April	3			1	5[1]
November	1				2
Two year cycle	3				3
Four year cycle	2				2
Unburned	3	1	1	2	2
Mowed and baled: March	1				
Mowed and left: July		1			1
Mowed and baled: July	1				2
Mowed and left: November					1
Mowed and baled: November				1	

[1]Includes 1 replicate sample site each of burned with and against the prevailing wind.

Table 2. Canopy coverage/frequency of plant species on Tully soil based on twenty 10 m² plots per replication. Number of replications in parentheses. Nomenclature follows the Great Plains Flora Association (1986), where authorities for scientific names may be found.

Species	*Annually burned* *Nov.* *(2)*	*March* *(2)*	*late Apr.* *(3)*	*2-year burns* *(3)*	*4-year burns* *(2)*	*Unburned* *(2)*	*July mowed & removed* *(2)*	*July mowed & left* *(1)*	*Nov. mowed & left* *(1)*
Tall Warm-Season Perennial Grasses:									
Andropogon gerardii big bluestem	98/100	97/100	98/100	98/100	98/100	96/100	97/100	83/100	98/100
Sorghastrum nutans indiangrass	35/100	54/100	43/83	39/100	36/100	14/88	59/100	50/100	23/95
Panicum virgatum switchgrass	6/40	23/70	7.5/38	2.6/18	5.6/42	18/72	2.8/30	15/75	
Total cover, above 3 grasses	139	174	148	140	140	128	159	133	136
Medium-Tall Warm-Season Grasses:									
Andropogon scoparius little bluestem	74/100	68/100	22/93	30/98	10/85	1.7/50	8.5/68	25/100	29/100
Bouteloua curtipendula sideoats grama	0.5/50	0.6/60	0.1/27	0.4/35	0.02/5	0.02/5	0.6/22	1.2/75	0.4/45
Sporobolus asper var. *asper* tall dropseed	13/72	25/95	0.2/10	0.9/17	15/65	3.0/25	2.0/20	6.9/65	34/100
Sporobolus heterolepis prairie dropseed		0.1/2		0.6/22	0.4/2				2.0/55
Eragrostis spectabilis prairie lovegrass		0.02/5		0.1/15	0.1/2				
Leptoloma cognatum fall witchgrass						0.01/2		0.8/70	
Muhlenbergia racemosa green muhly						1.0/5			
Tridens flavus purpletop							0.4/38	0.08/15	
Total cover, above 8 grasses	88	94	22	32	25	5.8	12	34	65
Short Warm-Season Perennial Grasses:									
Bouteloua hirsuta hairy grama								0.02/5	
Cool-Season Perennial Grasses:									
Poa pratensis Kentucky bluegrass[1]	0.2/5			0.1/15	29/50	47/100	80/100	82/100	27/100
Dicanthelium oligosanthes var. *scribnerianum*, scribner panicum	0.6/95	1.0/88	0.4/62	0.6/78	0.6/85	0.7/85	0.6/95	1.6/100	0.2/40
D. acuminatum var. *villo- sissimum*, early panicum	0.01/2	0.04/8		0.8/52	0.2/12	0.01/2	0.01/2	0.02/5	
Koeleria pyramidata prairie junegrass	1.4/88	0.2/45		0.1/27	0.02/5	0.06/12	0.01/2	0.05/10	0.4/55
Sphenopholis obtusata prairie wedgescale				0.07/7	0.04/8	0.3/28	1.6/40	1.6/80	0.02/5
Elymus canadensis Canada wildrye						0.1/5	0.1/5	0.02/5	0.4/25
Total cover, above 6 grasses	2.2	1.2	0.4	1.7	30	48	82	85	28
Introduced Cool-Season Perennial Grasses:									
Bromus inermis smooth bromegrass[1]							1.4/22	0.02/5	
Festuca arundinacea tall fescue[1]							0.1/5		
Cyperaceae and Juncaceae:									
Carex brevior straw sedge	3.6/100	0.8/50	0.02/3	0.2/37	0.5/58	0.2/22	0.06/15		
Carex gravida var. *lupulina* hop sedge	0.02/5	0.01/2	0.01/2	0.02/15	1.0/48	0.8/55		0.6/85	0.05/10
Carex heliophyla pennsylvania sedge	0.2/28	0.6/48	0.01/2	0.03/5	0.01/2				
Carex meadii mead sedge	42/100	38/100	0.07/17	26/87	5.8/70	0.9/58	0.1/30	0.2/30	64/100

Table 2. Continued

Species	Annually Nov. (2)	March (2)	burned late Apr. (3)	2-year burns (3)	4-year burns (2)	Unburned (2)	July mowed & removed (2)	July mowed & left (1)	Nov. mowed & left (1)
Carex spp.			0.07/10				0.1/8		
Cyperus lupulinus spp. *lupulinus*, fern flatsedge			0.03/5	0.02/5					
Eleocharis compressa flatstem spikesedge	0.04/8	0.01/2		0.1/8					
Juncus interior inland rush				0.03/5					
Total cover, Cyperaceae and Juncaceae	46	38	0.2	27	7.3	1.9	0.3	0.8	64
Annual Grasses:									
Bromus japonicus Japanese brome[1]							46/100	0.1/20	
Perennial Forbs:									
Achillea millifolium var. *lanulosa*, western yarrow	0.06/15	0.04/8	0.01/2	0.09/20	0.1/18	0.5/32	0.2/40	0.6/85	0.1/25
Ambrosia psilostachya western ragweed	5.2/92	12/98	13/88	3.6/98	3.2/100	2.0/100	0.04/8	0.2/30	2.8/100
Antennaria neglecta var. *neglecta*, field pussytoes	0.05/10	0.2/15		0.2/18				0.05/10	0.05/10
Apocynum cannabinum hemp dogbane					0.01/2				
Artemisia ludoviciana Louisiana sagewort	1.5/75	0.4/42		0.05/10	1.2/40	1.9/82	0.2/28	0.7/95	
Asclepias stenophylla narrowleaf milkweed		0.01/2		0.01/2		0.02/5			
Asclepias syriaca common milkweed			0.01/2						
Asclepias tuberosa ssp. *interior*, butterfly milkweed	0.01/2		0.07/5		0.01/2				
Asclepias verticillata whorled milkweed		0.05/10	0.5/40	0.03/5	0.5/20	0.09/18	0.3/40	0.1/20	0.6/65
Aslepias viridiflora green milkweed		0.01/2		0.01/3					
Asclepias viridis green antelopehorn	0.5/32	0.2/25	0.2/22	0.3/33	0.5/40	0.7/40	0.6/48	0.7/60	0.2/20
Aster ericoides heath aster	19/100	18/100	0.3/22	13/98	9.3/98	2.7/95	0.7/98	0.8/100	25/100
Aster laevis smooth aster					0.02/5				
Aster oblongifolius aromatic aster									0.3/15
Aster sericeus silky aster									0.2/10
Astragalus crassicarpus groundplum milkvetch	0.01/2								0.6/35
Baptisia australis var. *minor*, blue wildindigo		0.8/12		0.4/7	0.2/12	0.01/2			0.3/10
Baptisia bracteata plains wildindigo	0.6/30	0.4/25	0.2/15	0.4/27	0.01/2	0.4/20	1.2/45	0.08/15	2.0/60
Cacalia plantaginea tuberous indianplantain					0.01/2			0.02/5	
Callirhoe involucrata purple poppymallow						0.1/8			
Cirsium altissimum tall thistle					0.01/2	0.02/5			
Cirsium undulatum wavyleaf thistle		0.04/8		0.04/10	0.01/2	0.01/2	0.02/5	0.02/5	
Convolvulus arvensis field bindweed[1]					0.01/2				
Dalea candida white prairieclover	3.7/62	1.6/32	0.3/12	0.6/32	0.04/8	0.2/15	0.2/15	0.2/5	0.4/30

Table 2. Continued

Species	*Annual Nov. (2)*	*March (2)*	*burned late Apr. (3)*	*2-year burns (3)*	*4-year burns (2)*	*Unburned (2)*	*July mowed & removed (2)*	*July mowed & left (1)*	*Nov. mowed & left (1)*
Dalea multiflora roundheaded prairieclover	0.01/2								0.02/5
Dalea purpurea var. *purpurea* purple prairieclover	1.4/50	0.5/35	0.1/12	0.04/8	0.2/10	0.4/5	0.2/15	0.4/50	0.6/50
Desmodium illinoense Illinois tickclover	0.6/18	0.3/25	0.5/17	0.3/7	0.1/5	0.02/5	0.09/20		0.1/20
Equisetum laevigatum smooth horsetail			0.2/33				0.4/50		
Hedyotis nigricans narrowleaf bluets								0.05/10	
Kuhnia eupatorioides var. *corymbulosa*, false boneset	0.2/20	0.1/8	0.3/27	0.2/20	0.2/32	0.02/5	0.04/8	0.08/15	0.5/50
Lespedeza capitata roundhead lespedeza	0.9.48	0.9/25	0.5/28	0.3/10	0.2/10	0.2/8	0.04/8	0.02/5	0.05/10
Lespedeza violacea violet lespedeza[1]	0.5/8	0.1/2	0.9/5	2.7/13	0.4/5	0.1/2	0.01/2		1.0/10
Liatris punctata dotted gayfeather					0.2/10				
Lithospermum incisum narrowleaf gromwell					0.01/2				
Monarda fistulosa var. fistulosa, mintleaf beebalm						0.4/2			
Oenothera speciosa white eveningprimrose					0.1/8	0.02/5	0.1/5	0.08/15	
Oxalis violacea violet woodsorrel oxalis		0.01/2	0.3/8	0.1/25	0.04/8	0.06/12		0.2/20	0.2/45
Physalis heterophylla clammy groundcherry						0.1/5	0.02/5		
Physalis pumila prairie groundcherry		0.05/10	0.07/5	0.01/2	0.04/8	1.5/15	0.4/40	0.08/15	0.02/5
Physalis virginiana Virginia groundcherry	0.09/18	0.1/20	0.07/15	0.2/28	0.8/40	0.7/45	0.05/10	0.1/25	0.2/40
Psoralea argophylla silverleaf scurfpea		0.05/10		0.07/2	0.2/10		1.5/12		
Psoralea esculenta common breadroot scrufpea	0.04/8			0.03/5			0.01/2		0.1/25
Psoralea tenuiflora manyflower scrufpea	0.8/20	0.4/5	0.2/8		0.02/5	0.3/28	0.1/22	2.9/70	
Ratibida columnifera upright prairieconeflower	0.02/5	0.01/2	0.01/3	0.03/7	0.01/2			0.08/15	0.02/5
Ruellia humilis fringeleaf ruellia	0.2/28	0.1/20	0.3/52	0.2/35	0.2/32	0.2/30	0.1/20	0.05/10	0.2/40
Salvia azurea Pitcher sage	0.1/2		0.04/10	0.1/22	0.2/12	0.7/28	0.1/8	0.02/5	0.1/25
Schrankia nuttallii catclaw sensitivebriar		0.4/2	0.07/2	0.3/2		0.01/2			
Senecio plattensis prairie groundsel	0.05/12	0.01/2		0.02/5	0.02/5		0.01/2	0.05/10	0.02/5
Silphium integrifolium wholeleaf rosinweed							0.1/5		
Sisyrinchium campestre prairie blueeyedgrass	0.9/92	0.8/100	0.02/52	0.2/43	0.2/25	0.2/32	0.02/5	0.7/85	0.1/25
Solanum carolinense horsenettle			0.01/2			0.01/2	0.6/22		
Solidago canadensis var. *scabra*, Canada goldenrod		1.0/5	0.07/2	0.01/2	0.4/8	4.6/18	0.01/2		1.7/20
Solidago missouriensis var. *fasciculata*, Missouri goldenrod	0.8/8	3.8/20	0.2/25	2.1/42	8.6/45	0.1/12		0.2/40	3.8/25
Solidago mollis ashy goldenrod						0.1/2			
Solidago rigida var. *humilis* stiff goldenrod		0.02/5	0.01/2		0.01/2				0.05/10

Table 2. Continued

Species	Annual		burned	2-year	4-year		July	July	Nov.
	Nov. (2)	March (2)	late Apr. (3)	burns (3)	burns (2)	Unburned (2)	mowed & removed (2)	mowed & left (1)	mowed & left (1)
Spiranthes vernalis upland ladiestresses		0.01/2	0.03/5	0.01/2					
Taraxacum officinale common dandelion1							0.02/5		
Teuchrium canadense var. *virginiana* American germander			0.02/3		0.01/2	0.1/5			
Verbena stricta woolly verbena	0.01/2	0.05/10	0.05/10	0.01/2		0.04/8		0.05/10	0.08/15
Vernonia valdwinii var. *interior*, inland ironweed	0.7/88	0.8/75	2.2/97	1.7/90	1.5/80	6.3/100	8.2/100	2.5/100	0.8/100
Vicia americana American vetch							0.6/12	0.05/10	0.2/35
Viola pedatifida prairie violet				0.1/22					0.2/50
Viola pratincola blue prairie violet									0.08/15
Zizia aurea golden zizia									1.1/30
Total cover, perennial forbs	38	43	20	27	29	25	16	11	44
Woody Plants:									
Amorpha canescens leadplant	1.9/38	2.9/35	10/37	11/77	21/95	0.4/22	0.02/5	0.02/5	7.2/95
Prunus americana American plum							0.01/2		
Rhus glabra smooth sumac			0.01/2						
Rosa arkansana Arkansas rose			0.07/3						
Symphoricarpos orbiculatus buckbrush	0.01/2		0.01/2	0.01/2	0.2/8	1.4/12	0.2/15		0.02/5
Total cover, woody plants	1.9	2.9	10	11	21	1.8 0.2	0.02	7.2	
Annual and Biennial Forbs:									
Ambrosia artemisiifolia common ragweed			0.01/2	0.01/3					
Conyza canadensis horseweed				0.01/2				0.02/5	
Erigeron strigosus var. *strigosus*, daisy fleabane	0.01/2		0.01/2	0.06/12		0.05/10	0.4/52	0.3/60	
Euphorbia marginata snow-on-the-mountain		0.01/2	0.02/5		0.01/2	0.04/8	0.01/2		0.02/5
Euphorbia spathulata warty spurge						0.02/5			
Helianthus annuus common sunflower			0.03/7	0.01/2					
Hymenopappus scabiosaeus whitebract hymenopappus								0.02/5	
Lactuca spp. wild lettuces[1]				0.02/3	0.01/2	0.1/25	0.01/2	0.3/65	0.02/5
Linum sulcatum grooved flax	0.02/5	0.02/5	0.01/2	0.07/17	0.1/22	0.01/2		0.02/5	0.05/10
Medicago lupulina black medic[1]							0.4/20		
Melilotus spp. sweetclovers[1]	20/38	0.2/10	0.01/2				37/100	0.3/10	0.02/5
Oenothera villosa spp. *villosa*, eveningprimrose					0.01/2				
Oxalis stricta common yellow oxalis				0.02/5	0.06/12	0.04/8	0.06/12	0.2/40	

Table 2. Continued

Species	Annually burned Nov. (2)	Annually burned March (2)	Annually burned late Apr. (3)	2-year burns (3)	4-year burns (2)	Unburned (2)	July mowed & removed (2)	July mowed & left (1)	Nov. mowed & left (1)
Plantago rhodosperma redseed plantain				0.01/2		0.01/2			
Spermolepis inermis spreading spermolepis							0.01/2	0.05/10	
Strophostyles leiosperma smoothseed wildbean	0.01/2	0.4/8	0.03/7						
Tragopogon dubius western salsify[1]			0.01/2	0.01/2		0.01/2	0.2/35	0.6/40	
Triodanis perfoliata clasping venus lookingglass					0.01/2			0.02/5	
Veronica arvensis common speedwell[1]							0.01/2		
Viola rafinesquii johnnyjumpup				0.02/3		0.02/5			
Total cover, annual and biennial forbs	20	0.6	0.1	0.2	0.2	0.3	38	1.8	0.1
Total cover, all plants	335	354	201	239	252	211	355	266	344
Average number of native species	38.5	39.5	34.3	45.0	47.5	48.0	40.0	54	53
Average number of exotic species	1.5	1.0	1.3	1.3	1.5	2.0	8.0	5	3
Shannon-Weaver diversity index, H', av.	2.01	2.08	1.46	1.80	2.00	1.81	1.91	1.78	2.27

[1]Exotic species

Table 3. Canopy coverage/frequency of plant species on Florence soil based on twenty 10 m² plots per replication. Number of replications in parentheses. Nomenclature follows the Great Plains Flora Association (1986), where authorities for scientific names may be found.

	Annually burned							
Species	*Nov. (1)*	*March (1)*	*late Apr. (3)*	*2-year burns (3)*	*4-year burns (2)*	*Unburned (3)*	*July mowed & removed (1)*	*March moved & removed (1)*
Tall Warm-Season Perennial Grasses:								
Andropogon gerardii big bluestem	69/100	77/100	94/100	93/100	94/100	93/100	94/100	90/100
Sorghastrum nutans indiangrass	35/100	21/100	43/95	53/100	34/95	34/100	57/100	26/75
Panicum virgatum switchgrass	2.3/40	7.5/60	3.5/17	3.5/18	0.2/10	2.8/17	9.0/30	4.3/25
Total cover, above 3 grasses	106	106	140	150	128	130	160	120
Medium-Tall Warm-Season Perennial Grasses:								
Andropogon scoparius little bluestem	67/100	63/100	28/95	31/100	36/100	38/100	51/100	25/95
Bouteloua curtipendula sideoats grama	0.9/100	1.5/100	6.4/100	1.8/95	2.8/95	0.4/38	11/100	5.7/95
Sporobolus asper var. *asper* tall dropseed	24/100	22/90	5.5/28	0.2/7	2.2/28	0.7/15	18/95	29/60
Sporobolus heterolepis prairie dropseed	6.1/75	6.2/75	0.3/15	1.0/37	2.8/52	1.0/13	2.4/45	5.4/70
Eragrostis spectabilis Prairie lovegrass			0.01/3			0.2/3	1.4/30	
Leptoloma cognatum fall witchgrass			0.06/13					
Muhlenbergia cuspidata plains muhly	2.4/50	1.6/40		0.07/8	0.7/22	0.8/15	0.2/25	0.7/45
Sporobolus cryptandrus		0.02/5	0.02/3	0.1/3	0.2/5			
Total cover, above 8 grasses	100	94	40	34	45	41	84	66
Short Warm-Season Perennial Grasses:								
Bouteloua gracilis blue grama	2.1/95	1.5/100	1.2/62	0.4/32	0.5/18	0.2/3	0.2/5	0.02/5
Bouteloua hirsuta hairy grama	1.6/100	1.6/95	0.3/23	0.1/15	0.1/5	0.1/3		
Buchloe dactyloides buffalograss	0.3/35	0.4/30	0.01/3		0.1/2			
Total cover, above 3 grasses	4.0	3.5	1.5	0.5	0.7	0.03	0.2	0.02
Cool-Season Perennial Grasses:								
Poa pratensis Kentucky bluegrass[1]		0.02/5	0.04/8	0.1/12	37/68	37/67	36/95	75/100
Dicanthelium oligosanthes var. *scribnerianum*, scribner panicum	0.2/30	0.4/45	0.2/37	0.3/38	0.4/78	1.0/72	4.6/90	0.2/45
D. acuminatum var. *villosissimum*, early panicum			0.01/2	0.02/5	0.05/10	0.02/5	0.3/35	
D. linearifolium slimleaf panicum		0.02/5	0.03/5	0.01/2				
Koeleria pyramidata prairie junegrass	1.6/100	1.4/95	0.6/47	0.7/70	0.2/42	0.2/28	0.1/25	0.1/25
Sphenopholis obtusata prairie wedgescale					0.01/2	0.03/7	12/95	
Elymus canadensis Canada wildrye	0.05/10		0.02/3			0.1/8		0.4/45
Total cover, above 7 grasses	1.8	1.8	0.9	1.1	38	38	53	76
Introduced Cool-Season Perennial Grasses:								
Bromus inermis smooth bromegrass[1]	0.08/15						3.4/25	0.6/50

Table 3. Continued

Species	Annually burned Nov. (1)	Annually burned March (1)	Annually burned late Apr. (3)	2-year burns (3)	4-year burns (2)	Unburned (3)	July mowed & removed (1)	March mowed & removed (1)
Cyyperaceae and Juncaceae:								
Carex brevior straw sedge			0.4/62	0.09/7	0.2/22	0.4/33	0.5/10	
Carex gravida var. *lupulina* hop sedge			0.2/13	0.1/12	0.9/40	0.2/17		
Carex heliophila pennsylvania sedge	5.2/100	1.0/100	0.02/3	0.3/38	0.3/40	0.2/22	0.2/30	
Carex meadii mead sedge	1.1/65	0.5/75	0.09/7	1.3/13	2.0/25	1.1/18	17/70	0.4/20
Cyperus lupulinus spp *lupulinus,* fern flatsedge		0.05/10	0.1/28	0.1/30	0.01/2	2.2/33		
Syperus schweinitzii schweinitz flatsedge			0.01/2					
Total cover, Cyperaceae and Juncaceae	6.3	1.5	0.8	1.9	3.4	4.1	18	0.4
Annual Grasses:								
Bromus japonicus Japanese brome[1]				0.01/2	3.0/15	0.4/22	15/100	12/100
Perennial Forbs:								
Achillea millifolium var. *lanulosa,* western yarrow			0.1/15	0.2/32	0.4/40	0.5/52	0.4/85	0.1/20
Ambrosia psilostachya western ragweed	0.2/30	0.4/50	0.9/77	1.4/87	1.2/80	4.5/93	0.3/40	0.2/40
Antennaria neglecta var. *neglecta,* field pussytoes	0.2/20	0.4/45	0.01/2	0.07/15	0.05/12	0.01/2	0.8/55	0.02/55
Artemisia ludoviciana Louisiana sagewort	0.5/70	0.2/40	0.3/17	7.5/63	3.6/40	4.1/32	0.1/20	12/85
Argemone polyanthemos pricklypoppy						0.07/2		
Asclepias stenophylla narrowleaf milkweed		0.02/5	0.04/8	0.03/7	0.02/5	0.04/8	0.2/30	
Asclepias verticillata whorled milkweed		0.05/10		0.01/2	0.02/5	0.01/2	0.2/40	0.1/20
Aslepias viridiflora green milkweed	0.2/30	0.3/65	0.08/18	0.2/23	0.1/22	0.1/27	0.2/30	0.1/20
Asclepias viridis green antelopehorn	0.4/25	0.05/10	0.3/35	0.07/8	0.04/8	0.08/12	0.5/20	0.2/20
Aster ericoides heath aster	0.5/70	0.4/90	0.1/27	0.2/42	1.6/95	3.4/88	0.4/80	5.1/100
Aster laevis smooth aster						0.01/2		
Aster oblongifolius aromatic aster	5.0/100	0.7/65	0.1/12	3.1/62	24/85	12/47	0.4/30	7.4/75
Aster sericeus silky aster	0.05/10	0.08/15	0.1/15	0.2/42	1.7/88	0.8/45	0.2/45	0.9/75
Astragalus crassicarpus groundplum milkvetch	2.7/90	0.3/35	0.01/2	0.02/3	0.01/2	0.01/2	0.5/20	0.7/40
Baptisia australis var. *minor* blue wildindigo	0.3/10	0.5/30	0.01/2	0.9/28	0.5/25	0.09/7	3.9/75	0.02/5
Baptisia bracteata plains wildindigo	0.02/5	0.4/20	0.3/23	0.5/27	0.1/15	0.5/27		0.7/40
Cacalia plantaginea tuberous indianplantain							0.02/5	
Callirhoe alceoides pale poppymallow								0.02/5
Cirsium undulatum wavyleaf thistle	0.2/35	0.4/65	0.3/35	0.1/15	0.4/34	0.3/22	0.2/30	0.08/15
Commandra umbellata var. *pallida,* pale comandra						0.01/2	0.02/5	

Table 3. Continued

Species	Annually burned Nov. (1)	Annually burned March (1)	Annually burned late Apr. (3)	2-year burns (3)	4-year burns (2)	Unburned (3)	July mowed & removed (1)	March mowed & removed (1)
Corypantha missouriensis Missouri mamillaria			0.01/2		0.01/2			
Dalea candida white prairieclover	1.3/35	0.2/25	0.1/8	0.1/12	0.1/5	0.1/7	0.8/50	0.02/5
Dalea multiflora roundheaded prairieclover	0.05/10	0.08/7	0.02/5	0.06/12	0.2/5			
Dalea purpurea var. *purpurea* purple prairieclover	19/100	20/95	2.3/73	1.2/88	0.4/58	0.4/60	0.8/50	0.3/60
Delphinium carolinianum plains larkspur				0.01/2		0.01/3		
Desmodium illinoense Illinois tickclover			0.02/3	0.01/2				
Echinachea augustifolia blacksampson echinachea	0.2/25	0.4/20	0.07/7	0.07/5	0.2/22	0.04/8	0.05/10	
Hieracium longipilum longbeard hawkweed				0.02/3		0.01/2		
Hybanthus verticillatus North American calceolaria	0.02/5		0.7/23		0.1/2	0.07/3		
Kuhnia eupatorioides var. *corymbulosa*, false boneset	0.2/35	0.3/40	0.5/30	2.0/70	1.0/58	1.0/78	0.7/70	1.0/55
Lespedeza capitata roundhead lespedeza			0.05/10	0.07/12	0.1/10	0.7/13	0.08/15	
Lespedeza violacea violet lespedeza[1]				0.07/2				
Liatris punctata dotted gayfeather				0.01/2	0.01/2	0.2/10		
Lithospermum incisum narrowleaf gromwell		0.02/5	0.01/2		0.03/7		0.02/5	
Lomatium foeniculaceum carrotleaf lomatium			0.03/7	0.5/53	0.01/2	0.07/17	4.0/50	0.08/15
Mirabilis linearis narrowleaf four-o'clock			0.02/3					
Opuntia macrorhiza var. *macrorhiza* bigroot pricklypear					0.01/2			
Oxalis violacea violet woodsorrel oxalis						0.08/5		
Penstemon cobaea cobaea penstemon	0.02/5	0.1/20		0.01/2		0.01/2		
Penstemon grandiflorus shell-leaf penstemon			0.02/5	0.1/15				
Physalis pumila prairie groundcherry	0.2/10	0.08/15	0.3/27	0.1/8	1.0/8	0.5/22	0.2/15	
Physalis virginiana Virginia groundcherry			0.02/3	0.01/3	0.05/10	0.01/2	0.1/25	0.2/10
Psoralea esculenta common breadroot scurfpea		0.05/10	0.05/10	0.1/17	0.06/12	0.04/8	0.2/20	0.2/30
Psoralea tenuiflora manyflower scurfpea				0.3/5	0.1/5	0.01/2		
Ratibida columnifera upright prairieconeflower	0.02/5	0.08/15	0.02/30	0.6/37	0.8/50	0.3/27	0.08/15	0.08/15
Ruellia humilis fringeleaf ruellia	0.1/20	0.08/15	0.3/43	0.04/8	0.1/22	0.2/38	0.2/45	0.08/15
Salvia azurea Pitcher sage	3.8/95	5.8/80	20/87	2.9/62	1.8/70	1.0/60	1.0/55	3.2/70
Schrankia nuttallii catclaw sensitivebriar	0.9/15	0.4/15	1.2/13	1.8/33	1.6/20	1.4/33		0.4/15
Senecio plattensis prairie groundsel	0.05/10	0.1/25	0.02/5	0.04/8		0.07/13	0.08/15	
Sisyrinchium campestre prairie blueeyedgrass	0.4/80	1.2/100	0.2/37	0.3/50	0.2/35	0.01/2	1.4/100	0.3/60
Solidago missouriensis var. *fasciculata*, Missouri goldenrod	0.2/45	0.2/30	0.4/30	0.3/48	1.4/52	1.3/22	3.4/60	0.9/35

Table 3. Continued

Species	Annually burned Nov. (1)	Annually burned March (1)	Annually burned late Apr. (3)	2-year burns (3)	4-year burns (2)	Unburned (3)	July mowed & removed (1)	March mowed & removed (1)
Solidago rigida var. *humilis* stiff goldenrod						0.02/3	0.2/10	
Stenosiphon linifolius stenosiphon						0.02/3		
Tragia betonicifolia nettleleaf noseburn			0.2/25	0.3/32	0.4/38	0.02/3		0.1/25
Verbena canadensis rose verbena				0.01/2				
Verbena stricta woolly verbena		0.02/5	0.02/3	0.01/2		0.03/7	0.02/5	
Vernonia baldwinii var. *interior*, inland ironweed	0.08/15	0.4/45	1.9/95	0.4/63	1.0/55	1.1/78	0.4/50	0.5/70
Total cover, perennial forbs	37	34	31	26	44	35	22	35
Woody Plants:								
Amorpha canescens leadplant	10/100	4.1/100	1.9/85	6.0/90	5.0/98	1.7/65	3.1/100	7.6/80
Ceanothus herbaceus var. *pubescens*, inland ceanothus	0.02/5		4.3/42	1.4/12	0.7/12	1.9/40	0.02/5	
Rosa arkansana Arkansas rose					0.02/5			
Symphoricarpos orbiculatus buckbrush						0.1/7		
Total cover, woody plants	10	4.1	6.2	7.4	5.7	3.7	3.1	7.6
Annual and Biennial Forbs:								
Androsace occidentalis western rockjasmine					0.01/2			
Conyza canadensis horseweed					0.01/2			
Descurainia pinnata pinnate tansymustard						0.06/12		
Erigeron Strigosus var. *strigosus*, daisy fleabane	0.02/5		0.04/8	0.2/30	0.2/38	0.1/28	0.02/5	0.02/5
Euphorbia marginata snow-on-the-mountain			0.01/2		0.02/5			
Euphorbia spathulata warty spurge						0.06/12		
Hedeoma hispidum rough falsepennyroyal				0.02/3				
Hymenopappus scabiosaeus whitebract hymenopappus			0.03/7	0.04/10	0.1/22	0.03/7	0.1/25	
Lactuca spp. wild lettuces[1]				0.04/8	0.05/10	0.2/35	0.08/15	0.05/10
Lepidium densiflorum peppergrass[1]					0.2/45	0.01/2	0.02/5	
Linum sulcatum grooved flax			0.2/32	0.2/33		0.07/13	0.4/70	
Melilotus spp. sweetclovers[1]	0.8/60	0.1/20		0.03/7			6.3/85	18/75
Oxalis stricta common yellow oxalis			0.01/2	0.03/5	0.3/52	0.1/23	0.4/85	0.02/5
Silene antirrhina sleepy catchfly				0.02/3	0.01/2	0.03/5		
Spermolepis inermis spreading spermolepis				0.01/2		0.02/5	0.02/5	
Strophostyles leiosperma smoothseed wildbean							0.02/5	
Tragopogon dubius salsify[1]			0.01/2	0.04/10	0.05/10	0.08/17	0.2/30	0.2/30

Table 3. Continued

Species	*Annually burned* *Nov.* *(1)*	*March* *(1)*	*late Apr.* *(3)*	*2-year burns* *(3)*	*4-year burns* *(2)*	*Unburned* *(3)*	*July mowed & removed* *(1)*	*March mowed & removed* *(1)*
Triodanis leptocarpa slimpod venus lookingglass				0.02/3	0.02/5	0.07/15		
Triodanis perfoliata clasping venus lookingglass				0.01/2	0.01/2	0.02/3		
Verbascum blattaria moth mullein[1]							0.02/5	
Viola rafinesquii johnnyjumpup						0.01/2		
Total cover, annual and biennial forbs	0.8	0.1	0.3	0.7	1.0	0.9	7.6	18
Total cover, all plants	266	245	221	222	269	253	366	336
Number of native species	46	51	54	53	58.5	59.3	61	48
Number of exotic species	2	1	1	2.7	1	2.7	7	5
Shannon-Weaver diversity index, H', av.	2.25	2.13	1.85	1.82	2.09	1.96	2.53	2.36

[1]Exotic species

Table 4. Canopy coverage/frequency of plant species on Irwin, Sogn, Benfield and Tully soils, based on twenty 10 m² plots per replication. Number of replications in parentheses. Nomenclature follows the Great Plains Flora Association (1986), where authorities for scientific names may be found.

	Irwin					Sogn		Benfield	Tully	
Species	Burned annually (1)	Unburned (2)	July mowed & left (1)	July mowed & removed (1)	Nov. mowed & removed (1)	Unburned (1)	July mowed & left (1)	Unburned (1)	Burned against wind (1)	Burned with wind (1)
Tall Warm-Season Perrenial Grasses:										
Andropogon gerardii big bluestem	94/100	96/100	91/100	96/100	93/100	92/100	91/100	98/100	98/100	96/100
Sorghastrum nutans indiangrass	13/40	14/70	56/95	72/100	30/90	39/100	28/95	18/95	39/100	43/100
Panicum virgatum switchgrass	6.4/20	0.6/18	6.8/65	0.9/15	5.2/20	13/70	5.3/40	4.3/25	10/60	12/55
Total cover, above 3 grasses	113	111	154	169	128	144	124	120	147	151
Medium-Tall Warm-Season Perennial Grasses:										
Agropyron scoparius little bluestem	25/95	2.6/58	1.0/35	44/100	4.9/70	2.2/60	0.9/35	23/100	38/100	58/100
Bouteloua curtipendula sideoats grama	1.8/80	0.2/15	0.08/15	7.0/95	0.4/30	7.4/90	5.2/100	0.2/50	0.4/45	0.7/85
Sporobolus asper var. *asper* tall dropseed	7.2/65	29/85	15/85	33/100	72/100	45/100	22/85	0.2/15	6.0/75	3.9/90
Sporobolus heterolepis prairie dropseed	0.2/10	4.1/18						0.3/10		
Eragrostis spectabilis prairie lovegrass		0.1/2		0.05/10		0.2/5	0.2/15	0.2/5	0.3/40	0.2/30
Leptoloma cognatum fall witchgrass		0.01/2								
Tridens flavus purpletop		0.01/2	1.7/20							
Total cover, above 7 grasses	34	36	18	84	77	55	28	24	45	63
Short Warm-Season Grasses:										
Bouteloua gracilis blue grama	0.02/5									
Bouteloua hirsuta hairy grama						0.2/5				
Buchloe dactyloides buffalograss						0.2/5				
Total cover, above 3 grasses	0.02					0.4				
Cool-Season Perennial Grasses:										
Poa pratensis Kentucky bluegrass[1]		46/75	98/100	78/100	98/100	35/100	91/100	4.6/30		
Dicanthelium oligosanthes var. *scribnerianum*, scribner panicum	0.6/85	1.1/78	0.6/90	1.5/100	0.5/55	0.2/35	0.05/10	4.5/100	1.0/100	0.6/100
D. acuminatum var. villo-sissimum, early panicum								0.05/10	0.08/15	0.05/10
Koeleria pyramidata prairie junegrass	0.05/10	0.1/18		0.02/5	0.02/5	0.02/5				0.02/5
Spenopholis obtusata prairie wedgescale		0.02/5		0.2/10				0.05/10		
Elymus canadensi Canada wildrye		1.0/5	0.1/20	0.02/5	0.5/50	0.6/30	0.4/60			
Elymus virginicus Virginia wildrye					0.02/5					
Total cover, above 7 grasses	0.6	48	99	80	99	36	91	9.2	1.1	0.7
Introduced Cool-Season Grasses:										
Bromus inermis spp. inermis smooth bromegrass[1]			3.2/10	0.08/15	0.8/5		3.2/10			

Table 4. Continued

			Irwin			*Sogn*		*Benfield*	*Tully*	
Species	*Burned annually (1)*	*Unburned (2)*	*July mowed & left (1)*	*July mowed & removed (1)*	*Nov. mowed & removed (1)*	*Unburned (1)*	*July mowed & left (1)*	*Unburned (1)*	*Burned against wind (1)*	*Burned with wind (1)*
Cyperaceae and Juncaceae:										
Carex brevior straw sedge		0.06/15	0.2/40	0.1/20	1.9/85	0.02/5	0.08/15	0.02/5	0.3/30	0.2/30
Carex gravida var. *lupulina* hop sedge	0.2/5	1.0/55	2.0/85	1.2/65	2.4/95	0.1/25	0.1/20		0.02/5	
Carex heliophila pennsylvania sedge				0.1/20						
Carex meadii mead sedge		11/48	2.0/95	0.6/80	42/95	9.6/90	0.6/60	6.4/80	1.4/55	8.2/85
Cyperus lupulinus spp. *lupulinus,* fern flatsedge	0.02/5								0.02/5	0.05/10
Eleocharis compressa flatstem spikesedge									0.02/5	
Total cover, Cyperaceae & Juncaceae	0.2	12	4.2	2.0	46	9.7	0.8	6.4	1.8	8.4
Annual Grasses:										
Bromus japonicus Japanese brome[1]		0.01/2	13/90	23/100	0.05/10		0.02/5			
Perennial Forbs:										
Achillea millefolium var. lanulosa, western yarrow		0.9/40	0.8/75	0.4/75	0.4/55	0.3/35	0.6/75	0.5/30		
Ambrosia psilostachya western ragweed	8.8/85	3.0/70	0.4/50	0.5/70	1.1/100	0.6/75	0.3/55	5.2/100	19/100	2.7/100
Antennaria neglecta var. neglecta, field pussytoes				0.05/10					0.02/5	
Artemisia ludoviciana Louisiana sagewort	0.02/5	3.6/90	1.9/90	0.3/55	0.9/80	8.6/100	2.6/90	0.02/5	0.1/25	0.2/40
Asclepias stenophylla narrowleaf milkweed		0.05/10			0.02/5			0.02/5	0.05/10	0.02/5
Asclepias verticillata whorled milkweed	2.0/25	0.2/38	4.2/30	0.05/10	0.5/70			0.1/25	0.05/10	0.1/25
Asclepias viridiflora green milkweed	0.02/5	0.02/5					0.05/10	0.05/10		
Asclepias viridis green antelopehorn	0.05/10	0.01/18	0.2/35	0.6/55	1.0/70	0.4/35	0.05/10	0.2/20	0.6/50	0.4/60
Aster ericoides heath aster	0.05/10	4.4/90	0.8/85	0.4/85	0.4/90	4.1/85	0.5/100	19/100	4.9/100	5.7/100
Aster laevis smooth aster		0.01/2					0.2/5			
Aster oblongifolius aromatic aster						9.9/75	0.1/20	0.8/5		
Aster sericeus silky aster								0.5/25		
Astragalus crassicarpus groundplum milkvetch	0.05/10	0.1/5		0.02/5		0.1/20	0.02/5	0.02/5		
Astragalus missouriensis Missouri milkvetch				0.02/5						
Baptisia australis var. *minor,* blue wildindigo		0.1/5		0.3/10		1.0/20	0.4/20	0.2/5		
Baptisia bracteata plains wildindigo		0.02/5	0.2/5	0.5/25	0.2/5	0.02/5	0.2/5	1.0/45	0.05/10	0.2/25
Cacalia plantaginea tuberous indianplantain							0.08/15			
Callirhoe involucrata purple poppymallow		0.1/8		0.02/5						
Cirsium undulatum wavyleaf thistle				0.08/15		0.3/40	0.7/45			
Dalea candida white prairieclover	0.5/30	0.2/20			0.05/10		0.02/5	0.3/30	1.5/50	0.1/20

Table 4. Continued

			Irwin			Sogn		Benfield	Tully	
Species	Burned annually (1)	Unburned (2)	*July mowed & left (1)*	*July mowed & removed (1)*	*Nov. mowed & removed (1)*	Unburned (1)	*July mowed & left (1)*	Unburned (1)	Burned against wind (1)	Burned with wind (1)
Dalea multiflora roundheaded prairieclover								0.05/10		
Dalea purpurea var. *purpurea* purple prairieclover	0.02/5	0.1/5	0.02/5	0.2/5	0.08/15	0.3/55	0.2/25	0.1/25	0.1/25	0.4/25
Delphinium carolinianum plains larkspur						0.05/10				
Desmodium illinoense Illinois tickclover	0.2/10				0.2/10				0.8/15	0.2/10
Echinachea angustifolia blacksampson echinachea							0.05/10			
Hieracium longipilum longbeard hawkweed										0.05/10
Kuhnia eupatorioides var. *corymbulosa,* falseboneset	0.1/20	0.02/5	0.02/5	0.02/5		0.7/60	3.6/90	0.5/75	0.2/30	
Lespedeza capitata roundhead lespedeza			0.02/5		0.05/10		0.02/5	0.2/45	1.0/35	1.0/25
Lespedeza violacea violet lespedeza[1]		0.01/2							8.6/35	
Lithospermum incisum narrowleaf gromwell				0.02/5			0.02/5			
Lomatium foeniculaceum carrotleaf lomatium						0.02/5				
Oenothera macrocara ssp. *macrocarpa,* Missouri eveningprimrose						0.05/10				
Oenothera speciosa white eveningprimrose		0.1/5	0.08/15		0.02/5	0.02/5				
Onosmodium molle var. *occidentale,* western marbleseed						0.2/5				
Oxalis violacea violet woodsorrel oxalis	0.1/20	0.01/2					0.02/5			0.02/5
Physalis heterophylla clammy groundcherry		0.1/2								
Physalis pumila prairie groundcherry		2.5/25	0.5/30	0.02/5	1.0/35	1.8/30	0.6/35	0.05/10		0.02/5
Physalis virginiana Virginia groundcherry	0.05/10	1.3/50	0.6/75	0.2/30	0.02/5	0.05/10	0.2/25		0.2/40	0.2/45
Psoralea argophylla silverleaf scurfpea				0.02/5						
Psoralea esculenta common breadroot scurfpea							0.05/10	0.02/5	0.02/5	
Psoralea tenuiflora manyflower scurfpea		0.2/5	0.5/30	3.4/60	1.3/35	3.5/70	4.3/75		2.3/50	3.2/80
Ratibida columnifera upright prairieconeflower	0.02/5		0.02/5	0.08/15	0.02/5	0.2/45	0.4/40	0.05/10		
Ruellia humilis fringeleaf ruellia	0.5/55	0.4/70	0.3/65	0.2/45	0.3/60	0.2/35	0.2/35	0.5/80	0.2/40	0.3/60
Salvia azurea Pitcher sage	0.4/20	0.1/15	0.05/10	0.3/15	0.02/5	1.1/30	0.2/35	0.4/35	0.02/5	
Schrankia nuttallii catclaw sensitivebriar	0.2/10	1.4/8						2.6/25		
Senecio plattensis prairie groundsel				0.02/5			0.02/5	0.1/20		
Sisyrinchium campestre prairie blueeyedgrass	0.2/40	0.2/30	0.3/60	0.2/45	0.05/10	0.2/35	0.4/60	0.2/30	0.4/85	0.3/65
Solanum carolinense horsenettle			0.4/30							
Solidago canadensis var. *scabra,* Canada goldenrod		1.3/5	0.02/5	0.05/10	0.02/5					
Solidago missouriensis var. *fasciculata,* Missouri goldenrod	0.02/5	11/40	0.4/55	0.2/35		1.6/85	0.6/50	1.9/5	6.8/45	0.08/15

Table 4. Continued

Species	Burned annually (1)	Unburned (2)	Irwin: July mowed & left (1)	Irwin: July mowed & removed (1)	Irwin: Nov. mowed & removed (1)	Sogn: Unburned (1)	Sogn: July mowed & left (1)	Benfield: Unburned (1)	Tully: Burned against wind (1)	Tully: Burned with wind (1)
Solidago mollis ashy roldenrod							0.02/5			
Solidago rigida var. *humilis* stiff goldenrod				0.05/10						
Spiranthes vernalis upland ladiestresses										0.05/10
Taraxacum officinale common dandelion[1]			0.1/25	0.02/5						
Teuchrium canadense var. *virginiana*. American germander		0.3/22			0.4/20					
Tragia betonicifolia nettleleaf noseburn								0.02/5		
Verbena canadensis rose verbena						0.05/10				
Verbena stricta woolly verbena		0.01/2	0.2/25			0.02/5			0.1/20	0.1/20
Vernonia baldwinii var. *interior*, inland ironweed		2.6/50	11/100	1.8/95	12/100	3.3/100	4.8/100	0.8/85	1.0/95	1.4/95
Vicia americana American vetch				0.05/10	0.02/5					
Viola pratincola blue prairie violet							0.2/35			
Total cover, perennial forbs	13	34	23	10	20	39	22	36	48	17
Woody Plants:										
Amorpha canescens leadplant	16/80	7.1/50		0.02/5	0.02/5	0.5/20	0.1/20	4.3/95	0.6/35	0.1/25
Ceanothus herbaceus var. *pubescens*, inland ceanothus						0.2/5		2.0/45		
Gymnocladus dioica Kentucky coffeetree		0.01/2			0.02/5					
Rosa arkansana Arkansas rose		2.2/18								0.2/5
Symphoricarpos orbiculatus buckbrush		0.4/12	0.4/40		3.1/35		0.2/25	0.05/10	0.02/5	
Total cover, woody plants	16	9.7	0.4	0.02	3.1	0.7	0.3	6.4	0.6	0.3
Annual and Biennial Forbs:										
Ambrosia artemisiifolia common ragweed					0.02/5					
Erigeron strigosus var. *strigosus*, daisy fleabane	0.02/5		0.1/25	0.2/50	0.02/5	0.1/25	0.2/30	0.02/5	0.02/5	0.02/5
Euphorbia marginata snow-on-the-mountain								0.02/5	0.02/5	
Euphorbia spathulata warty spurge						0.05/10				
Galium aparine catchweed bedstraw		0.02/5	0.02/5							
Hymenopappus scabiosaeus whitebract hymenopappus						0.05/10	0.08/15			
Lactuca spp. wild lettuces[1]			0.08/15	0.05/10	0.3/30	0.1/25	0.6/70	0.1/20		
Linum sulcatum grooved flax		0.02/5		0.2/45	0.02/5	0.02/5		0.08/15	0.05/10	0.02/5
Melilotus sweetclovers[1]				0.2/5						
Oxalis stricta common yellow oxalis		0.02/5	0.2/30	0.3/65			0.05/10		0.02/5	
Plantago rhodosperma redseed plantain				0.05/10						

Table 4. Continued

Species	Burned annually (1)	Unburned (2)	Irwin July mowed & left (1)	Irwin July mowed & removed (1)	Irwin Nov. mowed & removed (1)	Sogn Unburned (1)	Sogn July mowed & left (1)	Benfield Unburned (1)	Tully Burned against wind (1)	Tully Burned with wind (1)
Spermolepis inermis spreading spermolepis		0.01/2		0.02/5		0.08/15				
Strophostyles leiosperma smoothseed wildbean									0.2/30	0.05/10
Tragopogon dubius western salsify[1]		0.01/2	4.9/100	0.6/50	0.02/5	0.1/20	1.5/95	0.02/5		
Triodanis perfoliat clasping venus lookingglass		0.01/2								
Verbascum blattaria moth mullein[1]			0.02/5							
Viola rafinesquii Johnnyjumpup		0.02/5		0.08/15						
Total cover, Annual & Biennial forbs	0.02	0.1	5.3	1.7	0.4	0.5	2.4	0.2	0.3	0.09
Total cover, all plants	177	251	320	370	374	285	272	202	244	240
Number of native species	33	42	53	40	43	51	50	50	43	41
Number of exotic species	0	1.5	6	6	4	2	4	2	1	0
Shannon-Weaver diversity index, H', av.	1.65	2.03	1.99	1.97	1.97	2.22	1.88	1.98		

[1]Exotic species

STUDY AREA

The study was conducted in the Geary County, "Old Konza Prairie", portion of Konza Prairie Research Natural Area in the Flint Hills of northeast Kansas (Hulbert 1985). Konza Prairie is a 3,487 ha tallgrass prairie site acquired by The Nature Conservancy in late 1971 and is leased to Kansas State University. A management plan, initiated in 1972, included prescribed burning in early April of watershed units at 1-, 2-, 4-, and 10-year intervals, as well as unburned units (Hulbert 1973). The area was never been plowed, except in a few lowland areas, and had been grazed by cattle since settlement. The sites studied by Hulbert were last grazed in 1971. Experimental mowing in March, July, and November began in 1971, with the hay removed on part and left on part of the mowed areas. With the acquisition of additional land in Riley County in 1977, Konza Prairie was much enlarged. Subsequently, some of the experimental treatments were modified in 1978 (Hulbert 1985).

METHODS

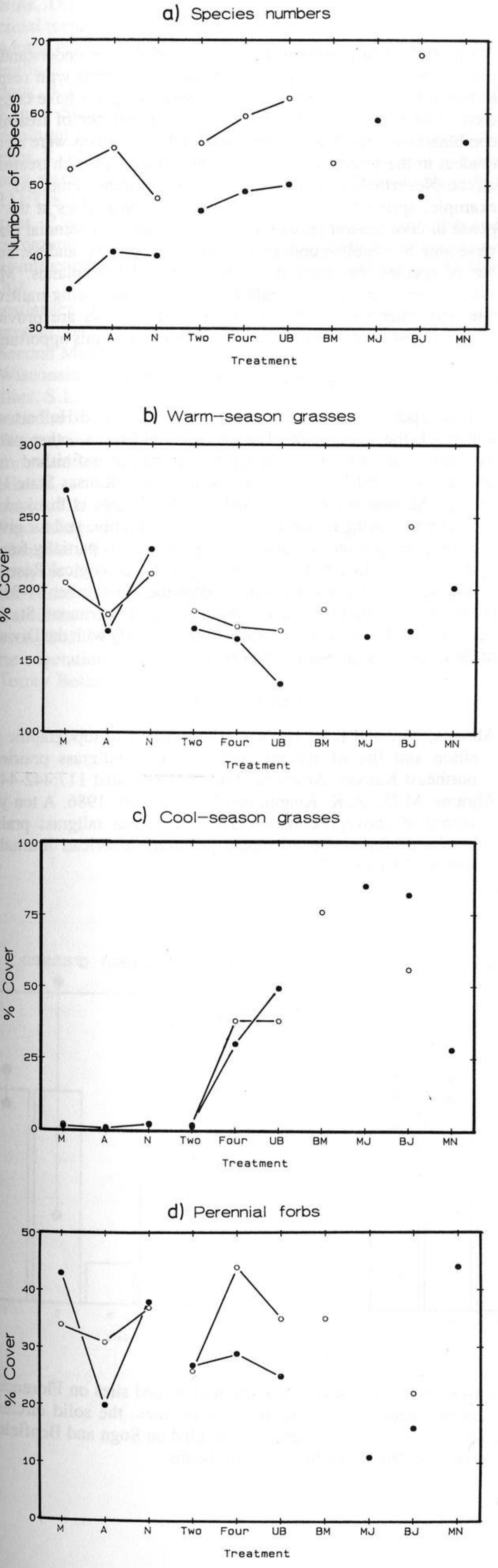
The relative cover of all vascular plant species was recorded in 1983 in twenty circular plots (10 m^2) in each of 27 soil-treatment combinations (Table 1). The plots were evenly distributed over each soil-treatment area. Each soil-treatment area was sampled in late spring, mid-summer, and late summer. Cover was estimated ocularly according to a modified Daubenmire (1959) scale (Abrams and Hulbert 1987). The maximum cover value attained for each species in each plot over the three dates was retained for subsequent analysis.

RESULTS AND DISCUSSION

In his unfinished manuscript, Hulbert pointed out that the six to ten years of treatments were insufficient to remove all effects of prior grazing and burning. In an analysis of other Konza Prairie data, Gibson (1988) came to a similar conclusion for watersheds subjected to a four-year burning cycle. Hulbert pointed out that rigorous statistical analyses would likely yield a number of significant differences between treatments that were not biologically useful. Furthermore, in-spite of the many hours spent gathering data, the number of replicate samples per soil-treatment combination was small ($n = 1$ to 5). Thus, for this report, only differences that occurred consistently between soil-treatment combinations were considered.

Effect of Season of Burning

Annual burning in March or November resulted in the highest total cover of warm-season grasses and perennial forbs (Figures 1b and 1c). In contrast, burning in late April led to a comparatively lower cover of these types of plants. Of the individual species, little bluestem (*Andropogon scoparius* Michx.) and tall dropseed [*Sporobolus asper* (Michx.) Kunth] were favored especially on Tully soils by burning in March compared with late April. In contrast, big bluestem (*Andropogon gerardii* Vitman) and indiangrass [*Sorghastrum nutans* (L.) Nash] were favored on Florence soils by burning in late April compared with March (Table 2). These results are comparable to those reported by Towne and Owensby (1984). Although the difference between burning in March or late April was only a few days, it apparently was critical because it coincided with the emergence of the warm-season perennial grasses (Aldous 1934, Towne and Owensby 1984).



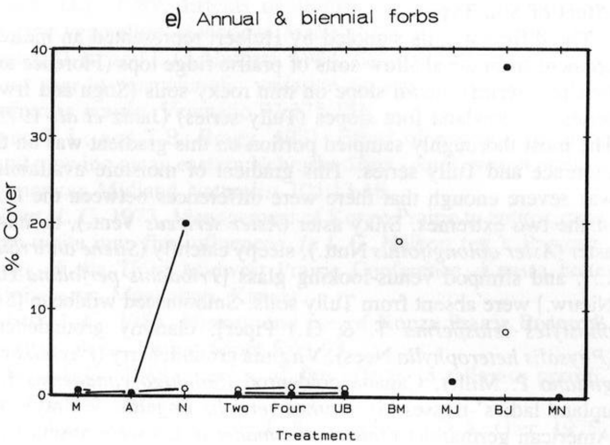


FIG. 1. a) Mean number of species, and b-e) percentage cover of different plant life forms according to different burning and mowing treatments on Florence (open circles) and Tully (solid circles) soils. M = burned annually in March, A = burned annually in April, N = burned annually in November, Two = burned every two years in April, Four = burned every four years in April, UB = unburned, BM = mowed and baled in March, MJ = mowed and left in July, BJ = mowed and baled in July, and MN = mowed and left in November.

Effect of Frequency of Burning

With more frequent burning, growth (cover) of warm-season grasses was favored (Figure 1a). Cool-season grasses and species richness increased with less frequent burning (Figures 1a and 1b). Of the cool-season grasses favored by less frequent burning, Kentucky bluegrass (*Poa pratensis* L.) showed a particularly strong response as it had in other studies (Towne and Owensby 1984, Abrams and Hulbert 1987). As a group, perennial forbs did not show a clear response to burning frequency (Figure 1d), although on Tully soils western ragweed (*Ambrosia psilostachya* DC.), and on Florence soils Canada goldenrod (*Solidago canadensis* var. *scabra* T. & G.) and inland ironweed [*Vernonia baldwinii* var. *interior* (Small) Faust] had highest cover values in less frequently burned areas. As shown in other studies (Gibson and Hulbert 1987), big bluestem showed little response to burning frequency, whereas indiangrass and little bluestem were most abundant under conditions of frequent burning.

Effect of Mowing

The effect of mowing was varied and depended on the season and whether or not the hay was removed. Annual and biennial forbs were favored by mowing and reached 38% cover on Florence soils in sites that had been mowed and baled in July. This was primarily due to the success of sweetclovers (*Melilotus* spp. P. Mill.), an exotic biennial species (Table 2). Japanese brome (*Bromus japonicus* Thunb. *ex* Murr.), an exotic annual grass, also reached maximum cover on sites that had been mowed in July (Tables 2 and 3). In the absence of mowing, annual species were normally most abundant on sites of animal disturbances (Collins and Glenn 1988, Gibson 1989). The maximum number of species was also recorded on Florence soils in sites that had been mowed and baled in July (Figure 1e). This reflected a large number (8) of exotic species (Table 2). Mowing and baling removed vegetative cover, and had the effect of increasing light levels at the soil surface. Increased surface light intensity was one of the factors which, in combination with higher soil temperatures, accounted for increased productivity following burning (Hulbert 1988). In this sense, mowing was similar to burning. However, an increase in species richness and cover of annual species was not noted in the burned sites in this study. Whereas burning killed seedlings and favored rapidly resprouting perennials, mowing allowed and favored annual species.

Effect of Soil Type

The different soils sampled by Hulbert represented an indirect gradient from the shallow soils of prairie ridge tops (Florence and Benfield series), down slope on thin rocky soils (Sogn and Irwin series), to lowland foot slopes (Tully series) (Jantz *et al.* 1975). The most thoroughly sampled portion on this gradient was on the Florence and Tully series. This gradient of moisture availability was severe enough that there were differences between the flora of the two extremes. Silky aster (*Aster sericeus* Vent.), aromatic aster (*Aster oblongifolius* Nutt.), sleepy catchfly (*Silene antirrhina* L.), and slimpod venus-looking glass [*Triodanis perfoliata* (L.) Nieuw.] were absent from Tully soils. Smoothseed wildbean [*Stophostyles leiosperma* T. & G.) Piper], clammy groundcherry (*Physalis heterophylla* Nees), Virginia groundcherry (*Physalis virginiana* P. Mill.), Canada goldenrod (*Solidago canadensis* L.), upland ladies'-tresses (*Sprianthes vernalis* Engelm. & Gray), and American germander (*Teucrium canadense* L.) were absent from Florence soils. Overall, more species occurred on Florence soils than on either Tully or Irwin soils irrespective of burning or mowing treatment (Figure 2). Other species showed quantitative differences in abundance on different soil types. For example, big bluestem, the dominant plant overall, was more abundant on Tully soils than on Florence soils under all burning and mowing treatments. Many species showed an interaction between a combination of burning, mowing, and soil type. For example, wild lettuces (*Lactuca* spp. L.) were more abundant on Florence soils compared with Tully soils when in treatments burned on a less frequent than annual burning regime. Prairie coneflower [*Ratibida columnifera* (Nutt.) Woot. & Standl.] was infrequent on Tully soils irrespective of burning treatment, but was more abundant on Florence soil that had been either left unburned or burned only every few years.

The unburned treatments allowed a comparison across all five soil series (Table 1). However, the variability in these data were large, in particular the mean cover of particular life form classes, such as cool- and warm-season grass cover (Figure 2). This variation reflects Hulbert's assertion and Gibson's (1988) observation, that influence from prior management may still be evident after several years of known management.

CONCLUSIONS

Hulbert's data represent a valuable resource for understanding plant community interactions on the tallgrass prairie with respect to burning, mowing, and soil type. Previous studies have considered these factors, but not in such a large number of treatment combinations. Prior management and landscape effects were clearly evident in these data and increased the variance of each treatment effect. Nevertheless, a number of consistent trends emerged. For example, spring burning favored warm-season grasses at the expense of cool-season grasses and forbs, annual and biennial plants were able to establish under the mowing treatments, and the number of species was highest on the soils of level uplands. More subtle effects and trends would be likely revealed using multivariate and other statistical procedures, and the data are provided (Tables 2 to 4) so that other researchers might have this opportunity.

ACKNOWLEDGEMENTS

This report is written in tribute to the late Lloyd Hulbert who undertook the field work. The original field notes, other partial summaries of these data and Hulbert's original unfinished manuscript are stored in the Konza Prairie Office, Kansas State University, Manhattan, Kansas 66506. J. M. Briggs is thanked for critically reviewing an early draft of the manuscript, and for giving the oral presentation. Manuscript preparation was partially funded by NSF Grant BSR-8514327 for Long-Term Ecological Research to Kansas State University. This is contribution number 89-31-A, Division of Biology, Kansas Agricultural Experiment Station, Kansas State University. The author was formerly with the Division of Biology, Kansas State University.

LITERATURE CITED

Abrams, M., and L.C. Hulbert. 1987. Effect of topographic position and fire of species composition in tallgrass prairie in northeast Kansas. American Midland Naturalist 117:442-445.

Abrams, M.D., A.K. Knapp, and L.C. Hulbert. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position. American Journal of Botany 73:1509-1515.

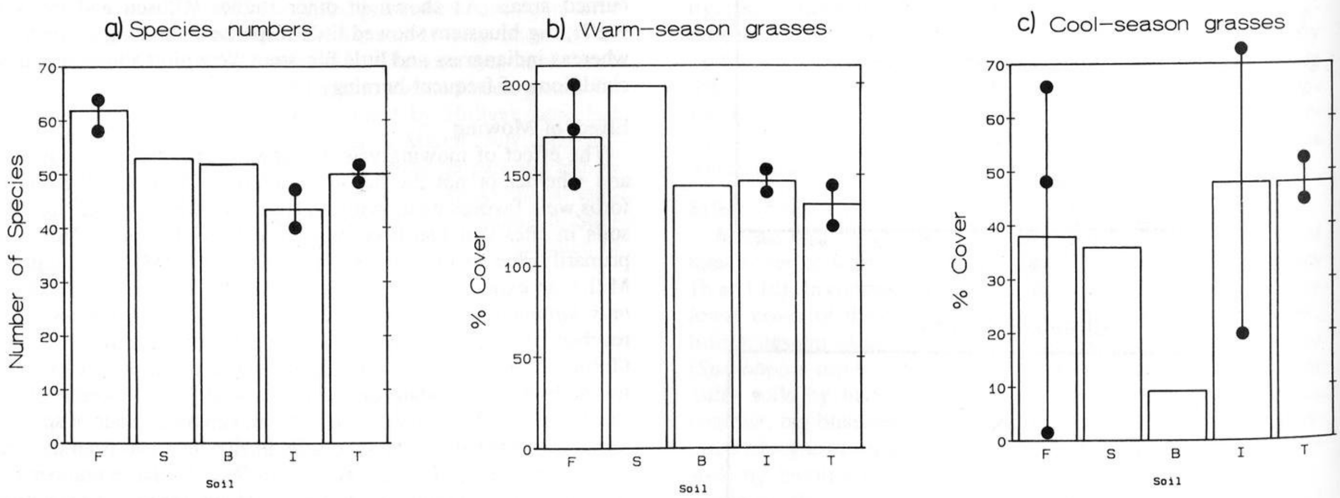


FIG. 2. Mean a) number of species, and percentage cover of b) warm-season and c) cool-season grasses in unburned sites on Florence (F), Sogn (S), Benfield (B), Irwin (I), and Tully (T) soils. The bars indicate mean values over all replicate sites, the solid circles indicate the mean values for each replicate site (e.g. three replicate sites on Florence soil). One site was sampled on Sogn and Benfield soils and so just the bars are drawn. The line joining the highest and lowest value indicates the range of means.

Adams, D.E., R.C. Anderson, and S.L. Collins. 1982. Differential response of woody and herbaceous species to summer and winter burning in an Oklahoma grassland. Southwestern Naturalist 27:55-61.

Aldous, A.E. 1934. Effect of burning Kansas bluestem pastures. Kansas State College of Agriculture and Applied Science, Agricultural Experimental Station Technical Bulletin Number 38.

Archer, S. 1984. The distribution of photosynthetic pathway types on a mixed-grass prairie hillside. American Midland Naturalist 111:138-142.

Barnes, P.W., and A.T. Harrison. 1982. Species distribution and community organization in a Nebraska Sandhills mixed prairie as influenced by plant/soil-water relationships. Oecologia 52:192-201.

Christiansen, P.A. 1972. Management on Hayden prairie: past, present and future. Pages 25-29. *In* J.H. Zimmerman (ed.). Second Midwest Prairie Conference Proceedings, University of Wisconsin, Madison.

Collins, S.L., and S.M. Glenn. 1988. Disturbance and community structure in North American Prairie. *In* H.J. During, M J.A. Werger, and J.H. Willems (eds.). Diversity and pattern in plant communities. SPB Academic Publishers, The Hague, The Netherlands.

Crockett, J.J. 1966. Effect of mowing on a relict tall grass prairie. Proceedings of the Oklahoma Academy of Science 46:1-4.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. Northwest Science 33:43-66.

Great Plains Flora Association. 1986. Flora of the Great Plains. University of Kansas Press, Lawrence.

Gibson, D.J. 1988. Regeneration and fluctuation of tallgrass prairie vegetation in response to burning frequency. Bulletin of the Torrey Botanical Club 115:1-12.

Gibson, D.J. 1989. Effects of animal disturbance on tallgrass prairie vegetation. American Midland Naturalist 121:144-154.

Gibson, D.J., and L.C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72:175-185.

Hover, E.I., and T.B. Bragg. 1981. Effect of season of burning and mowing on an eastern Nebraska *Stipa - Andropogon* prairie. American Midland Naturalist 105:13-18.

Hulbert, L.C. 1973. Management of Konza Prairie to approximate pre-white man fire influences. *In* L.C. Hulbert (ed.). Proceedings of the Third Midwest Prairie Conference. Kansas State University, Manhattan, Kansas.

Hulbert, L.C. 1985. History and use of Konza Prairie Research Natural Area. Prairie Scout 5:63-93.

Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69:46-58.

Jantz, D.R., R.F. Harner, H.T. Rowland, and D.A. Gier. 1975. Soil survey of Riley County and part of Geary County, Kansas. Soil Conservation Service, U. S. Department of Agriculture, Washington, D.C.

Knapp, A.K., and T.R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience 36:662-668.

Owensby, C.E., and K.L. Anderson. 1967. Yield response to time of burning in the Kansas Flint Hills. Journal of Range Management 20:12-16.

Platt, D.R. 1988. Dedication to Dr. Lloyd C. Hulbert. Transactions of the Kansas Academy of Science 91:2-3.

Towne, G., and C.E. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. Journal of Range Management 37:392-397.

Zimmerman, U.D., and C.L. Kucera. 1977. Effects of compositional changes on productivity and biomass relationships in tallgrass prairie. American Midland Naturalist 97:465-469.

REMNANT AND RESTORED PRAIRIE RESPONSE TO FIRE, FERTILIZATION, AND ATRAZINE

Robert A. Masters and Kenneth P. Vogel
U.S. Department of Agriculture, Agricultural Research Service, Department of Agronomy, University of Nebraska, Lincoln, Nebraska 68583

Abstract. The effect of spring burning, fertilization, and atrazine on herbage yield of warm- and cool-season grasses, flowering stalk density, and seed yield of selected warm-season grasses was determined on a remnant prairie and a restored prairie located near Lincoln and Center, Nebraska, respectively. Sites were burned in mid-April 1987 and followed by application of fertilizer (112 kg N/ha at the remnant prairie and 112-22 kg N-P/ha at the restored prairie) and atrazine (2.2 kg active ingredient/ha). Herbage yield of warm-season grasses increased more than 100% following burning in combination with fertilization at both sites and atrazine application alone at the restored prairie. Warm-season grass flowering stalk density increased more than 3 and 2 times following burning combined with fertilization and fertilization only at the remnant and restored prairies, respectively. Germinable seed numbers increased over 600% following a combination of burning, fertilization, and atrazine application at the remnant prairie and more than doubled following atrazine application at the restored prairie. Evidence provided by this research indicates that spring burning, fertilization, and atrazine can be used to renovate and improve productivity of tallgrass prairie in Nebraska.

Key Words. prairie renovation, flowering stalk density, warm-season grasses, cool-season grasses, Nebraska

INTRODUCTION

Areas of remnant and restored tallgrass prairies occur throughout eastern Nebraska. Renovation of these prairies is often necessary because of encroachment of non-endemic cool-season grasses, Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss.), which compete with desirable warm-season native mid- and tall grasses. Generally, these cool-season species occur on prairies with a history of grazing mismanagement and/or where fire has been excluded.

Methods used to renovate degraded grasslands include spring burning, fertilization, and application of the herbicide, atrazine [6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine]. Vegetation composition and successional status were important factors influencing grassland community response to these treatments (Gillen *et al.* 1987). Time of spring burning and fertilizer application influenced the response of the warm-season grass component of grassland communities. Burning at the time of warm-season grass growth initiation favored warm-season grasses and suppressed undesirable cool-season plants that initiated growth earlier in the spring (Anderson *et al.* 1970). Warm-season grass herbage production increased following late spring application of nitrogen as compared to early spring application that promoted growth of less desirable introduced cool-season grasses (Rehm 1984). Atrazine selectively controlled cool-season grasses and some broadleaf plants and improved productivity of warm-season grasses (Morrow et al . 1977, Waller and Schmidt 1983).

Information regarding the combined effect of burning, fertilization, and atrazine application on remnant and restored tallgrass prairie is limited. Therefore, this study was conducted to evaluate the influence of these treatments alone and in combination on herbage yield of warm- and cool-season grasses, flowering stalk density, and seed yield of selected warm-season grasses.

METHODS

Study sites were established on a remnant native grassland located on Nine-Mile Prairie, 15 km northwest of Lincoln, Nebraska in Lancaster County and on a restored overgrazed pasture, 6 km east of Center, Nebraska in Knox County. The restored prairie was revegetated with a mixture of native warm-season grasses following a brief period of use as cropland in the 1950's. The remnant prairie had not been grazed since 1968, but had been burned in the spring at two- to three-year intervals. The restored prairie was grazed up to 1986, but had not been burned. The study sites were not grazed during the experiment. Soils on the remnant and restored prairie sites are classified as a Sharpsburg silty clay loam (montmorillonitic, mesic, Typic Argiudolls) and a Dickinson loamy sand (mixed, mesic, Typic Hapludolls), respectively. Common grasses on the sites included big bluestem (*Andropogon gerardii* Vitman-var. *gerardii* Vitman), indiangrass [*Sorghastrum nutans* (L.) Nash], switchgrass (*Panicum virgatum* L.), little bluestem [*Schizachyrium scoparium* (Michx.) Nash], sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], Scribner panicum [*Dicanthelium oligosanthes* (Schult.) Gould var. *scribnerianum* (Nash) Gould], smooth brome, and Kentucky bluegrass.

One-half of an area (148 x 54 m) was burned at the remnant and restored prairies on 18 April and 23 April 1987, respectively. After burning, three plots (74 x 18 m) were delineated within the burned and unburned areas at each site. In May 1987, one-half of each plot was fertilized with 112 kg/ha of nitrogen. In addition, 22 kg/ha of phosphorus was applied at the Center, Nebraska site because soils in this area are phosphorus deficient. Following fertilizer application, 2.2 kg active ingredient/ha of atrazine was applied to half of each fertilized and unfertilized plot in the burned and unburned areas.

After treatment application a subplot (4 x 8 m) was delineated within each plot to facilitate sampling. In early August 1987, a quadrat (0.5 m^2) was located along each of the longest sides of the sampling subplot within each plot. Vegetation within the quadrats was clipped to a 2 cm stubble height, separated by species, oven-dried, and weighed.

Flowering stalk density was determined in early October by counting number of big bluestem and indiangrass flowering stalks within two quadrats (0.5 m^2) randomly placed within each sampling subplot. After counting, flowering stalks of the two species within each sampling subplot were harvested by hand and air dried. Seeds were threshed, weighed, and stored at room temperature (25 C) until germinability was determined. One gram of threshed seed from each sampling subplot was placed in a petri dish between two pieces of filter paper. Five ml of a solution of 2% KNO_3 and 1% captan N-[(trichloromethyl)-thio]-4-cyclohexene-1,2-dicarboximide, a fungicide, were added to each petri dish. The petri dishes were placed in cold storage (5 C) for two weeks to break seed dormancy (Crosier 1970). Following cold storage, the petri dishes were placed in a germination chamber for four weeks where temperature and light alternated from 20 C and 30 C for 16 (dark) and 8 (light) hr, respectively. After four weeks, the total number of germinated seeds was determined. Total number of germinable seed produced within each sampling subplot was then calculated by multiplying number of germinated seed within a petri dish by weight of the threshed seed harvested from the appropriate sampling subplot.

The experiment was designed as a split block with three replications per treatment combination. Hierarchical analysis of variance was applied to warm- and cool-season grass herbage yields and flowering stalk density and yield of germinable seed of selected warm-season grasses. Sources of variation in descending order were burning, fertilization, and atrazine application. Since randomization associated with placement of the burning treatment was restricted at both sites, the main effect of burning could not be statistically tested. Remaining main effects and interactions were evaluated using standard analysis of variance procedures, and treatment means were compared using Fisher's protected least significant difference test (Steel and Torrie 1980).

RESULTS AND DISCUSSION

Forb response to the various treatments was not determined. Apparently, the technique used to sample the vegetation was not sensitive enough to characterize the forb component of the prairie communities. In other studies, atrazine had an adverse (Gillen *et al.* 1987) or no effect (Peterson *et al.* 1983) on forbs in grasslands of the southern Great Plains. In the following presentation, information will be limited to the response of warm- and cool-season grasses within the remnant and restored prairie study sites.

Warm- and Cool-Season Grass Yields

Warm-season grass yield at the remnant and restored prairies increased following a combination of burning and fertilization (Tables 1, 2, 3, and 4). The two-fold increase in yield was partially the result of removal of standing dead plant biomass and litter by burning. Standing dead and litter yields from unburned areas averaged 6,480 and 1,438 kg/ha as compared to only 333 and 311 kg/ha on the burned sites at the remnant and restored prairies, respectively. Although the main effect of burning cannot be statistically evaluated in this study, it is apparent that burning had an effect on the standing dead and litter biomass components of the remnant and restored prairies.

Excessive accumulation of standing dead and litter depressed plant yields by maintaining low soil temperatures (Sharrow and Wright 1977, Rice and Parenti 1978). Higher soil temperatures following burning stimulated plant growth initiation and enhanced soil microflora growth which hastened organic matter decomposition and increased nutrient availability (Neuenschwander and Wright 1984). Others have found that fire-induced removal of standing dead and litter increased tallgrass productivity by im-

Table 1. Mean dry matter yields (kg/ha) of warm-season grasses, cool-season grasses, and standing dead and litter at the remnant prairie near Lincoln, Nebraska.

Treatment[1]	*Warm-season grasses*	*Cool-season grasses*	*Standing dead and litter*
		kg/ha	
BFA	10,049	125	350
BF	9,372	537	472
BA	5,548	90	258
B	5,146	281	255
FA	7,088	50	6,849
F	6,026	197	5,562
A	4,855	19	7,033
0	4,773	153	6,481
LSD (0.05)[2]	1,891	293	NS
LSD (0.05)[3]	NS	NS	504

[1]Treatments are: B = burned, F = fertilized with 112-0-0 kg N-P-K/ha, A = atrazine applied at 2.2 kg a.i./ha, and 0 = no treatment.
[2]Least significant difference (LSD) for comparing between means of fertilizer main treatment effect and means of fertilizer by burning treatment interaction.
[3]LSD for comparing between means of herbicide main effect and all interaction terms that include the herbicide effect.

Table 2. Mean squares and levels of significance for the treatment effects in the analysis of variance for dry matter yields of warm-season grasses, cool-season grasses, and standing dead and litter at the remnant prairie near Lincoln, Nebraska.

Source of variation[1]	*df*	*Warm-season grasses*	*Cool-season grasses*	*Standing dead and litter*
Burning (B)[2]	1	20383212	140975	226738243
Fertilizer (F)	1	55943784 **	50106 *	235541 NS
F X B	1	10300006 **	17550 NS	747231 NS
Error (a)	4	1008195	24237	632933
Herbicide (H)	1	1852926 NS	292737 NS	1109572 **
H X B	1	1624 NS	39091 NS	1438249 **
H X F	1	590509 NS	20662 NS	139843 NS
H X B X F	1	186949 NS	16214 NS	277780 NS
Error (b)	8	448045	58032	71512

[1]The ** and * indicate significance at the 0.01 and 0.05 levels of probability. NS indicates lack of statistical significance at these levels of probability.
[2]The main effect of burning could not be statistically evaluated.

Table 3. Mean dry matter yields (kg/ha) of warm-season grasses, cool-season grasses, and standing dead and litter at the restored prairie near Center, Nebraska.

Treatment[1]	*Warm-season grasses*	*Cool-season grasses*	*Standing dead and litter*
		kg/ha	
BFA	7,905	12	306
BF	4,944	373	260
BA	4,340	35	437
B	2,091	86	240
FA	5,458	77	1,843
F	1,379	433	952
A	3,401	6	1,635
0	2,355	180	1,325
LSD (0.05)[2]	1,259	NS	NS
LSD (0.05)[3]	2,142	239	NS

[1]Treatments are: B = burned, F = fertilized with 112-22-0 kg N-P-K/ha, A = atrazine applied at 2.2 kg a.i./ha, and 0 = no treatment.
[2]Least significant difference (LSD) for comparing between means of fertilizer main treatment effect and means of fertilizer by burning treatment interaction.
[3]LSD for comparing between means of herbicide main effect and all interaction terms that include the herbicide effect.

Table 4. Mean squares and levels of significance for the treatment effects in the analysis of variance for dry matter yields of warm-season grasses, cool-season grasses, and standing dead and litter at the restored prairie near Center, Nebraska.

Source of variation[1]	*df*	*Warm-season grasses*	*Cool-season grasses*	*Standing dead and litter*
Burning (B)[2]	1	16770495	13614	7634078
Fertilizer (F)	1	21086626 **	130420 NS	28635 NS
F X B	1	10690413 **	1380 NS	1107 NS
Error (a)	4	446891	33098	627218
Herbicide (H)	1	40056651 **	332762 **	782865 NS
H X B	1	2786 NS	5198 NS	343827 NS
H X F	1	5262381 NS	90921 *	69876 NS
H X B X F	1	2018516 NS	6286 NS	200531 NS
Error (b)	8	1293842	16149	182951

[1]The ** and * indicate significance at the 0.01 and 0.05 levels of probability. NS indicates lack of statistical significance at these levels of probability.
[2]The main effect of burning could not be statistically evaluated.

proving the light environment of emerging shoots (Knapp 1984, Hulbert 1988).

Cool-season grass yields were low at both sites when sampled in early August. However, despite time of sampling, yield of cool-season grasses was increased by fertilization at both sites and declined following atrazine application at the restored prairie (Tables 1, 2, 3, and 4). Others determined that atrazine selectively controlled cool-season grasses, but did not have an adverse affect on most warm-season grasses (Waller and Schmidt 1983, Rehm 1984, Gillen *et al.* 1987). As a result of this selectivity, application of atrazine is an effective practice to rejuvenate warm-season grasses in prairie communities dominated by less desirable cool-season grasses.

Table 5. Mean flowering stalk density (number/m^2) and germinable seed numbers (number/m^2) of selected warm-season grass at remnant and restored prairies in eastern Nebraska.

Treatment[1]	*Flowering Stalk Density*		*Germinable Seed Number*	
	Remnant	*Restored*	*Remnant*	*Restored*
	Number/m^2			
BFA	109	49	2,822	534
BF	86	29	1,201	166
BA	56	23	707	597
B	45	13	754	350
FA	37	21	475	631
F	20	12	316	87
A	38	12	466	577
0	21	6	389	225
LSD (0.05)[2]	28	12	NS	NS
LSD (0.05)[2]	22	NS	614	565

[1]Treatments are: B = burned, F = fertilized with 112-0-0 (remnant prairie) or 112-22-0 (restored prairie) kg N-P-K/ha, A = atrazine applied at 2.2 kg a.i./ha, and 0 = no treatment.
[2]Least significant difference (LSD) for comparing between means of fertilizer main treatment effect and means of fertilizer by burning treatment interaction.
[3]LSD for comparing between means of herbicide main effect and all interaction terms that include the herbicide effect.

Flowering Stalk Density and Germinable Seed Number

Flowering stalk density increased at both sites when burning was combined with fertilization, but only at the remnant prairie when atrazine was applied (Tables 5 and 6). At the remnant prairie, the increase due to burning and fertilization (30 to 98 stalks/m^2), was greater than that attributed to atrazine application alone (43 to 60 stalks/m^2). Increases in tallgrass flowering stalk density following burning may be explained in part by plant growth enhancement caused by standing dead and litter removal. The positive influence of atrazine on flowering stalk density may result from suppression of competing plants, such as, cool-season annual and perennial grasses, and/or a stimulatory effect of the herbicide on plant growth and development. Reis (1976) determined that sublethal doses of S-triazine herbicides enhanced physiological processes within perennial and annual grasses.

Influence of treatments on germinable seed yield varied by site. At the remnant prairie, number of germinable seeds increased 7-fold following treatment with a combination of burning, fertilizer, and atrazine as compared to no treatment (Tables 5 and 6). Others have observed that burning and fertilization improved warm-season grass seed yield. Burton (1944) found that seed yield of the introduced grasses bahiagrass (*Paspalum notatum* Flugge) and bermudagrass [*Cynodon dactylon* (L.) Pers.] increased following burning. In cultivated grass seed production fields, nitrogen fertilization and burning increased seed production of several grasses including switchgrass, big bluestem, little bluestem, and indiangrass (Cornelius 1950). In contrast to the remnant prairie, germinable seed numbers at the restored prairie site were significantly affected only by atrazine. Atrazine treated areas produced 585 seeds/m^2 as compared to only 207 seeds/m^2 from areas not treated with atrazine.

In this study, depending on site and plant parameter evaluated, spring burning, fertilization, and atrazine enhanced tallgrass productivity. These treatments not only facilitated prairie renovation, but also improved seed yield of selected warm-season grasses. Feasibility of atrazine use as part of a renovation program depends on whether the objective is to suppress introduced cool-season grasses and restore warm-season grass dominance or promote forb population expansion. Although not conclusively determined in this study, other research (Gillen *et al.* 1987) indicated that atrazine application should be avoided if rejuvenation of the forb component of the prairie community is a primary objective of a renovation program.

Table 6. Mean squares and levels of significance for the treatment effects in the analysis of variance for flowering stem density and germinable seed number of selected warm-season grasses at remnant and restored prairies in eastern Nebraska.

Source of variation[1]	*df*	*Flowering stem density*		*Germinable seed number*	
		Remnant	*Restored*	*Remnant*	*Restored*
Burning (B)[2]	1	12150	1430	5675875	11417
Fertilizer (F)	1	3220 **	1175 *	2431351 NS	27900 NS
F X B	1	3553 **	225 *	2487128 NS	16426 NS
Error (a)	4	228	40	1328334	49633
Herbicide (H)	1	1734 **	642 NS	1297902 **	718382 *
H X B	1	1 NS	86 NS	621400 *	18792 NS
H X F	1	54 NS	93 NS	1082024 *	43752 NS
H X B X F	1	48 NS	15 NS	1004939 *	5070 NS
Error (b)	8	48	173	106475	85717

[1]The ** and * indicate significance at the 0.01 and 0.05 levels of probability. NS indicates lack of statistical significance at these levels of probability.
[2]The main effect of burning could not be statistically evaluated.

ACKNOWLEDGEMENTS

The authors would like to thank Terry Gompert (Knox County Extension Specialist), Kevin Grams, and Jim Kube for their assistance. Contribution Number 8781 of the Agricultural Research Division, University of Nebraska, Lincoln, and the Agricultural Research Service, U.S. Department of Agriculture.

LITERATURE CITED

Anderson, K.L., E.F. Smith, and C.E. Owensby. 1970. Burning bluestem range. Journal of Range Management 23:81-92.

Burton, G.W. 1944. Seed production of several southern grasses as influenced by burning and fertilization. Journal American Society of Agronomy 36:523-529.

Cornelius, D.R. 1950. Seed production of native grasses under cultivation in eastern Kansas. Ecological Monographs 20:1-29.

Crosier, W.F. (ed.). 1970. Rules for testing seeds. Proceedings of the Association of Official Seed Analysts. Graphic Publishing Company, Lake Mills, Iowa.

Gillen, R.L., D. Rollins, and J.F. Stritzke. 1987. Atrazine, spring burning, and nitrogen for improvement of tallgrass prairie. Journal of Range Management 40:444-447.

Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69:46-58.

Knapp, A.K. 1984. Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. American Journal of Botany 71:220-227.

Morrow, L.A., C.R. Fenster, and M.K. McCarty. 1977. Control of downy brome on Nebraska rangeland. Journal of Range Management 30:293-296.

Neuenschwander, L.F., and H.A. Wright. 1984. Edaphic and microclimate factors affecting tobosagrass regrowth after fire. Journal of Range Management 37:116-122.

Peterson, J.L., R.L. Potter, and D.N. Ueckert. 1983. Evaluation of herbicides for manipulating herbaceous rangeland vegetation. Weed Science 31:735-739.

Rehm, G.W. 1984. Yield and quality of a warm-season grass mixture treated with N, P, and atrazine. Agronomy Journal 76:731-733.

Reis, S.K. 1976. Subtoxic effects on plants. Pages 313-340. *In* L.J. Audus (ed.). Herbicides: Physiology, biochemistry, ecology. Academic Press, London.

Rice, E.L., and R.L. Parenti. 1978. Causes of decreases in productivity in undisturbed tall grass prairie. American Journal of Botany 65:1091-1097.

Steel, R.G.D., and J.H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill Book Company, New York.

Waller, S.S., and D.K. Schmidt. 1983. Improvement of eastern Nebraska tallgrass range using atrazine and glyphosate. Journal of Range Management 36:87-90.

INFLUENCE OF HARVEST AND NITROGEN FERTILIZER ON FOUR WARM-SEASON GRASSES

James Stubbendieck and Cheryl A. Nielsen
Department of Agronomy, University of Nebraska, Lincoln, Nebraska 68583

Abstract. Two cultivars each of four warm-season grass species under three N fertilizer treatments and three harvesting regimes were studied to determine the effect of nitrogen fertilizer and harvest date on forage yield. Research was conducted in eastern Nebraska on an alluvial soil. The eight grasses studied were 'Blaze' and 'PM-K-129' little bluestem [*Schizachyrium scoparium* (Michx.) Nash], 'Cave-in-Rock' and 'Pathfinder' switchgrass (*Panicum virgatum* L.), 'Holt' and 'Oto' indiangrass [*Sorghastrum nutans* (L.) Nash], and 'Kaw' and 'Pawnee' big bluestem (*Andropogon gerardii* var. *gerardii* Vitman). Dates of harvest were mid-July, mid-August, and early October. Regrowth from plots harvested in mid-July and mid-August was harvested in early October. Yields, analyzed by orthogonal comparisons, tested quadratic and linear effects of harvest date and N treatments. Total yields of all cultivars, except 'Cave-in-Rock', showed quadratic effects. Mid-August yields were greater than the averaged yields of mid-July and early October harvests. Yields of 'Blaze', 'Pathfinder', and 'Holt' exhibited no significant differences between mid-July and early October harvests. Nitrogen was applied at the rates of 0, 100, and 200 kg/ha. These high rates of nitrogen were applied to determine yield potential of the grasses. A large increase in dry matter production occurred following the addition of 100 kg/ha of N fertilizer. For most cultivars, a slight yield increase occurred as N was increased from 100 to 200 kg/ha. Yields obtained in this research indicate a high yield potential for these warm-season grasses.

Key Words. little bluestem, *Schizachyrium scoparium*, big bluestem, *Andropogon gerardii*, indiangrass, *Sorghastrum nutans*, switchgrass, *Panicum virgatum*, nitrogen fertilizer, harvest dates, Nebraska

INTRODUCTION

Eastern Nebraska was once occupied by tallgrass prairie, which was dominated by perennial warm-season grasses (Stubbendieck 1988). Big bluestem (*Andropogon gerardii* var. *gerardii* Vitman), indiangrass [*Sorghastrum nutans* (L.) Nash], switchgrass (*Panicum virgatum* L.), and little bluestem [*Schizachyrium scoparium* (Michx.) Nash] were the primary species (Weaver 1954). Most of eastern Nebraska is under cultivation today, and little native prairie remains. Due to improper management, much of this uncultivated land is now dominated by introduced cool-season grasses, such as Kentucky bluegrass (*Poa pratensis* L.).

Warm-season grasses have often been overlooked as a potential forage source in the tallgrass prairie region because they are typically found on sites that have little opportunity for high yields due to low fertility and low levels of management. Relatively little research has been done to find the maximum potential yields of warm-season grasses growing on a favorable site. The objective of this study was to determine the yield response and potential of several warm-season grass cultivars as affected by harvest date and nitrogen fertilizer.

Increased forage production following application of nitrogen (N) fertilizer has been shown in numerous studies (Johnson *et al.* 1948, Rogler and Lorenz 1957, Moser and Anderson 1965, Reardon and Huss 1965, Lorenz and Rogler 1967, Cosper *et al.* 1967, Rehm *et al.* 1972, Perry and Baltensperger 1979). Factors affecting plant response to fertilization were soil type, soil fertility, soil temperature, and the amount of precipitation. Length of grazing period and date and rate of application can alter effectiveness of nitrogen fertilizer (Goetz 1969).

Vogel and Bjugstad (1968) reported that clipping of little bluestem, big bluestem, and indiangrass during the mature seed stage or later increased yield and stimulated spring tillering, as compared to clipping during the summer which reduced yields. Clipping between floral initiation and anthesis caused the greatest reduction in yields of the warm-season grasses. On bluestem range in North Dakota, maximum yields were obtained with harvest dates between 15 July and 1 August. Plots harvested on 1 June declined in yield over the eight-year experiment (Lorenz and Rogler 1973). Significant yield reductions occurred when forage was removed twice, rather than once, during the growing season.

Near Manhattan, Kansas, a four-year study was conducted on irrigated and fertilized big bluestem growing on uplands (Owensby *et al.* 1970). Plots clipped during both July and August resulted in increased herbage production, as compared to plots clipped only at the end of the growing season. Clipping during the growing season conserved moisture and increased water use efficiency. Conversely, yields were decreased with two or three clippings during a five-year study of pure stands of big bluestem and switchgrass near Lincoln, Nebraska (Newell and Keim 1947). Yields from these plots were 1,270 kg/ha for big bluestem and 550 kg/ha for switchgrass. With a single clipping at the end of August, big bluestem and switchgrass produced 1,500 and 1,020 kg/ha, respectively.

A five-year clipping study was conducted in northcentral Oklahoma on pure stands of indiangrass, big bluestem, little bluestem, and switchgrass (Dwyer *et al.* 1963). Four clipping treatments were applied with clipping heights of 5 and 10 cm. The annual clipping treatment dates were: 1) July; 2) June and September; 3) June, July, August, and September; and 4) January. Greatest forage yields for all species occurred under the annual July clipping, followed by the June and September clipping treatment.

METHODS

The study area was on the Desoto National Wildlife Refuge, located about 32 km north of Omaha in Washington County, Nebraska. The soil was a course-silty, mixed (calcareous), mesic Mollic Udifluvent (DaMoude 1980). This nearly level, imperfectly drained, alluvial soil was formed in sediments recently deposited by the Missouri River. The soil series was Haynie. Texture of the top soil varied from a silt loam to a silty clay loam. The subsoil was stratified sand and silt. The pH of the top soil was 7.9, and the organic matter was 1.5%. The water table was a depth of approximately 2.5 m.

Long-term, average annual precipitation at the DeSoto National Wildlife Refuge is 770 mm. Precipitation for the two years of the study was 790 and 750 mm. An average of 66% of the precipitation is recorded during the active growth period (May 1-October 1) of the warm-season grasses.

The Soil Conservation Service (SCS) seeded a group of 18 x 160 m plots to various warm-season grasses seven years prior to the start of this experiment. Unpublished SCS data indicated that rather high forage yields were harvested from most plots. Plots were grazed at low stocking levels by wildlife prior to this study. Plots had not been fertilized. Based on yield potential and widespread usage, two cultivars within each of four species were selected for this experiment: 'PM-K-129' and 'Blaze' little bluestem, 'Pathfinder' and 'Cave-in-Rock' switchgrass, 'Holt' and 'Oto' indiangrass, and 'Pawnee' and 'Kaw' big bluestem.

The design of this experiment was a split plot with four replications within each cultivar. Harvest dates were the main plots and rates of N fertilizer were the subplots. Dimensions of the main plot were 9 x 18 m. Three fertilizer treatments were applied, which divided the main plots into 3 x 6 m subplots.

Plots were burned in April of each year of the study to remove the accumulated plant material. Plots were sprayed in early June with 2,4-D (2,4-dichlorophenoxyacetic acid) amine at the rate of 0.35 liter/ha to control broadleaf weeds.

Subplots were fertilized with ammonium nitrate (NH_4NO_3) at rates of 0 (N_0), 100 (N_{100}), and 200 (N_{200}) kg/ha on 20 May of each year of the experiment. Harvest dates were 15 July, 15 August, and 10 October. Regrowth following the first two harvests was harvested 10 October. Only total yields are addressed in this paper.

Plots were harvested with a flail-type harvester which cut a 0.9 x 3.0 m strip out of the center of the subplots at a height of approximately 10 cm. The forage was collected, and a wet field weight was obtained. From this sample, a subsample of approximately 500 gm was selected and weighed. This subsample was placed into a forced air oven at 65 C until a constant weight was reached. Dry matter was determined, and hay yields (12% moisture) were calculated.

A separate statistical analysis was conducted for each grass variety. Two years of data were combined for analysis because of the absence of year interactions. This also created more degrees of freedom which decreased the mean square error term. An analysis of variance (ANOVA) and F tests were computed for each variable. Responses to nitrogen and harvest dates were analyzed for each variable using orthogonal comparisons. Contrasts were not adjusted for unequal spacing of harvest dates.

Orthogonal comparisons tested linear and quadratic effects of N and harvest date on total yield. The orthogonal comparison used to test linear effects of N compared N_0 to N_{200}. The orthogonal comparisons used to test quadratic effects compared the N_{100} treatment with the yield averages from the N_0 and N_{200} treatments. Quadratic effects were considered significant when the yield of N_{100} was significantly different ($P > 0.05$) than the averaged yields of N_0 and N_{200}. The N treatments were averaged over harvest date.

The effect of harvest date on hay yield was evaluated using orthogonal comparisons. Total yields compared 15 August harvests plus regrowth with averaged yields of 15 July harvests plus regrowth and 10 October harvests. Harvest dates were averaged over N treatments.

RESULTS AND DISCUSSION

Little Bluestem

Little bluestem fertilized with nitrogen exhibited a significant quadratic effect for total yield (Table 1). 'Blaze' and 'PM-K-129' N_{100} yields were greater than the averaged yields of N_0 and N_{200}. Nitrogen was apparently not a limiting factor for grass production at the N_{200} treatment level.

Nitrogen generally increases leaf area which will increase evapotransportation. This could result in limiting growth due to moisture stress. However, on this study site, moisture limitation is probably not a major factor. Water table depth is approximately 2.5 m. The soil is not classified as a subirrigated site by the SCS because the major portion of the grass root system will not have free access to water. However, the lower portion of the grass roots will reach the water table. Consequently, the genetic potential for N response may occur near 100 kg/ha.

Harvest dates tested by orthogonal comparisons exhibited a significant quadratic effect for total yield (Table 1). Highest total yield for 'Blaze' occurred on 15 August. The maturity of 'Blaze' was probably the main reason for the total yield on 10 October being less than on 15 August. By October, 'Blaze' was dormant.

Table 1. Yield (tonnes/ha) of 'Blaze' and 'PMK-129' little bluestem with three harvest regimes and three levels of nitrogen fertilizer.

Harvest regime or fertilizer rate	*Little bluestem* *'Blaze'*	*'PMK-129'*
	----------tonnes/ha----------	
Harvest Regimes:		
7/15 and 10/10	6.89	6.50
8/15 and 10/10	10.89	10.15
10/10	8.87	10.19
Nitrogen Rate:		
0 kg/ha	6.55	7.21
100 kg/ha	10.23	10.00
200 kg/ha	9.88	9.62
Treatment Contrasts	Pr > F	
Quadratic effect of harvest regime	0.02	0.04
Quadratic effect of nitrogen regime	0.02	0.03

Dry matter production had ceased, and leaves were senescing. Thus, total dry matter yield was reduced.

Due to the later maturity of 'PM-K-129' than that of 'Blaze', only a small amount of leaf loss had occurred. Therefore, total yield did not decrease by the 10 October harvest date.

Little bluestem total yields on 15 July produced the least amount of dry matter. Lowered yields may be partly due to low carbohydrate reserves. Little bluestem was rapidly growing, so energy was being used for dry matter production. Carbohydrate reserves were used to initiate growth and perhaps to maintain rapid production. After clipping, plants may have been slow to recover from defoliation due to low availability of carbohydrates and/or few remaining nonelongated tillers.

Switchgrass

Switchgrass fertilized with nitrogen exhibited a significant quadratic effect for total yield (Table 2). Switchgrass N_{100} yields were greater than the averaged yields of N_0 and N_{200}. Nitrogen was apparently not the first limiting factor for grass production at the N_{200} treatment. As with the little bluestem cultivars, it appears that the genetic potential for N response for 'Cave-in-Rock' and 'Pathfinder' under the conditions of this experiment occurred near 100 kg/ha.

Harvest dates, tested by orthogonal comparisons, exhibited a significant quadratic effect for total yield of 'Pathfinder' switchgrass (Table 2). Yields of 'Pathfinder' on 15 August were greater than the average yields of the other two harvest dates. Total yield on 10 October was slightly lower than on 15 July. Harvest dates for 'Cave-in-Rock' exhibited a linear effect for yield.

Indiangrass

'Holt' indiangrass fertilized with nitrogen exhibited a significant quadratic effect for total yield (Table 3). The N_{100} yields were greater than the averaged yields of N_0 and N_{200}. 'Oto' indiangrass fertilized with nitrogen exhibited a significant linear increase for total yield (Table 3).

Both indiangrass cultivars exhibited a large yield increase with the high rate of N. McKendrich *et al.* (1975) reported indiangrass to have biennial tillers. The tillers remained active in the fall. Perhaps this longer growth period allowed indiangrass to respond to the high levels of N.

Table 2. Yield (tonnes/ha) of 'Cave-in-Rock' and 'Pathfinder' switchgrass with three harvest regimes and three levels of nitrogen fertilizer.

Harvest regime or fertilizer rate	*Switchgrass* 'Cave-in-Rock'	*Switchgrass* 'Pathfinder'
	------------ tonnes/ha ------------	
Harvest Regimes:		
7/15 and 10/10	11.10	10.93
8/15 and 10/10	11.78	13.95
10/10	9.11	10.19
Nitrogen Rate:		
0 kg/ha	8.91	8.80
100 kg/ha	12.25	13.82
200 kg/ha	10.82	12.45
Treatment Contrasts	Pr > F	
Quadratic effect of harvest regime	0.13	0.04
Quadratic effect of nitrogen regime	0.02	0.05

Table 3. Yield (tonnes/ha) of 'Holt' and 'Oto' indiangrass with three harvest regimes and three levels of nitrogen fertilizer.

Harvest regime or fertilizer rate	*Indiangrass* 'Holt'	*Indiangrass* 'Oto'
	---------- tonnes/ha ----------	
Harvest Regimes:		
7/15 and 10/10	6.60	7.26
8/15 and 10/10	9.33	10.60
10/10	7.94	10.16
Nitrogen Rate:		
0 kg/ha	3.50	3.78
100 kg/ha	9.20	10.22
200 kg/ha	11.17	14.02
Treatment Contrasts	Pr > F	
Quadratic effect of harvest regime	0.03	0.05
Quadratic effect of nitrogen regime	0.05	0.11

Harvest dates tested by orthogonal comparisons exhibited a significant quadratic effect for total yield (Table 3). Yields on 15 August were greater than the averaged yields on the other two harvest dates. Yields on 10 October were less than those on 15 August probably because of the maturity stage of the plants by October. Dry matter was reduced due to leaf loss.

The least amount of dry matter was harvested on 15 July. Indiangrass has few basal nodes, and the growing point is elevated above the ground soon after growth starts (Rechenthin 1956). Therefore, many growing points were probably removed during the first harvest. Cutting below the growing point prevents leaf initiation and expansion except by the slower process of tillering (Dahl and Hyder 1977). Regrowth may have been slowed by the tillering process, reducing dry matter yields of the regrowth. Lower 15 July yields may have been partly due to low carbohydrate reserves. Carbohydrate reserves were used to initiate growth and, perhaps, to maintain rapid production. After clipping, plants may have taken longer than normal to recover from defoliation due to low available carbohydrates.

Big Bluestem

Big bluestem fertilized with N exhibited a significant quadratic effect for total yield (Table 4). Big bluestem N_{100} yields were greater than the averaged yields of N_0 and N_{200}. Nitrogen was apparently not a limiting factor for grass production at the N_{200} treatment.

Table 4. Yield (tonnes/ha) of 'Kaw' and 'Pawnee' big bluestem with three harvest regimes and three levels of nitrogen fertilizer.

Harvest regime or fertilizer rate	*Big bluestem* 'Kaw'	*Big bluestem* 'Pawnee'
	---------- tonnes/ha ----------	
Harvest Regimes:		
7/15 and 10/10	8.14	9.38
8/15 and 10/10	13.06	12.49
10/10	10.13	7.84
Nitrogen Rate:		
0 kg/ha	6.45	6.26
100 kg/ha	11.57	11.37
200 kg/ha	13.31	12.08
Treatment Contrasts	Pr > F	
Quadratic effect of harvest regime	0.01	0.02
Quadratic effect of nitrogen regime	0.05	0.05

Harvest date orthogonal comparisons exhibited a significant quadratic effect for total yields of big bluestem (Table 4). The 15 August yields were greater than the average yields on 15 July and 10 October. Highest yields occurred with the 15 August harvest. The 10 October harvest severely reduced yields of 'Pawnee'. By October, big bluestem was dormant. Dry matter production had ceased. Since leaves were senescing, a reduction in total dry matter yield resulted.

Branson (1953) observed big bluestem to be somewhat more resistant than switchgrass to grazing. The growing points remained below the ground level until late July. Also, about two-thirds of big bluestems' shoots are vegetative rather than fertile (Branson 1953). July 15 yields were less than yields on August 15. Owensby *et al.* (1971) reported reduced carbohydrate percentages in rhizomes and stem bases in mid-July in big bluestem due to rapid vegetative growth. Reduction in carbohydrates from rapid growth plus harvesting at that time may have slowed recovery, reducing regrowth yields. Maximum carbohydrate accumulation occurred during mid-August to early September in big bluestem (Owensby *et al.* 1971). Carbohydrate levels were probably high at the 15 August harvest.

CONCLUSIONS

Yields of native, warm-season prairie grasses growing under favorable conditions, including added nitrogen, were exceptionally high. Some yields were similar to dry matter yields reported for corn (*Zea mays* L.) silage (Goodrich and Meiske 1985). Further research on yield potential and research on forage quality are warranted. High producing perennial species may be more economical and practical than use of annual species for production of dry matter for livestock.

ACKNOWLEDGEMENTS

Appreciation is expressed to the personnel with the DeSoto National Wildlife Refuge, Bureau of Sport Fisheries and Wildlife for their cooperation and assistance during the study. Journal Series Number 8411, of the Agricultural Research Division, University of Nebraska.

LITERATURE CITED

Branson, F.A. 1953. Two new factors affecting resistance of grasses to grazing. Journal of Range Management 6:165-171.

Cosper, H.R., J.R. Thomas, and A.Y. Alsayegh. 1967. Fertilization and its effect on range improvement in the Northern Great Plains. Journal of Range Management 20:216-222.

Dahl, B.E., and D.N. Hyder. 1977. Developmental morphology and management implications. Pages 257-290. *In* R.E. Sosebee (ed.). Rangeland plant physiology. Society for Range Management, Denver, Colorado.

DaMoude, D.W. 1980. Soil survey of Burt County, Nebraska. United States Department of Agriculture, Soil Conservation Service, Washington, DC.

Dwyer, D.S., W.C. Elder, and G. Singh. 1963. Effects of height and frequency of clipping on pure stands of range grasses in North Central Oklahoma. Oklahoma Agricultural Experiment Station Bulletin B-614.

Goetz, H. 1969. Composition and yields of native grassland sites fertilized at different rates of nitrogen. Journal of Range Management 22:384-390.

Goodrich, R.D., and J.C. Meiske. 1985. Corn and sorghum silages. Pages 527-536. *In* M.E. Heath, R.F. Barnes, and D.S. Metcalfe (eds.). Forages. Iowa State University Press, Ames.

Johnson, A., A.D. Smith, L.E. Lutwick, and S. Smoliak. 1948. Fertilizer response of native and seeded ranges. Canadian Journal of Plant Science 48:467-472.

Lorenz, R.J., and G.A. Rogler. 1967. Grazing and fertilization affect root development on range grasses. Journal of Range Management 10:129-132.

Lorenz, R.J., and G.A. Rogler. 1973. Interaction of fertility level with harvest date and frequency on productiveness of Mixed Prairie. Journal of Range Management 26:50-54.

McKendrich, J.E., C.E. Owensby, and R.M. Hyde. 1975. Big bluestem and indiangrass, vegetative reproduction and annual reserve CH_{20} and nitrogen cycles. Agro-Ecosystems 2:75-93.

Moser, L.W., and K.L. Anderson. 1965. Nitrogen and phosphorus fertilization of bluestem range. Transactions of the Kansas Academy of Sciences 67:613-616.

Newell, L.C., and F.D. Keim. 1947. Effects of mowing frequency on the yield and protein content of several grasses grown in pure stands. Nebraska Agricultural Experiment Station Research Bulletin 150.

Owensby, C.E., R.M. Hyde, and K.L. Anderson. 1970. Effects of clipping and supplemental nitrogen and water on loamy upland bluestem range. Journal of Range Management 23:341-346.

Owensby, C.E., G.M. Paulsen, and J.D. McKendrick. 1971. Effect of burning and clipping on big bluestem reserve carbohydrates. Journal of Range Management 24:358-362.

Perry, L.J., and D. Baltensperger. 1979. Leaf and stem yields and forage quality of three nitrogen fertilized warm-season grasses. Agronomy Journal 71:355-358.

Reardon, P.O., and D.L. Huss. 1965. Effects of fertilization on a little bluestem community. Journal of Range Management 18:238-241.

Rechenthin, C.A. 1956. Elementary morphology of grass growth and how it affects utilization. Journal of Range Management 9:167-170.

Rehm, G.W., W.J. Moline, and E.J. Schwartz. 1972. Response of a seeded mixture of warm-season prairie grasses to fertilization. Journal of Range Management 25:452-456.

Rogler, G.A., and R.J. Lorenz. 1957. Nitrogen fertilization of Northern Great Plains rangelands. Journal of Range Management 10:156-160.

Stubbendieck, J. 1988. Historical development of native vegetation on the Great Plains. Pages 21-28. *In* J. Mitchell (ed.). Impacts of the Conservation Reserve Program in the Great Plains. United States Department of Agriculture Forest Service General Technical Report RM-158.

Vogel, W.G., and A.J. Bjugstad. 1968. Effects of clipping on yield and tillering of little bluestem, big bluestem, and indiangrass. Journal of Range Management 21:136-140.

Weaver, J.E. 1954. North American prairie. Johnsen Publishing Company, Lincoln, Nebraska.

EFFECTS OF MANIPULATION ON FOLIAGE CHARACTERISTICS OF *ANDROPOGON GERARDII* VITMAN

Rosemary A. Ramundo, T. Dawn Shapley, C. L. Turner
Division of Biology, Kansas State University, Manhattan, Kansas 66506

M. I. Dyer
Biosphere Research Inc., Route 2, Box 330-A, Lenoir City, Tennessee 37771
and
T. R. Seastedt
Division of Biology, Kansas State University, Manhattan, Kansas 66506

Abstract. The effects of burning, mowing, and nitrogen fertilizer on the chlorophyll, nitrogen, and phosphorus content of big bluestem were measured using a factorial experimental design at Konza Prairie Research Natural Area. While spring burning usually increased foliage production, burning had no effect on mid-season chlorophyll or nitrogen concentrations. Chlorophyll concentrations were significantly increased by fertilizer and mowing treatments. Nitrogen concentrations of foliage were higher on fertilized and mowed plots. Mowing also increased phosphorus concentrations of foliage, but nitrogen fertilizer significantly reduced phosphorus concentrations. These results support other research indicating that: 1) nitrogen use efficiency (grams biomass produced per gram of foliage nitrogen) is higher on burned prairie, 2) removal of foliage by mowing results in more nutrient-rich regrowth, and 3) the amount of phosphorus available to big bluestem foliage is limited. The dilution of phosphorus caused by added nitrogen was a consequence of increased productivity on these plots and suggests phosphorus uptake in excess of requirements for maximum growth. The relationships between burning, mowing, and nitrogen on the spectral reflectance patterns of vegetation indicated that chlorophyll (or nitrogen) concentrations of foliage appeared to more strongly affect indices of greenness and plant vigor than did the amount of plant biomass.

Key Words. biomass, burning, mowing, big bluestem, *Andropogon gerardii*, chlorophyll, nitrogen, phosphorus, Kansas

INTRODUCTION

Publications on the factors controlling the productivity of tallgrass prairie are abundant (Knapp and Seastedt 1986, Ojima 1987, Hulbert 1988). Current scientific emphasis is directed at understanding spatial patterns of productivity in relation to topography, fire, and grazing. Interest is increasing in the use of remote sensing procedures in these efforts. Spectral reflectance patterns have been used to monitor seasonal patterns of productivity both within and among terrestrial ecosystems (Goward *et al*. 1985, Asrar *et al*. 1986). For this type of approach to be useful in tallgrass prairie, knowledge of burning, mowing, and grazing on plant spectral reflectance characteristics must be understood on a basis of both per unit of foliage and per unit of vegetation area. Plant physiology and morphology, in conjunction with the absolute amounts of living and dead foliage, will affect the spectral reflectance measurements (Sellers 1985, Waring *et al*. 1985).

This study evaluated the effects of burning, mowing and fertilizer on the chlorophyll, nitrogen, and phosphorus content of the dominant tallgrass species, big bluestem (*Andropogon gerardii* Vitman). These results are then related to the effects of the respective treatments on prairie productivity and the spectral reflectance properties of this vegetation.

STUDY SITE AND METHODS

Research was conducted on the Konza Prairie Research Natural Area in the Flint Hills region of northeastern Kansas. The study area consisted of 32 plots (100 m²) that had been: 1) annually burned or unburned since 1985, 2) mowed and raked twice per growing season or unmowed since 1985, and 3) fertilized with 10 g/m² of nitrogen as ammonium nitrate (NH_4NO_3) or untreated. This experiment consisted of four replicates of eight combinations of burning, mowing, and fertilizer additions. Mowing was conducted in late May and in mid-July. Species composition of these plots is similar to that reported by Hulbert (1988). Big bluestem was the dominant grass, but indiangrass [*Sorghastrum nutans* (L.) Nash] was also abundant. Forbs, including several milkweeds (*Asclepias* spp.) and goldenrods (*Solidago* spp.), were also common, particularly in unmowed plots.

Samples of big bluestem foliage for chlorophyll and nutrient analyses were collected on 3 July 1987 and immediately placed in refrigerated bags and returned to the laboratory. Leaf sheaths were removed prior to measurements. Wet weights of these samples were obtained and samples were then frozen until other analyses were conducted. Quantitative samples for biomass estimates were obtained on 15 July by clipping 0.1 m² of vegetation from each plot. Biomass from mowed plots represented regrowth after one mowing while biomass from unmowed plots represented total foliage production.

Methods of both extraction and spectrophotometric analysis of chlorophyll were based on the Delaney technique as used by Knapp and Gilliam (1985). The leaves were taken from the freezer one at a time, thawed by warming gently between the palms, then cut into 1 cm pieces, and weighed on a Mettler balance to 0.01 g. Chlorophyll A, chlorophyll B, and beta carotene were then extracted using 85% acetone, sand, and calcium chloride ($CaCO_3$) with a foil-covered mortar in a pestle. The leaves were ground for 1-2 minutes with a Talboy blender. The ground tissue and acetone were poured into a foil- covered, graduated centrifuge tube, and diluted to 10 ml with acetone. Each sample was centrifuged for 5 minutes and allowed to settle for 1 hour before measured in wavelengths of 750, 663, 644, and 452 nm on a Beckmann DB-GT spectrophotometer (Robbelen 1957).

Nitrogen and phosphorus values for foliage samples were obtained by drying and grinding additional foliage, digesting this tissue with a micro-Kjeldahl method, and determining nitrogen and phosphorus colorimetrically on a Technicon Autoanalyzer.

Spectral reflectance measurements were concurrently obtained by personnel involved on the NASA-FIFE experiment (FIFE = First ISLSCP Field Experiment, ISLSCP = International Satellite Land Surface Climatology Project). The spectral measurements determined total amount of reflected light at specific wavelengths. Here, an index of "greenness" or Green Vegetation Index (GVI) (Kauth and Thomas 1976) based on a linear combination of reflectances of various wavelengths, is used to describe the plots. Another index of plant vigor used to describe the plots, the normalized difference, is a ratio estimator created by subtracting red reflectance from the near-infrared reflectance and dividing this value by the sum of these reflectances (Goward *et al*. 1985).

Statistical analysis of these data employed a three-way ANOVA, using fire, mowing, and nitrogen as main effects. All possible interactions among the treatments were also evaluated. Due to the configuration of the plots, fire effects were tested using a block*fire interaction term. Other effects were evaluated with the error term.

RESULTS

An analysis of variance of nitrogen concentrations indicated no interactions among the main treatments of burning, mowing, and nitrogen additions. Nitrogen concentrations in foliage of big bluestem were higher in the fertilized plots than in control plots (Figure 1). Significantly higher nitrogen concentrations also occurred in mowed than in unmowed plots. Spring burning, however, did not significantly affect nitrogen concentrations (Figure 1).

An analysis of variance also indicated no interactions among the main treatment effects for phosphorus concentrations of foliage. Phosphorus increased in mowed plots at about the same ratio as the increase in nitrogen (Figure 2). In contrast, phosphorus significantly decreased in plots where nitrogen fertilizer was added (Figure 2).

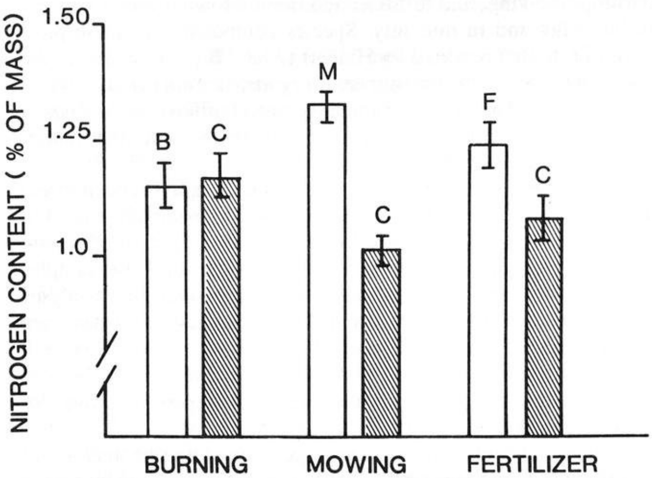


FIG. 1. Nitrogen concentrations of big bluestem foliage. Controls (C), represented by hatched bars, are compared to burned (B) plots, mowed (M) plots, or fertilized (F) plots. Error bars represent one standard error for l6 replicates.

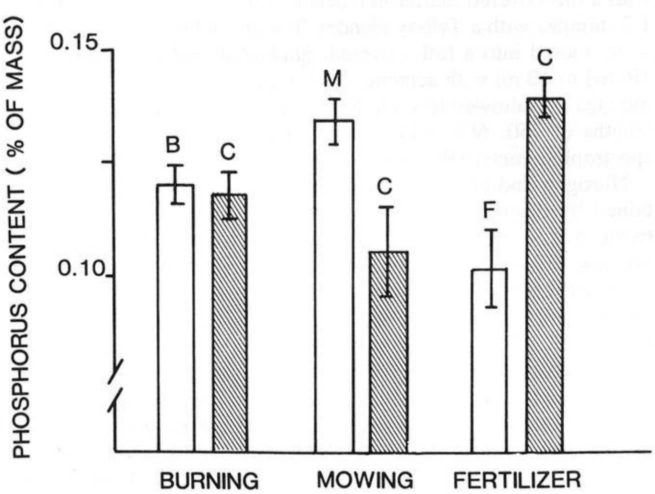


FIG. 2. Phosphorus concentrations of big bluestem foliage. Symbols are same as those used in Figure 1.

Fertilization with ammonium nitrate resulted in higher chlorophyll A and total pigment concentrations in big bluestem foliage (Figures 3 and 4). Mowing also significantly increased pigment concentrations while spring burning had no effect. An analysis of variance indicated modest ($p = 0.05$) interactions between mowing and fertilizer additions (for chlorophyll A concentrations) and for mowing and burning (for total pigment concentrations). Unmowed, unfertilized vegetation had lower chlorophyll A concentrations than mowed, unfertilized vegetation. Concentrations of chlorophyll A were similar for mowed or unmowed but fertilized vegetation. Burning tended to increase pigment concentrations on unmowed sites, but, it decreased concentrations on mowed sites.

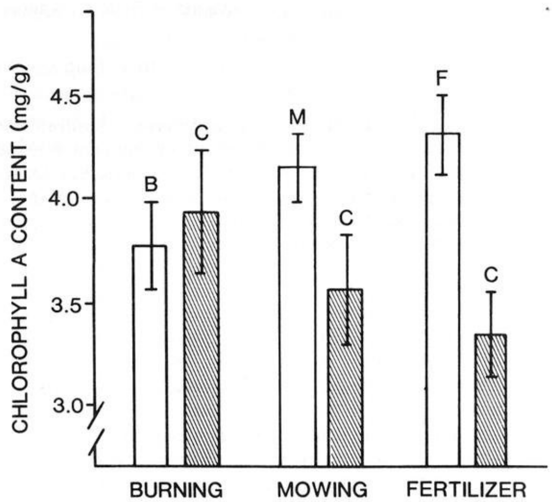


FIG. 3. Chlorophyll A concentrations of big bluestem foliage. Symbols are same as those used in Figure 1.

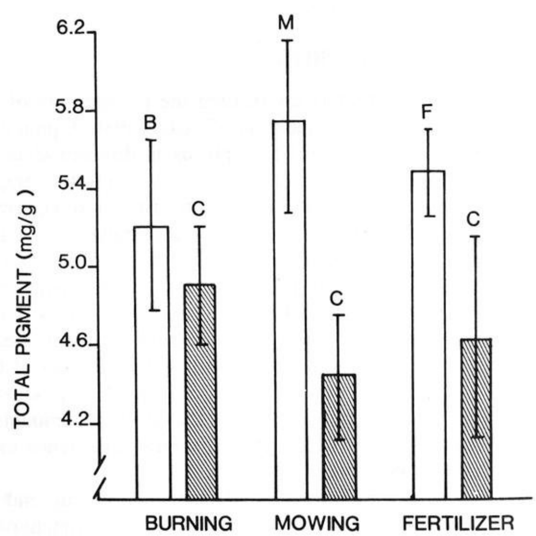


FIG. 4. Total pigment (chlorophyll A, chlorophyll B, and beta carotenes) of big bluestem foliage. Symbols are same as those used in Figure 1.

Plant biomass on the various plots was harvested on 15 July (Figure 5). Regrowth after mowing in late May on mowed plots was much greater on fertilized than on unfertilized plots. Overall, these midseason values show a strong mowing and fertilizer effect, and a non-significant effect of spring burning on plant biomass. Indices of plant greenness and plant vigor associated with this biomass are shown in Figures 6 and 7. When these values are compared with plant biomass (Figure 5), ''greenness'' appears to be more closely associated with nitrogen additions than with biomass. An analysis of variance of the reflectance-derived values indicated that all treatments except mowing and all two-way interactions among treatments were statistically significant. However, the amount of variance attributed to fertilizer was much more significant than any other variable or combination of treatments.

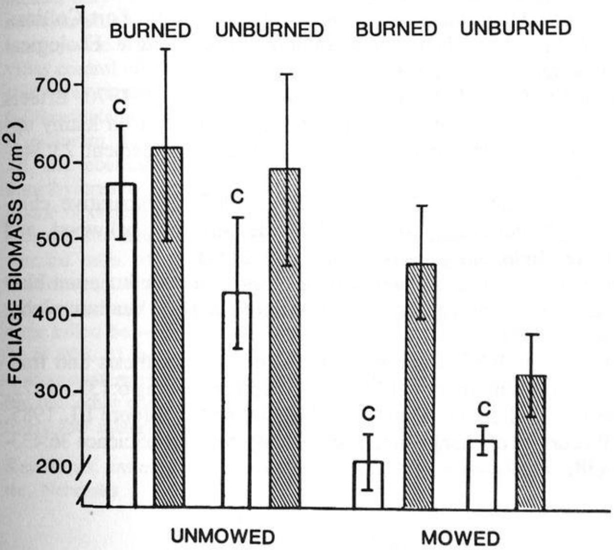


FIG. 5. Midseason foliage biomass on burned, mowed, and fertilized plots. Hatched bars represent the fertilized plots within each mowing and burning treatments.

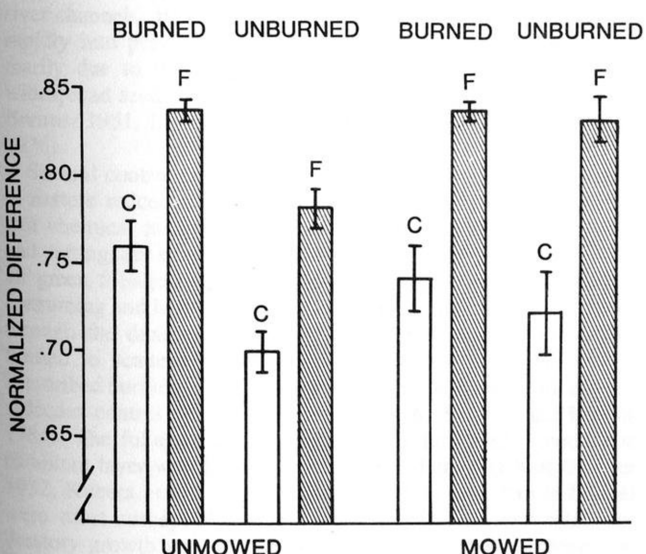


FIG. 6. Normalized difference, another index of plant vigor, for burned, mowed, and fertilized plots. Symbols are the same as those used in Figure 5.

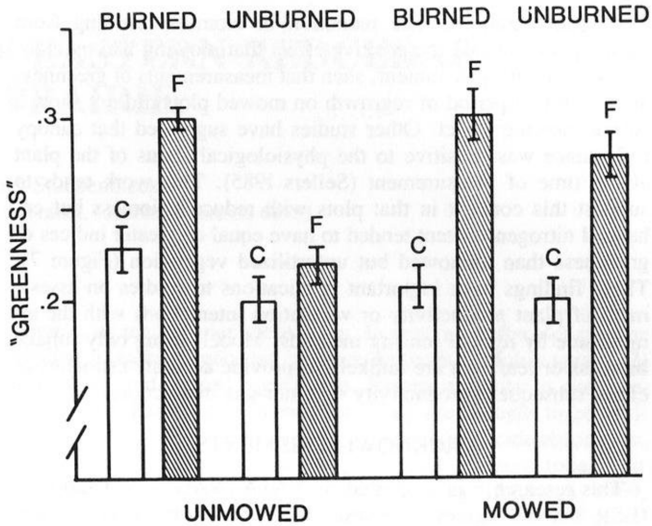


FIG. 7. ''Greenness'' in relation to burning, mowing, and fertilizer treatments. Controls (C), are compared to fertilized plots (F) within each mowing and burning treatment. Bars are one standard error for 8 replicates.

DISCUSSION

Midseason chlorophyll concentrations measured here for big bluestem are, on average, somewhat higher than values reported by other investigators (Bray 1960, Ovington and Lawrence 1967, Old 1969, Knapp and Gilliam 1985). These higher values reported in this study may reflect differences in methodologies rather than actual species differences or differences attributed to site effects. The age of the foliage at the time the chlorophyll measurements were made is important, although Ovington and Lawrence (1967) found little seasonal dynamics in concentrations of total chlorophyll in a Minnesota prairie.

Spring burning did not affect midseason chlorophyll or nitrogen concentrations. While the seasonality of nitrogen content of burned and unburned vegetation may differ markedly (Owensby *et al.* 1970), the overall amount of nitrogen available to vegetation on burned sites is not markedly different from unburned sites, and may in fact be less on burned sites (Ojima 1987). This implies that the increased productivity observed on burned sites in most years corresponds to increased nitrogen use efficiency by this vegetation.

Old (1969) measured the effects of nitrogen addition on midseason chlorophyll content and reported about a 20% increase in chlorophyll, a relative difference similar to that found in this study (Figure 3). This increase appears to be linearly related to the nitrogen content of this tissue. In contrast, phosphorus concentrations were not related to chlorophyll concentrations. While mowing increased chlorophyll, nitrogen, and phosphorus concentrations, addition of ammonium nitrate increased chlorophyll and nitrogen concentrations, but decreased phosphorus content. These data therefore suggest that big bluestem will accumulate phosphorus in concentrations higher than those limiting growth. Therefore, these plants exhibit luxury uptake of this element relative to nitrogen and/or other elements.

These results indicate that ''greenness'' as measured with the normalized difference procedure was sensitive to both burning and chlorophyll (nitrogen) content of the vegetation. The former treatment, which in this study did not significantly affect nitrogen concentrations, removed standing dead plant materials and litter and, thereby, changed the reflectance properties of the soil surface. Fertilization and mowing strongly affected nitrogen and chlorophyll concentrations. The reduction in biomass resulting from mowing may negate the positive effect that mowing had on chlorophyll and nitrogen content, such that measurements of greenness after a certain period of regrowth on mowed plots did not show a strong mowing effect. Other studies have suggested that canopy reflectance was sensitive to the physiological status of the plant at the time of measurement (Sellers 1985). This work tends to support this concept in that plots with reduced biomass but enhanced nitrogen content tended to have equal or greater indices of greenness than unmowed but unfertilized vegetation (Figure 7). These findings have important implications to studies on assessment of plant productivity or vegetation interactions with the atmosphere by remote sensing methods. Models using only foliage biomass or leaf area are unlikely to provide accurate estimates of either subsequent productivity or water-gas interactions.

ACKNOWLEDGEMENTS

This research was supported by NASA (NAG-5-897) and NSF (BSR-8514327) grants to Kansas State University. T. Dawn Shapley's current address is University of Kansas Medical Center, Kansas City, Kansas 66103.

LITERATURE CITED

Asrar, G., E.T. Kanemasu, G.P. Miller, and R.L. Weiser. 1986. Light B, Binterception and leaf area estimates from measurements of grass canopy reflectance. IEEE Transactions Geoscience and Remote Sensing 24:76-82.

Bray, J.R. 1960. The chlorophyll content of some native and managed plant communities in central Minnesota. American Journal Botany 38:313-333.

Goward, S.N., C.J. Tucker, and D.G. Dye. 1985. North American vegetation patterns observed with meteorological satellite data. Vegetatio 64:3-14.

Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69:46-58.

Kauth, R.J., and C.S. Thomas. 1976. The tassel cap - a graphic description of the spectral-temporal development of agricultural crops as seen by Landsat. Proceedings of the Symposium on Machine Processing of Remotely Sensed Data. Purdue University, West Lafayette, Indiana.

Knapp, A.K., and F.S. Gilliam. 1985. Response of *Andropogon gerardii* (Poaceae) to fire-induced high *vs.* low irradiance environments in tallgrass prairie: leaf structure and photosynthetic pigments. American Journal of Botany 72:1668-1671.

Knapp, A.K., and T.R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience 36:662-668.

Ojima, D.S. 1987. The short-term and long-term effects of burning on tallgrass ecosystem properties and dynamics. Doctor of Philosophy Dissertation, Colorado State University, Fort Collins.

Old, S.M. 1969. Plant production in an Illinois prairie. Ecological Monographs 39:353-383.

Owensby, C.E., R.M. Hyde, and K.L. Anderson. 1970. Effects of clipping and supplemental nitrogen and water on loamy upland bluestem range. Journal of Range Management 23:341-346.

Ovington, J.D., and D.B. Lawrence. 1967. Comparative chlorophyll and energy studies of prairie, savanna, oakwood, and maize field ecosystems. Ecology 48:515-522.

Robbelen, G. 1957. Untersuchungen an strahleninduzierten blattarbumutanten von *Arabidopsis thaliana* (L.) Verebungslehre 88:189-193.

Sellers, P.J. 1985. Canopy reflectance, photosynthesis and transpiration. International Journal of Remote Sensing 6:1335-1372.

Waring, R.H., J.D. Aber, J.M. Melillo, and B. Moore III. 1985. Precursors of change in terrestrial ecosystems. BioScience 36:433-438.

CHEMICAL CONTROL OF EASTERN REDCEDAR IN MIXED PRAIRIE

S. D. Smith and James Stubbendieck
Department of Agronomy, University of Nebraska, Lincoln, Nebraska 68583

Abstract. Stands of eastern redcedar (*Juniperus virginiana* L.) have been increasing in prairies, often to the detriment of valuable prairie species. Initial control of dense stands of relatively tall eastern redcedar by herbicides may be necessary to alter population demographics before more environmentally sound mechanical methods and prescribed burning can be employed to maintain acceptable populations of this woody species. Previous control effectiveness with herbicides has been highly variable. This study was conducted to determine the effect of hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione] as Velpar L, picloram (4-amino-3,5,6-trichlora-2-pyridinecarboxylic acid) as Tordon 2K, and tebuthiuron N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]N,N′-dimethylurea as Graslan brush bullets on eastern redcedar in the mixed prairie of central Nebraska. Each herbicide was soil applied at three rates, adjusted for tree height, spanning the manufacturers' range of recommended rates. Picloram and tebuthiuron were applied in October, and hexazinone was applied in May. Success of control was recorded after two growing seasons. Depending on application rate and tree height, hexazinone killed between 68 and 90%, picloram 70 to 94%, and tebuthiuron 71 to 90% of the trees. Although all herbicides preformed well in controlling eastern redcedar, picloram generally provided greater control than the two other chemicals. Picloram also achieved this control with a relatively low material cost.

Key Words. eastern redcedar, *Juniperus virginiana*, herbicides, mixed prairie, Nebraska

INTRODUCTION

Eastern redcedar (*Juniperus virginiana* L.) is a medium-sized conifer occurring in all states east of the Rocky Mountains. Historical records indicated that eastern redcedar was not common in Nebraska prior to European settlement (Miller 1902, Kellogg 1905, Harper 1912), growing only on a few protected ridges and along river channels. In more recent years, eastern redcedar has spread rapidly into previously unoccupied prairie. This increase is primarily due to the absence of naturally reoccurring fires and a widespread seed source from shelterbelt plantings (Beilmann and Brenner 1951, Bragg and Hulbert 1976, Van Haverbeke and Read 1976).

Several control techniques are available to limit the occurrence of eastern redcedar. These include mechanical, pyric, biological, and chemical methods. Mechanical methods, including digging and cutting, are effective since the trees will not resprout provided all green foliage is removed. However, these methods are time consuming and labor intensive, and access to individual tree trunks through the dense foliage is difficult. Thus, their usefulness is limited to scattered or extremely large trees (Owensby 1975). Prescribed burning can also be effective and economical for eastern redcedar control (Bragg and Hulbert 1976, Stritzke and Rollins 1984). The foliage burns readily, and the thin bark provides the cambium layer with little protection from damaging heat (Starker 1932, Kucera *et al.* 1963). Small trees (less than 2 m in height) were most susceptible to fire, since larger trees prevented understory growth and its associated fuel accumulation. Stevens *et al.* (1975) proposed biological methods, notably insects and fungi, as potential alternative controls for junipers. However, eastern redcedar has few natural enemies, reducing the potential for biological control (Williamson 1965).

Chemical control may be an alternative in those cases where the previous three methods are inappropriate due to location, economics, or management objectives. In general, herbicides may be applied to eastern redcedar by three methods: 1) foliar sprays, 2) injections, and 3) soil application. Eastern redcedar is quite resistant to foliar applied herbicides. They are thought to be inefficient due to foliar cuticle waxes preventing herbicide absorption, lack of translocation within the plant, and/or dense foliage arrangement preventing complete canopy wetting (Dalrymple 1969, Buehring *et al.* 1971, Owensby *et al.* 1973, Stritzke 1985). Control of eastern redcedar with herbicide injection into trunks is difficult, since access to the tree trunk thought the low, dense branches is difficult. Response to injection was highly variable, depending upon both the herbicide and the rate applied (Buehring *et al.* 1971)

Results from soil applied herbicides have also been variable (Scifres *et al.* 1981). Broadcast application onto soil is generally not desirable, since rates required to control eastern redcedar also damage non-target species (Hamilton and Scifres 1983). Direct application of the herbicide under individual trees was recommended to avoid this problem (Meyer 1982, Ueckert and Whisenant 1982), because few desirable prairie species grow under eastern redcedar trees. However, past research indicated considerable inconsistency in control success with this technique (Buehring *et al.* 1971, Owensby *et al.* 1973, Link *et al.* 1979, Crathorne *et al.* 1982). Therefore, more information is required to determine proper techniques for chemical control of this species. The objective of this study was to compare relative abilities of the herbicides hexazinone [3-cyclohexyl-6-(dimethylamino)-1-methyl-1,3,5-triazine-2,4(1H,3H)-dione] as Velpar L, picloram (4-amino-3,5,6-trichlora-2-pyridinecarboxylic acid) as Tordon 2K, and tebuthiuron N-[5-(1,1-dimethylethyl)-1,3,4-thiadiazol-2-yl]N,N′-dimethylurea to control eastern redcedar when applied a individual tree treatments.

METHODS AND MATERIALS

Experimental Site

The study site was located about 12 km west of Oconto, Custer County, Nebraska (Township 14 North, Range 23 West, Section 24). The location was on steeply dissected, upland hills with slopes ranging between 20 and 60%. Soils were a Uly-Coly [fine-silty, mixed mesic Typic Haplustoll and fine-silty, mixed (calcareous), mesic Typic Ustorthent, respectively] silt loam aggregate derived from loess parent material. Average precipitation at this location is about 530 mm. The native vegetation, following the descriptions of Weaver and Albertson (1956), was a mixed prairie consisting of western wheatgrass (*Agropyron smithii* Rydb.), big bluestem (*Andropogon gerardii* Vitman), sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], and little bluestem [*Schizachyrium scoparium* (Michx.) Nash]. The oldest eastern redcedar trees on the site were about 80 years in age. Aerial photographs taken since 1938 indicated a steady spread of eastern redcedar, with a particularly dramatic increase during the last three decades. The area now supports a dense eastern redcedar stand.

Experimental Procedure

The experimental design was a randomized complete block. Ten treatments, replicated twice, were created; three herbicides, each at three application rates (low, medium, and high), plus a control. These rates were selected to span each of the manufacturers' recommended ranges for this species. Plots were located on the slopes of two adjacent canyons, with canyon location considered to be a blocking criteria. Each block contained a complete set of randomly applied treatment/replication combinations. The plots were 8 m wide and extended from the bottom of the canyon to the top of the slope, a distance varying from 50 to 75 m in length. These canyon sides were oriented to a northeast aspect.

Within each plot, the particular herbicide/rate/replication treatment combination was applied to all trees. Chemicals were distributed on the ground evenly within the canopy outline. The hexazinone was applied at full concentration in a liquid form (Velpar L) via a metered "spot gun." Picloram and tebuthiuron were applied in dry formulations as Tordon 2K and Graslan brush bullets, respectively. To compensate for differences in herbicide effectiveness with varying three size, five height classes (< 0.25, 0.25-1, 1-2, 2-4, and > 4 m) were established. Treatments were adjusted accordingly for each height class (Table 1).

Table 1. Herbicide application rates for each eastern redcedar tree height category.

Herbicide	*Tree Height*	*Rate*		
		Low	*Medium*	*High*
		ml of commercial product per tree		
Hexazinone[1]	0 to 0.25 m	1	2	3
	0.25 to 1 m	1	2	3
	1 to 2 m	1	2	3
	2 to 4 m	8	12	16
	> 4 m	16	24	32
		g of commercial product per tree		
Picloram[2]	0 to 0.25 m	11	22	33
	0.25 to 1 m	22	44	66
	1 to 2 m	44	66	88
	2 to 4 m	66	88	110
	> 4 m	88	110	176
		number of brush bullets per tree		
Tebuthiuron[3]	0 to 0.25 m	1	2	3
	0.25 to 1 m	2	4	6
	1 to 2 m	4	6	8
	2 to 4 m	6	9	12
	> 4 m	9	12	15

[1]25% active ingredient in a liquid as Velpar L (E. I. Du Pont De Nemours and Company)
[2]2.3% active ingredient in pellets as Tordon 2K (The Dow Chemical Company)
[3]1.0 g active ingredient in brush bullets as Graslan (Eli Lilly and Company)

Picloram and tebuthiuron rates were supplied by the manufacturer on a height basis. However, the hexazinone manufacturer's suggested application rate was based on rates of 0.79 to 1.57 ml/cm stem diameter at breast height (DBH). To convert this to a tree height basis for use in this study, diameter and height measurements were taken for eastern redcedar of various sizes on the site. From this, a regression equation [$Y = 0.225 (X) + 2.15$] was developed, where Y = tree height in meters, and X = DBH in centimeters. The coefficient of determination equalled 0.94. Dosages were applied on a height basis according to this equation. Since trees less than 1.5 m have no DBH, application rates of 1 to 3 ml were used for all height classes equal to or less than 2 m. Applications of less than 1 ml were not possible, since that was the minimum application the hexazinone "spot gun" would deliver. Following manufacturers' recommendations, picloram and tebuthiuron were applied in the fall (28 and 29 October), and hexazinone was applied the following spring (15 May).

Each tree was subsequently examined for mortality through the following two growing seasons. A tree was considered dead if less than 25% of its foliage was rated as green by a visual estimate. During the second growing season following application, many new eastern redcedar seedlings in the < 0.25 m height class were observed. This height class was not included in data analyses, because it was impossible to visually separate treated seedlings from untreated seedlings. Results presented in this paper are from the final evaluation at the end of the second growing season following treatment.

A total of 6,601 trees > 0.25 m in height were treated with herbicides. Hexazinone was applied to 1,780, picloram was applied to 2,666, and tebuthiuron was applied to 2,155. Each plot (control and treated) contained an average of 180 trees, equalling a stand density of 3,600 trees/ha.

Categorical data analysis procedures were utilized, with observations for each tree recorded as either "alive" or "dead." Following the weighted least squares procedures of Grizzle *et al.* (1969) and Koch *et al.* (1977), log-linear models of the categorical data were created, using Chi-square statistics to test for differences among response (dead or alive) probabilities. This analysis, distinguishing between dependent and independent variables in a multilevel contingency table format, was analogous to the analysis of variance approach used for testing continuous data. Orthogonal single degree of freedom contrasts were constructed to test for linear and quadratic relationships between response and the three application rates within each herbicide. Although analyses were conducted utilizing the observed and expected values of the number of alive and dead, results were standardized to percentages for ease of presentation.

Control rates were combined with herbicide costs in an economic analysis of herbicide effectiveness. This analysis was based on raw material costs of $15.85 per l for hexazinone, $3.37 per kg for picloram, and $0.12 per g for tebuthiuron. Average percentage kill for each herbicide was used as a weighting factor to adjust material costs required to kill one tree. The 2-4 m tree height class was selected for these comparisons.

RESULTS

All herbicide by rate interactions were significant. Given the precision due to the number of observations, analysis was therefore conducted on individual herbicides.

Combining percentage kill over tree height and rate generated an overall response to each herbicide (Table 2). Hexazinone and tebuthiuron each killed 83% of all trees, while picloram killed 88%. Although herbicide rate was adjusted for tree height, treatment by tree height interactions still occurred. Therefore, analysis was conducted separately by height class. A comparison averaged over application rate gave and indication of how well treatments were adjusted to fit individual height classes (Table 2). Hexazinone at the low, medium, and high rates killed 80, 82, and 88% of the trees, respectively (Table 2). While this showed a trend towards increased kill with increasing rate, no linear or quadratic relationships were significant at a probability of a greater Chi-square = 0.05 level (Table 3). Picloram killed 88, 87, and 87% of all trees at the low, medium, and high application rates, respectively (Table 2). No significant relationships were detected (Table 3). Low rates of hexazinone and picloram were, therefore, just as effective as the high rate. Tebuthiuron killed 80, 86, and 82%, respectively, at the low, medium, and high rates (Table 2). This increase at the medium level was depicted by a quadratic response (Table 3). The linear response over rate was not significant. All three herbicides provided good control when tree height classes were combined. However, picloram consistently provided control levels that were higher than the other two chemicals. It was the most effective herbicide against eastern redcedar when tree heights were combined.

Table 2. Percentage of eastern redcedar trees killed by tree height and application rate of hexazinone, picloram, and tebuthiuron.

Herbicide	*Rate*	*Tree Height (m)*				
		0.25-1	*1-2*	*2-4*	*>4*	*Average*
		%				
Hexazinone	low	90	68	78	76	80
	medium	79	78	87	84	82
	high	85	83	88	82	85
	Average	85	81	82	82	83
Picloram	low	88	90	88	88	88
	medium	86	94	90	70	87
	high	86	89	89	83	87
	Average	86	91	89	80	88
Tebuthiuron	low	73	90	81	71	80
	medium	88	82	81	89	86
	high	77	82	84	84	82
	Average	77	85	82	81	83

Table 3. Probabilities of > Chi-square for linear and quadratic contrasts of percentages of eastern redcedar trees killed following application of hexazinone, picloram, or tebuthiuron.

Comparison	*Constrast*	*Probability > Chi-square*		
		Hexazinone	*Picloram*	*Tebuthiuron*
All tree heights	Linear	0.09	0.39	0.41
combined:	Quadratic	0.51	0.97	0.01
0.25 to 1 m	Linear	0.17	0.95	0.31
tree height:	Quadratic	0.01	0.42	0.01
1 to 2 m	Linear	0.90	0.45	0.02
tree height:	Quadratic	0.30	0.04	0.16
2 to 4 m	Linear	0.01	0.79	0.47
tree height:	Quadratic	0.39	0.88	0.65
Greater than	Linear	0.50	0.13	0.01
4 m tree height:	Quadratic	0.35	0.01	0.01

Table 2 also provides percentage kill for individual tree height classes within each herbicide/rate combination. Control among all herbicide/rate/tree height combinations ranged from 68 to 94%, with a majority of responses in the 80 to 90% range. Hexazinone applied to 0.25-1 m trees generated a negative quadratic response (Tables 2 and 3) across rate, with the medium rate providing the least control at 79%. No linear relationship was evident, with low and high rates providing statistically equivalent control at 90 and 85%, respectively. Trees treated with picloram responded equally across rate, with no significant linear or quadratic relationships (Table 3). Control from the three rates varied only between 86 and 88% (Table 2). The response rates for tebuthiuron followed a positive quadratic relationship, with the medium rate generating greater control at 88% than either the low or high rates at 73 and 77%, respectively (Tables 2 and 3). The low and high rates were statistically equivalent, with no linear relationship apparent. For this height class, low rates of either hexazinone or picloram resulted in the greatest control.

No linear or quadratic relationships occurred for hexazinone treated trees in the 1-2 m height class (Table 3), with all rates providing equivalent control between 78 and 83% (Table 2). Picloram generated a positive quadratic response, with the medium rate resulting in the greatest control at 94% (Tables 2 and 3). No linear response occurred for picloram, with the low and high rates providing equivalent control at 90 and 89% respectively. The lowest tebuthiuron application rate generated greater control (90%) than did the medium (82%) or high (82%) rates, evidenced by a significant linear contrast (Table 3). Over the three application rates used with this tree height class, picloram consistently killed more trees, the highest control of 94% was at its medium rate (Table 2).

Increasing the hexazinone application rate corresponded with a linear increase in control of the 2-4 m height category from 68% at the low rate to 88% at the high rate (Tables 2 and 3). No linear or quadratic relationships were found for either picloram or tebuthiuron (Table 3). However, picloram generated greater control at all application rates than did tebuthiuron. Eighty-eight to 90% of the trees treated with picloram died, while 81 to 84% were killed with tebuthiuron (Table 2).

Hexazinone and tebuthiuron acted alike in their ability to control eastern redcedar in the > 4 m height class (Table 2). Both showed a curvilinear response to increasing rate, with maximum control at the medium rate. The curvilinear trend, however, was not significant for hexazinone, which provided 78 to 84% control (Tables 2 and 3). Tebuthiuron had both significant linear and quadratic relationships between response and application rate, with control varying between 71 and 89% (Tables 2 and 3). Picloram generated a significant quadratic response across rate. This arose from an unexplained low level of kill (70%) at the medium application rate. However, the low rate of picloram did provide 88% control (Table 2). The medium rate of tebuthiuron (89%) was the only other combination providing control near that level.

Herbicide material costs, adjusted for each herbicide's effectiveness, varied widely. Using the 2-4 m tree height class, hexazinone cost from $0.16 to $0.29/tree, picloram cost $0.17 to $0.32/tree, and tebuthiuron cost $0.75 to $1.47/tree. The range of costs reflects low and high application rates, respectively. The hexazinone costs did not include the initial $80 expense for the spot gun applicator.

DISCUSSION AND CONCLUSIONS

Although this study utilized a dense eastern redcedar stand for experimental purposes, these herbicides would also be suited to individual tree treatment of scattered individuals. Application of the dry formulations (picloram and tebuthiuron) was particularly easy, requiring little preparation or calibration for delivery. Directed application to the understory soil minimized the negative effect to non-target species that is often associated with herbicide use.

Hexazinone, picloram, and tebuthiuron all performed well in controlling eastern redcedar when applied to the soil under individual trees. Control levels were commonly greater than 80%. Whether viewed over all tree height classes or within individual height classes, picloram generally provided higher percentage kills than the two other chemicals. Overall, picloram killed 86% of the trees, while hexazinone and tebuthiuron each killed an average of 83%. In addition to providing a higher control level, picloram achieved this with a relatively low material cost of $0.17 to $0.32/tree for individuals in the 2 to 4 m height class. Hexazinone was slightly less expensive ($0.16 to $0.29), but did require an initial expense for the spot gun applicator. Comparative costs for tebuthiuron ranged from $0.75 to $1.47/ tree.

Increasing the application rate for picloram did not always result in greater control. Commonly, lower rates were just as effective as higher rates, indicating that the chemical was already producing its maximum effectiveness at the lower rate. This pattern was generally consistent throughout the four height classes. Further investigation of reduced rates of this chemical may result in eastern redcedar control at lower material costs.

Tebuthiuron showed a greater overall kill at the medium rate than either the low or high rates. This overall response was influenced by results occurring in the shortest (0.25-1 m) and the tallest (> 4 m) height classes. The reason for this pattern is unclear, although similar performance decreases with increasing herbicide rate on juniper species have been reported for picloram (Buehring *et al.* 1971) and tebuthiuron (Ueckert and Whisenant 1982).

Larger hexazinone application rates resulted in increases in overall percentage kill. However, this increase was not significant. Hexazinone appeared to be providing near maximum effectiveness at the lower application rate.

The inconsistent performances generated by some of the herbicide/rate combinations (e.g. increased herbicide rates did not always result in increased kill) over the tree height classes may have been due to unequal ranges of actual tree sizes within a particular height class. This would be particularly evident in the > 4 m class, where a particular treatment combination exhibiting reduced performance may have been applied to a greater number of trees much exceeding the 4 m minimum.

Yearly environmental variability will probably change the magnitude, but not the relative ranking, of these treatments. No environment by herbicide interaction would be expected within the scope of inference of this study, since all herbicides are soil applied during the preceding dormant season.

This research indicated that follow up treatments will be necessary if control levels greater than about 85% are desired. In addition, a large influx of seedlings was noticed within the treated areas during the second growing season following treatment. The seedling source was probably from a soil seed bank provided by the eastern redcedar over story. Visual observation showed no corresponding increase outside the treated areas, leading to the conclusion that removal of the over story may have been the causative factor. Therefore, use of herbicides will only be the first step in controlling eastern redcedar in prairies. Other control methods, such as periodic prescribed burning, will be necessary to maintain acceptable populations of eastern redcedar.

ACKNOWLEDGEMENTS

The authors wish to express their gratitude to Clifford Ward for providing the research site. Field help was provided by Susie Oldfather, Eric Kocher, Abderrahim Arif, Dick Gebhardt, and Toloumbaye Tadingar. Herbicides were provided by Eli Lilly and Company, E. I. Du Pont De Nemours and Company, and The Dow Chemical Company. This article was assigned Journal Series Number 8311, Agricultural Research Division, University of Nebraska. Dr. Smith's current address is P.O. Box 7206, Olympia, Washington 98507.

LITERATURE CITED

Bielmann, A.P., and L.G. Brenner. 1951. The resent intrusion of forests in the Ozarks. Annuals of the Missouri Botanical Garden 38:261-282.

Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19-24.

Buehring, N., P.W. Santelmann, and H.M. Elwell. 1971. Responses of eastern red cedar to control procedures. Journal of Range Management 24:378-382.

Crathorne, G.L., W.T. Scott, and P.M. Ritty. 1982. Eastern red cedar control in Kansas. Down to Earth 38:1-6.

Dalrymple, R.L. 1969. Cedar control in southern Oklahoma. Proceedings of the Southern Weed Science Society 22:272-273.

Grizzle, J.E., C.F. Starmer, and G.G. Koch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Hamilton, W.T., and C.J. Scifres. 1983. Buffelgrass (*Cenchrus ciliaris*) responses to tebuthiuron. Weed Science 31:634-638.

Harper, R.M. 1912. The diverse habitats of the eastern red cedar and their interpretation. Torreya 12:145-154.

Kellogg, R.S. 1905. Forest belts of western Kansas and Nebraska. U. S. Department of Agriculture, Forest Service Bulletin Number 66.

Koch, G.G., J.R. Landis, J.L. Freeman, D.H. Freeman, and R.G. Lehnen. 1977. A general methodology for the analysis of experiments with repeated measurement of categorical data. Biometrics 33:133-158.

Kucera, C.L., J. H. Ehrenreich, and C. Brown. 1963. Some effects of fire on tree species in Missouri prairie. Iowa State Journal of Science 38:179-185.

Link, M.L., W.E. Chappel, P.L. Hipkins, and J.G. Coartney. 1979. Control of eastern redcedar. Proceedings of the Southern Weed Science Society 32:238-240.

Meyer, R.E. 1982. Brush response to spacing and individual-plant herbicide treatments. Weed Science 30:378-384.

Miller, L.C. 1902. The red cedar in Nebraska. Forestry and Irrigation 8:282-285.

Owensby, C.E. 1975. Controlling eastern redcedar. Kansas State University Cooperative Extension Service Publication L-457.

Owensby, C.E., K.R. Blan, B.J. Eaton, and O.G. Russ. 1973. Evaluation of eastern redcedar infestations in the northern Kansas Flint Hills. Journal of Range Management 26:256-260.

Scifres, C.J., J.W. Stuth, and R.W. Bovey. 1981. Control of oaks and associated woody species on rangeland with tebuthiuron. Weed Science 29:270-275.

Starker, T.J. 1932. Fire resistance of trees on the northeast United States. Forest Worker 3:8-9.

Stevens, R.C., B.C. Giunta, and A.P. Plummer. 1975. Some aspects in the biological control of juniper and pinyon. Pages 77-81. *In* The pinyon-juniper ecosystem: A symposium. Utah State University, Logan.

Stritzke, J.F. 1985. Chemical and mechanical control of eastern redcedar. Pages 61-69. *In* D.M. Engle and R.F. Wittwer (eds.). Eastern redcedar in Oklahoma. Oklahoma State University Cooperative Extension Service Publication E-849.

Stritzke, J.F., and D. Rollins. 1984. Eastern redcedar and its control. Weeds Today 15:7-8.

Ueckert, D.N., and S.G. Whisenant. 1982. Individual plant treatments for controlling juniper seedlings. Journal of Range Management 35:419-423.

Van Haverbeke, D.F., and R.A. Read. 1976. Genetics of eastern redcedar. U. S. Department of Agriculture Forest Service Research Paper WO-32.

Weaver. J.E., and F.W. Albertson. 1956. Grasslands of the Great Plains. Johnsen Publishing Company, Lincoln, Nebraska.

Williamson, M.J. 1965. *Juniperus* (junipers). Pages 211-216. *In* Silvics of forest trees of the United States. U. S. Department of Agriculture Forest Service Agricultural Handbook Number 271.

EFFECT OF TWO CUTTING TREATMENTS ON ASPEN IN PRAIRIE

Virginia M. Kline
University of Wisconsin Arboretum, 1207 Seminole Highway, Madison, Wisconsin 53711

Abstract. Two cutting treatments were tested for aspen control in two southern Wisconsin prairies: Pasque Flower Hill (PFH), a steep hillside remnant, and Greene Prairie (GP), a restored prairie on sandy soil. The treatments, applied 25-26 June 1984, were: (1) A single cut at the base of the stem and (2) A cut that removed about one-third of the stem, followed 20-24 hours later by a basal cut. In 1986, both sites were burned in early spring, the usual management procedure for these prairies. At GP, aspen stem densities at the end of the experiment were similar in the control and both cut plots and were about 145% higher than at the start. Density increases at PFH were 171% in the plot cut once and 188% in the plot cut twice. In the PFH control plot, stem density at the end was 85% that at the start, but the stems had grown large enough to prevent top kill by the prescribed burn and to shade the prairie species. It was concluded that cutting aspen in June is not worthwhile in prairies managed with dormant season prescribed burns, except to remove any stems not top killed by the burns.

Key Words. aspen, *Populus tremuloides*, control, management, sucker, Wisconsin

INTRODUCTION

Trembling aspen (*Populus tremuloides*) is a troublesome invader of prairies in the tallgrass prairie region. Dormant season (spring or fall) burning, the usual management procedure to maintain prairies in this region, top kills aspen but stimulates root suckering. Suckering is favored by a high cytokinin/auxin ratio; top killing reduces auxin production because auxins are produced in the leaves, while the levels of cytokinins, produced in the roots, are increased because of increased soil temperature after the burn (Svedarsky *et al.* 1986).

Observations after a trial burn 23 June 1972, in an aspen-infested portion of a restored tallgrass prairie in the Arboretum, suggested that summer burning produces fewer suckers. Suppression of the aspen in the area burned in June was still apparent ten years later after several routine early spring burns. However, June burns produce thick smoke that is troublesome to burn crews, and it is sometimes difficult to obtain a burn permit at that time of year because of fire hazard.

Cutting aspen in June is a possible alternative to burning. In this experiment two June cutting techniques tested were: (1) each aspen shoot was cut off at the base and (2) about one-third of each shoot was cut off first and the remainder cut off at the base 20 hours later, a technique found by Stoeckeler (1947) to inhibit resprouting in aspen.

STUDY SITES

Two prairie sites having extensive aspen clones were selected. The first, Pasque Flower Hill (PFH), is a small, dry, natural prairie with dolomite close to the surface. Dominant grasses are little bluestem (*Andropogon scoparius* Michx.), prairie dropseed (*Sporobolus heterolepis* A. Gray), needle grass (*Stipa spartea* Trin.), and several small species of panic grass (*Panicum* L.). It had last been burned in 1981. The second, Greene Prairie (GP), is a 45-year-old restored prairie planted on sandy level soil. Dominant grasses include little bluestem, big bluestem (*Andropogon gerardii* Vitman), and prairie dropseed. It had last been burned in 1983.

METHODS

At each site three contiguous plots (7 x 12 m) plots were delineated in an area of dense aspen shoots. Three treatments were randomly dispersed: control (no cutting), cut once (1x), and cut twice (2x). The cutting was done on June 24 and 25, 1984. All plots were burned in early spring 1986.

Data were recorded in 1984, before treatment, and in 1985 and 1986 at the end of the growing season. Fifteen quadrats, each 0.5m², were located in each plot, using a stratified random technique. The number of stems in each of two size classes, height <1 m and >1 m, was recorded for each quadrat.

RESULTS

In Greene Prairie, aspen densities at the end of the experiment were similar for the three treatments (Table 1), and were approximately 145% higher than at the start (Table 2). At Pasque Flower Hill, the final density of the control was substantially lower than that of the two cut plots (Table 1). This was the only plot in the experiment in which density decreased. Density of stems in the cut plots increased more in PFH than in GP (Table 2).

Table 1. *Populus tremuloides* stems per 0.5 m².

	PFH			GP		
Treatment	*1984*	*1985*	*1986*	*1984*	*1985*	*1986*
Control	9.1	4.1	7.8	8.9	6.5	12.7
Cut 1x	8.9	14.6	15.3	9.3	12.9	13.6
Cut 2x	6.9	7.9	12.9	9.4	10.5	13.7

Table 2. Density of stems of *Populus tremuloides* in 1986 as percent of density of stems in 1984, by size class.

	Total		*Ht.* > 1 m	
Treatment	PFH	GP	PFH	GP
	%			
Control	85	143	33	78
Cut 1x	171	147	32	84
Cut 2x	188	146	30	74

Density of tall stems decreased in all plots, but especially in those at PFH where there were only 30-33% as many tall stems at the end of the experiment as at the start (Table 2). At both sites, fewer sprouts were produced the first year after cutting (1985 data, Table 1) in the plots cut twice than in those cut once; the difference was greatest at PFH. After the 1986 burn, no difference occurred between the two cutting treatments at GP, but a small difference persisted at PFH.

DISCUSSION

At GP clearly no advantage was gained by the extra labor of cutting. The 1986 burn was a clean burn that top killed all aspen stems in all three plots. This was also true of prescribed burns in 1987 and 1988.

The decrease in density of aspen in the PFH control was associated with an increase in the size of a few of the large stems. By 1986, 5 years after the last burn, some of these large stems were producing enough shade to discourage growth of grasses; fuel was insufficient to sustain a hot fire, and the larger stems were not set back by the fire that year. The 1987 and 1988 prescribed burns also failed to top kill the larger aspen, which were 2-3 cm dbh. Other woody species including black cherry (*Prunus serotina* Ehrh.) were coming into the plot, and prairie species were declining. In contrast, both the cut plots had sufficient fuel to carry the fire in all three burns.

Both the early spring burn and the single cut tended to produce densities of 25-30 stems/m², 250,000-300,000 per hectare, on both sites while the double cut resulted in densities of 16-21 stems/m². It is possible that double cutting 2 or 3 consecutive years would result in densities low enough that the difference between cut and uncut areas would persist after the next early spring burn. Densities after both treatments were ten times those reported by Svedarsky *et al.* (1986) and Buckman and Blankenship (1965).

In terms of practical management it appears that if dormant season burns can be applied frequently enough to obtain a top kill each time, there is no advantage to supplementing the burns with cutting. However, it is important after each burn to cut any stems that are not top killed. In that situation, or where burning is not appropriate, cutting is an alternative for aspen control. Double cutting may cause less suckering than single cutting.

ACKNOWLEDGEMENTS

The help of Carol Reott and Marion Dunn in collecting field data was greatly appreciated. Grant Cottam and Evelyn Howell read the manuscript and made helpful suggestions.

LITERATURE CITED

Buckman, R.E., and L.H. Blankenship. 1965. Repeated spring burning reduces abundance and vigor of aspen root suckering. Journal of Forestry 63:23-25.

Stoeckeler, J.H. 1947. When is plantation release most effective? Journal of Forestry 45:265-271.

Svedarsky, W.D., P.E.Buckley and T.A.Feiro. 1986. The effect of 13 years of annual burning on an aspen-prairie ecotone in northwestern Minnesota. Pages 118-122. *In* G.K. Clambey and R.H. Pemble (eds.). Proceedings of the Ninth North American Prairie Conference, Tri-College University, Moorhead, Minnesota.

IMPACT OF RAILROAD MANAGEMENT AND ABANDONMENT ON PRAIRIE RELICTS

John A. Harrington and Mark Leach
Department of Landscape Architecture, 25 Agriculture Hall, University of Wisconsin, Madison, Wisconsin 53706

Abstract. A field survey was begun in 1986 to determine the status of prairie vegetation on railroad rights-of-way in Wisconsin. Two % of 849 sample points located at 1.6 km intervals along railroads were found to contain relatively high quality prairie, and 23 % contained slightly degraded prairie. A significant proportion of these remnants contained mesic prairie, a community type which today is almost non-existent in Wisconsin and neighboring states. The linearity and fragmented state of these remnants, however, increase their susceptibility to invasion by woodland edge species. The lack of management that accompanies railroad abandonment has dramatically affected the ability of these prairie remnants to sustain themselves. This paper discusses the impact railroads have had on prairie remnants by examining 1) construction and abandonment trends, 2) the management history of railroad rights-of-way based on survey observations and interviews with maintenance personnel, and 3) the importance of the management techniques utilized through the 1950s in the preservation of prairie remnants.

Key Words. railroad, abandonment, prairie relicts, prairie remnants, rights-of-way, management, Wisconsin

INTRODUCTION

Remnants within railroad rights-of-way (ROW) have been found in all states that are recognized as containing portions of the original tallgrass prairie. These remnants tend to occur in patches and may extend for a few hundred meters or several kilometers, often to end abruptly in exotic grasses or trees and shrubs. While conducting a survey to determine the extent and quality of prairies still remaining along ROW, the authors became curious as to the effects that the construction and management of railroads must have had on the continuing existence of prairies that bordered them. This seemed particularly important because of the scarcity of remnants found along railroads and the potential for their loss as railroad companies halt management and abandon lines.

In the past 30 years, railroad companies increasingly abandoned lines that were no longer economically efficient. Management of vegetation ceases in railroad ROW with abandonment. Management generally maintained open community habitats, and as management ends, the invasion of canopy species often begins immediately. The extent to which vegetation management by railroad companies aids or impairs the stability of open grassland communities is important in understanding the effect high rates of abandonment may have on prairie remnants. The extent to which abandonment of lines and their management impact on desired native vegetation in ROW is of immediate concern if such remnants are to be preserved and acquired for conservation.

This paper will review survey results of the status of railroad prairies located in southern Wisconsin and then examine the methods used in the construction and management of railroads and adjacent ROW in the survey area. The paper will also review abandonment history and conclude by discussing the impacts that management and abandonment have had on these prairie relicts.

METHODS

A field survey was initiated in 1986 to determine the status of prairie vegetation in ROW of Wisconsin. About 2,100 km of ROW were surveyed that were built prior to 1901 and occurred within the prairie regions south of the tension zone of Wisconsin as delineated by Finley (1976) (Figure 1). Sampling points were located every 1.6 km along both abandoned and active railroad lines. A distance of 0.4 km was covered in each direction, and notes were taken on the vegetation type. If prairie was found, several walk-throughs were conducted to note the species and their relative abundance.

FIG. 1. Wisconsin presettlement vegetation map of both prairie and savanna combined occurring south of the tension zone. Stippled areas equal areas either in prairie or savanna. Adapted from Finley (1976).

Construction, management, and abandonment histories were investigated by reviewing historical records and government documents and through interviews conducted with former and current railroad personnel. Literature was of limited value as it did not address specific management techniques for an area. Early records by many of the railroad companies no longer exist or are scattered throughout cities of the Midwest. Railroad personnel generally did not seem to know of specific record locations. The majority of information discussed in this paper has been gathered from the interviews which have been corroborated by other individuals or writings.

RESULTS

Survey of Southern Wisconsin Railroads

A number of articles have discussed the importance of preserving railroad prairie remnants (Reed and Schwarzmeier 1978, Borowske and Heitlinger 1980, White 1986). This survey of Wisconsin railroad ROW suggests that another major reason for preservation is the ability of remnants to represent prairie communities and species no longer found elsewhere in the landscape.

Approximately 1,600 km of railroads were surveyed during the summers of 1986 and 1987. Each sampling point in the survey was placed into a category based on the number of grass and forb species it contained, the percentage of native species found, and the length of the area. Using the criteria outlined in Table 1, 2% of the 849 stops were categorized as a class 1, 7.5% as class 2, 15.5% as class 3, and 75% as class 4.

Table 1. Site category definitions of prairie remnant survey.

Site categories	*Definition*	*Proportion of total remnants*
		------------%------------
1	3 grass species >15 forb species >75% vegetative cover >0.4 km	2.0
3	grass species 10-15 forb species 50-75% vegetative cover 0.2-0.4 km	7.5
3	2 grass species 5-10 forb species 25-50% vegetative cover 60-220 m	15.5
4	1 grass species <5 forb species <25% vegetative cover <60 m	75.0

Although all types of prairie communities were found in the ROW mesic prairie dominated the class categories; 69%, 55%, and 65% for class 1, 2, and 3, respectively. This high abundance of mesic prairies is unique, because they are quite rare due to their high agricultural productivity.

Railroad Construction

Railroad construction began in Wisconsin between 1840 and 1850. By 1860, 1,341 km of track had been laid (Wisconsin Transportation Planning Program 1983). After the Civil War, with substantial land grant offerings available, the length of Wisconsin track increased 89% to a peak of 12,098 km in 1921. During this time, a three-fold increase in farms occurred, which were dependent on cities growing in tandem with the railroads.

In southern Wisconsin much of the land adjacent to railroad lines was in prairie until the late 1800s. These remnants were preserved through railroad ownership which isolated the ROW from agricultural use and development. By 1900 much of the land in southern Wisconsin was involved in cultivated agriculture, severely limiting the number of prairie sites available to reinvade disturbed railroad sites.

The amount of surface disturbance created over the 12 to 31 m wide ROW varied depending on construction needs. Early construction was kept to the actual rail bed. As technologies and the financial status of the railroads improved, road beds were raised creating damage to plant communities through direct disturbance of the soil and through the altering of the drainage pattern. Scattered damage to soils and vegetation occurred outside of the immediate construction zone with the erection of housing for equipment and personnel. Before 1900 rapid revegetation of ROW occurred wherever the adjacent land cover was still in prairie (Vestal 1918). However, it is likely that those plants which recolonized the sites, often from seeds and rootstocks, were a select group and did not represent the total original site vegetation. These field observations support Thomson's (1940) suggestions that trains, which travelled these lines, also transported and dropped native and exotic seeds along the tracks through the freighting of marsh hay. This dispersal of seed would further alter the prairie composition found along the tracks.

Management History

Management objectives.

Management objectives for the railroads were 1) to maintain open sight lines, 2) to remove physical obstacles, and 3) to reduce friction on track rails caused by adjacent grasses and herbs leaning onto the rails. The removal of tall material close to the rails, including the tall prairie grasses, was important so the trains could move smoothly over the tracks.

Management treatments.

Railroads utilized four main management treatments, each of which had a significant impact on the number and quality of prairie remnants still in existence. The four management treatments used were steaming, cutting, burning, and treating vegetation with herbicide.

Vegetation management between the late 1800s and the 1950s was labor intensive. It consisted largely of hand cutting, but a number of companies also used steam directed from locomotives onto the tracks to remove encroaching plants. Cutting often occurred from fence row to fence row with particular emphasis on vegetation growing close to the tracks. From the early 1900s to the 1960s major Wisconsin railroad lines, such as Chicago North Western (CNW), employed five to six road masters, or maintenance personnel, for each 8 to 16 km section of line. It was during this time that Shimek (1931) and others reported finding high quality tracts of prairie along 30- to 60-year-old railroads.

After World War II as people began to build on and cultivate open lands, state and local governments pressured companies to control accidental fires (Lanz 1985). Vegetation control as a means to eliminate wildfire became a fourth goal of maintenance. The railroads continued the practice of intensive brush control by annual cutting and controlled burns through the 1950s. Both manual cutting of brush and burning were typically done from fence line to fence line. Later as brushing machines became prevalent, maintenance was restricted to 3 m or less on either side of the track.

Brush was typically cut in winter and left where it had fallen until it was burned along with the vegetation in the right-of-way the following year. Prescribed burns typically occurred in the fall, as spring and summer were reserved for track maintenance and reconstruction.

As the intensity of management began to drop due to rising labor costs and declining revenues during the 1950s and 1960s, aromatic oils became the predominant treatment for ROW vegetation. After 1960 sprays were targeted for the center of the track, approximately 2 m on either side, and 1.5 m above the ground. The 12 m remaining on either side of the road were then mowed. From 1960 to 1968 intense brush killers, such as prometon [2,4-bis(isopropylamino)-6-methoxy-*s*-triazine], were used with observations that such treatments readily killed large trees and shrubs but did not eliminate sprouting. Soil sterilants were used by some companies within 100 m of bridge and road crossings.

A fifth technique was used by some lines for controlling vegetation along tracks. Two meter swaths were plowed or disked on either side of the tracks.

Current management varies among lines. Many lines use herbicide treatments on brush only at intersections and bridges, conducting mechanical maintenance along the line only when needed. Other lines use herbicides along the entire track length and still others disk along each side of the track. Management is typically greatest on the major freight lines. In contrast, the major short line operator in Wisconsin remarked that brush maintenance was at least five years behind schedule.

Interviews with former road masters yielded information, still relevant today, on remnant stability in geographic regions. For example, according to one interviewee, brush was not a problem along major lines west of Montfort in southwestern Wisconsin. The land remained open with little management. This area presently contains drier prairie sites and sandy sites. Although limited both in number, several lengthy and relatively high quality remnants occur along this track. In the Madison area, along the same track, brush was said to be aggressive, requiring frequent removal. This is still true today and has been a major problem in preserving remnants in this area.

Wildfires

In addition to prescribed management, many ROW burned by accident. In 1929, 11% of wildfires in Wisconsin were caused by trains (Wisconsin State Conservation Department 1946-1966). This figure rose to 16% in 1936 and continued to rise into the 1960s when railroads caused between 30 and 40 of all wildfires (Wisconsin State Conservation Department 1946-1966) (Figure 2). Railroads went from being the fourth or fifth cause of wildfires to the number one cause during the 1960s and 1970s (Figure 3). Fires in nonforested areas typically comprised 60 % or more of wildfires in the state each year. Grass was the initial starting fuel for more than 80% of these fires (Wisconsin State Conservation Department 1946-1966, Wisconsin Department of Natural Resources 1967-1987).

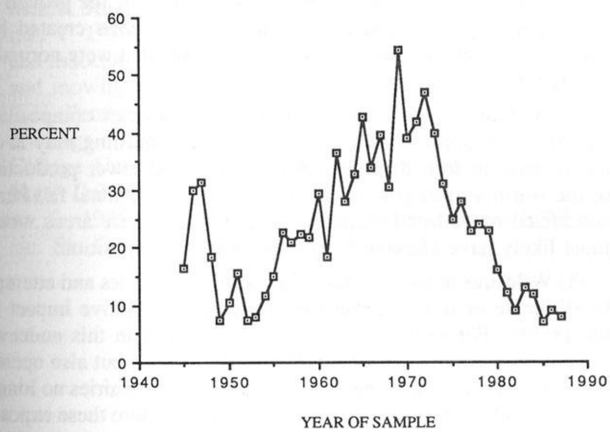


FIG. 2. Percent of Wisconsin wildfires caused by railroads for the years 1945 to 1987.

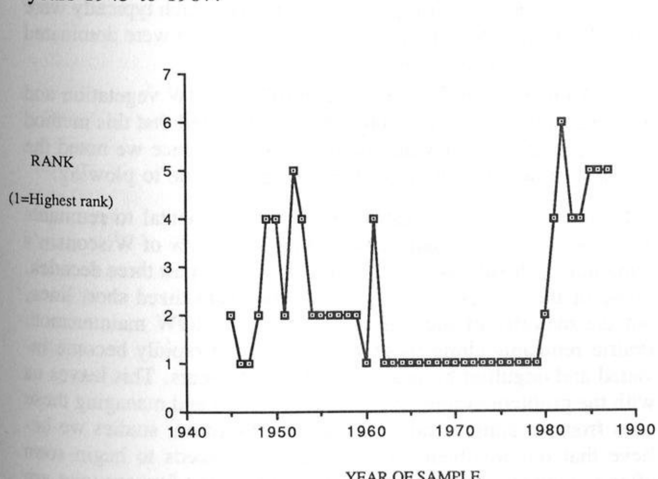


FIG. 3. Ranking of railroads as a cause of all wildfires in Wisconsin for the years 1945 to 1987.

A daily fire log, found during the vacating of a depot in Eau Claire, Wisconsin, contained fire records from 1915 to 1958 for four CNW lines. The recordings in the log indicate that many sections along lines may have burned at least once every two years. In addition to providing dates, locations, and causes of fires, the daily fire log provided the acreage that burned and the type of fuel existing at the burn location. Our searches for additional logs have not been successful.

Prescribed burning of ROW seldom resulted in wildfires. In 1946 three out of 470 fires were started during prescribed burns, and 463 fires were started from train exhaust and movement (Wisconsin State Conservation Department 1947). The trend of over 90% of the railroad-related wildfires starting from train movement and exhaust has remained constant. Causes of railroad-related wildfires were typically linked to poorly maintained wheels and exhaust systems. During the mid-1950s railroad companies began to switch from steam locomotives to diesel. It was assumed by most fire prevention officials that this switch would result in fewer fires. However, in 1955 railroad-caused fires rose 3.4% with 61.9% of the fires originating from the ejection of burning carbon deposits released by diesel engines (Wisconsin State Conservation Department 1956). A major cause of fire came from one type of diesel engine that vented the crankcase down onto the tracks. It was not uncommon to have 150 ignitions of ROW vegetation by such engines in a single day.

In 1958 the Annual Wisconsin Forest Fire Report noted that the curtailment of the number of ROW maintenance crews and an increase in the distances assigned to each crew had affected fire prevention efforts of eliminating natural fuels. Recommendations of the 1960 Railroad Fire Conference sponsored by the Michigan Department of Conservation were for companies to fireproof their ROW and to cut down on the fire-causing characteristics of diesel locomotives. The railroad fire prevention inspector stated that the present methods of prescribed burns were slow, unsatisfactory, and expensive; because of this ROW burning has nearly been abandoned (Wisconsin State Conservation Department 1962). The State of Wisconsin, however, began a few years later to pressure railroad companies to conduct prescribed burns. In the majority of its fire reports the Wisconsin State Conservation Department and later the Department of Natural Resources cited a need for properly cleaned and burned ROW. Few companies gave in to this pressure but some did apply greater use of herbicides and brush cutting on troublesome lines. The type and degree of management varied greatly among the companies.

In response to high rates of escaped wildfires, the Milwaukee Road in 1974 disked its ROW in Monroe, Juneau, and Columbia counties, all areas where prairie remnants would have been expected to be found (Wisconsin Department of Natural Resources 1975). Annual state fire reports encouraged disking elsewhere. In 1977 new forest fire laws required that fire-prone ROW be burned and cleared of debris at least once each year (Wisconsin Department of Natural Resources 1978). In 1981 as railroad fires began to decline, due to improvements in engine design, a special committee recommended that coordination of ROW management begin with the State Scientific Areas Director to deal with remnant prairie populations (Wisconsin Department of Natural Resources 1982).

Abandonment

Abandonments began almost immediately after the start of railroad construction but have become increasingly more frequent since 1934. Between 1920 and 1982 Wisconsin railroad mileage declined by 37% (Wisconsin Transportation Planning Project 1983). Thirty percent or more of this decline occurred in the last two decades of this period.

Until the 1970s the majority of abandoned lines were returned to adjacent land owners. These were quickly cultivated and used to increase or connect agricultural lands. Over the last two decades, however, federal and state laws have given first option of purchase to the state (East Central Wisconsin Regional Planning Commission 1978, Wisconsin Transportation Planning Project 1983). In

Wisconsin state options to acquire these lands are first considered by the Department of Transportation and then considered by other state agencies including the Department of Natural Resources. Wisconsin has converted approximately 720 km of track to biking and pedestrian trails, which includes several large stretches of prairies of various quality.

Cessation of Management

The time length of the abandonment process may have a tremendous impact on the vegetative condition of a prairie remnant. Ten years or more may pass from the time a company begins to contemplate abandonment to the time abandonment actually occurs. The legal abandonment process typically takes three years or more to occur. However, most rail companies after determining that a line is no longer economically productive will halt the majority of maintenance activities well in advance of the actual abandonment. During this time significant encroachment of shrubs or weedy species can occur.

The results of an abrupt halt in management are readily apparent on remnants along many lines. The Sugar River State Trail between New Glarus and Brodhead follows a rail line built in 1887 and abandoned in 1972. Along the line are considerable tracts of class 1 to class 3 prairies. Invading into a section of good prairie is a stand of black oak (*Quercus velutina* Lam.). The ages of these trees, which range between 22 and 25 years, would suggest that maintenance of this line was discontinued before 1965. The last major industry along the line ended operations in 1962. Freight earnings for the rail line dropped by $300,000 the next year. Due to this loss of revenue the rail line began preparing for abandonment in the early 1960s, although abandonment was not granted until 1972 (Lanz 1985).

Other lines show similar histories. In 1981 the Military Ridge route between Madison and Dodgeville was abandoned, however, according to maintenance personnel all management along this line had ended by 1974. A railroad line near Cambria, Wisconsin has proposed abandonment for the past decade. In 1979 the prairies along this line were rated fair to excellent by personnel of the Department of Natural Resources. Their report also notes concern for potential invasion by black locust (*Robinia pseudoacacia* L.) and grey dogwood [*Cornus foemina* subsp. *racemosa* (Lam.) J.S. Wils.]. A 1986 visit to the semi-active site found remnants in poor condition being replaced by solid stands of black locust saplings and grey dogwood.

SUMMARY AND DISCUSSION

In recent years the value of prairie remnants along railroad tracks has come into question. In view of the costs and logistics involved in acquiring and maintaining these remnants relative to the purchase of additional land of more pristine stands, one must ask if they are worth saving. Part of this concern may be linked to views on the inability of highly fragmented habitats to sustain themselves. How well the theories of island biogeography and fragmented habitats apply to the plant species in small prairie remnants has not been determined (Noss 1983 and 1987, Simberloff and Gottelli 1984, Wilcove 1987). Many small prairie remnants with a relatively high diversity of prairie forbs and grasses still exist while other nearby remnants are highly degraded.

Prairie remnants east of the Mississippi River are typically small, less than 0.5 ha to about 400 ha. These remnants are generally surrounded by distinctly different land uses that can have a detrimental impact on the health of a prairie. The potential effects of severe fragmentation include the inability to recover from internal disturbances due to wildlife or climatic elements, poor competitive ability with edge species, and loss of diversity in insect and wildlife populations resulting in lower dispersal rates of pollens and seeds. Although a number of sites found along railroads appear to be not changing, at least some form of management is needed to maintain most sites as open communities.

These studies to date suggest that management along with construction has been significant to the existence, composition, and quality of remnants. Activities that have been and are still significant in preserving or slowing decline in remaining prairies are linked to maintaining ROW as open space devoid of trees and brush. These include:

(1) The isolation of ROW lands in Wisconsin (many which included prairie) from agriculture and industrial development in the mid to late 1800s.

(2) Maintenance of railroad ROW (prescribed burns and brush cutting) that kept many areas free of brush and trees. Prairie communities remained fairly stable in many of these locations. Unfortunately due to rising labor costs, burning was not continued even though former road masters believed it provided the greatest brush control of the tools used.

(3) Wildfires, often started by trains, which would burn an area as frequently as once every two years and remove or set back brush and cool season plants.

Although railroads did maintain open ROW, particularly during the first part of this century, both management and construction had several undesirable effects on the quality and quantity of prairie remaining along railroads.

(1) Brush and ties which were allowed to lay in the ROW throughout a growing season would severely limit the growth of many plant species, and the burning of this debris created hot smoldering fires that would kill buds and roots that were normally resistant to fire.

(2) Annual fall burning would also affect species composition significantly. Studies indicate that annual fall burning may favor an increase in forb diversity (Kline 1986) and lower production of the warm season grasses (Hulbert 1986). The annual fall burns conducted by railroad maintenance crews in prairie areas would most likely have affected long-term species composition.

(3) Wildfires helped to maintain open communities and attempts to eliminate or reduce these fires have had a negative impact on the prairie. For example, the use of herbicides in this endeavor did not only impact and eliminate specific species but also opened the soil to reinvasion by pioneering plants. Since prairies no longer exist adjacent to the railroads, species that move into these exposed soils are often undesirable opportunists. An increase in brush invasion after the use of herbicides was noted by one former maintenance officer during our interviews. During our surveys we noticed that areas adjacent to bridges and crossroads, which typically were treated with soil sterilants, consisted of bare soil or were dominated by pioneering weed species.

(4) Another method noted for controlling ROW vegetation and limiting wildfires was plowing. Our survey noted that this method is still continuing today and in at least one instance we noted the recent destruction of a large stretch of prairie due to plowing.

Lack of management can often be as detrimental to remnants as the wrong type of management. More than 30% of Wisconsin's remaining railroads have been abandoned in the past three decades. Some of these lines are reopened as state subsidized short lines, but the majority of these lines receive little ROW maintenance. Prairie remnants along these short lines have rapidly become invaded and engulfed by brush in the past ten years. This leaves us with the problem of how to go about acquiring and managing these sites from an administrative standpoint. From our studies we believe that our involvement in management needs to begin soon after a company contemplates abandonment, but few agencies are willing to put time into managing land they do not own. Garden clubs and volunteer groups in Grant, Rock, and Green counties of Wisconsin have successfully organized work parties to manage prairie remnants in ROW that have been neglected by the railroads. However, volunteer groups willing to do this are few and other types of management plans need to be sought.

Site histories help to explain the present conditions of railroad prairies. Site histories can also help in making decisions as to which remnants have the greatest chance of being saved or even rejuvenated; and site histories may also help us determine which types of management have been most successful in maintaining prairie. Additional studies are needed, however, to determine if management of these narrow and unbuffered strips of prairie are actually preserving them or simply slowing their decline.

LITERATURE CITED

Borowske, J., and M. Heitlinger, M. 1980. A survey of native prairie remnants on railroad rights-of-way in Minnesota. Transportation Research Record 822: Landscape and Environmental Design. Transportation Research Board. National Academy of Science.

East Central Wisconsin Regional Planning Commission. 1978. Rail characteristics of East Central Wisconsin.

Finley, R. 1976. Original vegetation cover of Wisconsin. North Central Forest Experimental Station. USDA Forest Service, St. Paul, Minnesota.

Hulbert, L. 1986. Fire effects on tallgrass prairie. Pages 138-142. *In* G.K. Clamby and R.H. Pemble (eds.). The prairie: past, present and future. Proceedings of the Ninth North American Prairie Conference. Tri-College University Center for Environmental Studies, Fargo, North Dakota.

Kline, V. 1986. Response to sweet clover (*Melilotus alba* Desr.) and associated prairie vegetation to seven experimental burning and mowing treatments. Pages 149-152. *In* G.K. Clamby and R.H. Pemble (eds.). The prairie: past, present and future. Proceedings of the Ninth North American Prairie Conference. Tri-College University Center for Environmental Studies, Fargo, North Dakota.

Lanz, D. 1985. Railroads of Southern and Southwestern Wisconsin. Ski Printers, Blanchardville, Wisconsin.

Noss, R. 1983. A regional landscape approach to maintain diversity. BioScience 33:700-706.

Noss, R. 1987. Protecting natural areas in fragmented landscapes. Natural Areas Journal 7:2-13.

Reed, D., and J. Schwarzmeier. 1975. The prairie corridor concept: possibilities for planning large scale preservation and restoration. Pages 158-165. *In* D.C. Glenn-Lewin and R.Q. Landers, Jr. (eds.). Proceedings of the Fifth Midwest Prairie Conference. Iowa State University. Ames.

Shimek, B. 1931. The relation between the migrant and native flora of the prairie region. University of Iowa Studies in Natural History 14:10-16.

Simberloff, D., and N. Gotelli. 1984. Effects of insularization on plant species richness in the prairie-forest ecotone. Biological Conservation 29:27-46.

Thomson, J.W. 1940. Relict prairie areas in central Wisconsin. Ecological Monographs 10:685-717.

Vestal, A. 1918. Invasion of forest land by prairie along railroads. Illinois Academy of Science 11:126-128.

White, J. 1986. Why bother to protect prairies along railroads. Pages 172-173. *In* G.K. Clamby and R.H. Pemble (eds.). The prairie: past, present and future. Proceedings of the Ninth North American Prairie Conference. Tri-College University Center for Environmental Studies, Fargo, North Dakota.

Wilcove, D.S. 1987. From fragmentation to extinction. Natural Areas Journal 7:23-21.

Wisconsin Department of Natural Resources. 1967-1987. Annual Wisconsin forest fire reports. Madison, Wisconsin.

Wisconsin State Conservation Department. 1946-1966. Annual Wisconsin forest fire reports. Madison, Wisconsin.

Wisconsin Transportation Planning Program. 1983. The Wisconsin state rail plan 1983 update. Wisconsin Department of Transportation-Division of Planning and Budget, Madison, Wisconsin.

IS FIRE A DISTURBANCE IN GRASSLANDS?

E. W. Evans, J. M. Briggs, E. J. Finck, D. J. Gibson, S. W. James,
D. W. Kaufman, and T. R. Seastedt
Division of Biology, Ackert Hall, Kansas State University, Manhattan, Kansas

Abstract. Many grasslands, and in particular the tallgrass prairies of North America, are generally thought to be maintained by periodic fire. Semantic disagreement among researchers, however, threatens to hamper discussion of fire as an ecological force in grassland ecosystems. Some authors emphasize that fires are disturbances (or perturbations) since these fires disrupt or alter ecosystem states, trends, and dynamics (e.g., accumulating nitrogen is volatilized, plant and animal communities change in composition). Other researchers point out that, because these fire-induced disruptions and alterations can maintain the status quo of the ecosystem (e.g., prevent it from becoming woodland), it is the lack of fire rather than fire itself that should be considered a disturbance. We argue that, since both points of view are useful, there is little to be gained by labeling loosely either fire or the lack thereof as a "disturbance" in grassland ecosystems.

Key Words. disturbance, fire, grasslands, perturbation, prairie, Kansas

INTRODUCTION

Recurrent fire is widely regarded as an important, natural phenomenon of many ecosystems (Mooney *et al.* 1981, Wright and Bailey 1982), including many of the world's grasslands (Vogl 1974, Kucera 1981, Anderson 1982, Axelrod 1985). Towne and Owensby (1984), for example, succinctly state the general sentiment that tallgrass prairie of North America is "fire-derived and fire-maintained." But a semantic problem is surfacing in the grassland literature that threatens to hamper understanding of how fire functions in ecosystems.

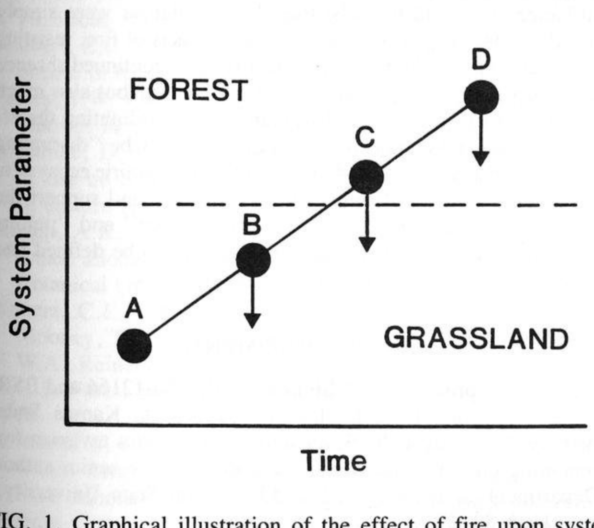


FIG. 1. Graphical illustration of the effect of fire upon system (ecosystem or community) parameters (e.g., biomass of woody tissue). The approximate bounds between a grassland and forest system are shown by the hatched line. The original state of the system is at position A, within the bounds of the grassland. Without fire, through time the system tends towards forest. A fire at B disrupts the system, but it remains as grassland; this could be repeated indefinitely. Without fire the system moves towards C, becoming forest. At C, a fire (of intensity as at B) moves the system back to grassland. In the continued absence of fire, the system reaches D, where after a fire of similar intensity the system remains a forest.

At issue is whether fires in grasslands (and other ecosystems) should or should not be considered (natural) disturbances/perturbations. Authors disagree more in semantics than in ecological substance. In fact, their disparate studies of nitrogen dynamics, plant succession, and grasshopper assemblages are linked conceptually by two common themes regarding grassland fires. Focus on one theme leads some researchers to label grassland fires as disturbances (Evans 1984, Collins and Barber 1985, Pickett and White 1985, and Collins 1987), while focus on the second theme leads other researchers to the opposite position, namely that it is the lack of fire that is the disturbance (Hulbert 1969, Lamotte 1983, van Andel and van den Bergh 1987).

The two themes can be stated simply. On the one hand, grassland fires disrupt or alter ecosystem states, trends, and dynamics. Accumulating nitrogen is volatilized (Seastedt 1988), expanding woody plant populations are reduced (Knapp 1986, Abrams and Hulbert 1987, Gibson and Hulbert 1987), animal communities change in composition (Kaufman *et al.* 1983, Evans 1984, Seastedt 1984a and 1984b, James 1988). These kinds of changes lead some researchers to label grassland fires as disturbances. On the other hand, these fire-induced disruptions and alterations can maintain the status quo of the ecosystem by preventing it from drifting beyond the loose bounds within which ecologists consider the ecosystem a grassland and outside of which it is recognized as a different system (Figure 1). The long-term result of the absence of fire in the North American tallgrass prairie region, for example, is the transformation of grassland to deciduous forest (Bragg and Hulbert 1976). It is this type of shift that leads some ecologists to view the absence rather than the occurrence of fire as a disturbance (White 1987).

Semantic difficulties arise in part from somewhat separate intellectual traditions. Ecosystem ecologists have used the terms disturbance and perturbation in comparing systems with differing degrees of what is now widely termed neighborhood stability. The system response to perturbation (used as a more neutral term than disturbance) has been described in terms of resistance and resilience (Webster *et al.* 1975, Swank and Waide 1980). This approach formally recognizes differences between the specific forcing function (the perturbation) and the system response. Lewis (1969) discussed state or controlling factors *vs.* dependent factors in ecosystems. As long as forcing variables such as climate do not deviate beyond a range of values, the system exhibiting neighborhood stability remains about the same. For example, Godron and Forman (1983) state that disturbance is "something that causes a community or ecosystem characteristic, such as species diversity, nutrient output, biomass, vertical or horizontal structure to exceed or drop below its common (homeostatic) range of variation." In this framework, the lack of fire can be usefully viewed as a disturbance to the grassland system. The tallgrass prairie without fire, for example, lacks both resistance (it takes no change in climate to change the system) and resilience (it does not return to its present state without fire). Ultimately, however, one's perception of stability and/or disturbance depends upon properties of the system as well as the forcing function, as illustrated for grasslands and fire in Figure 2.

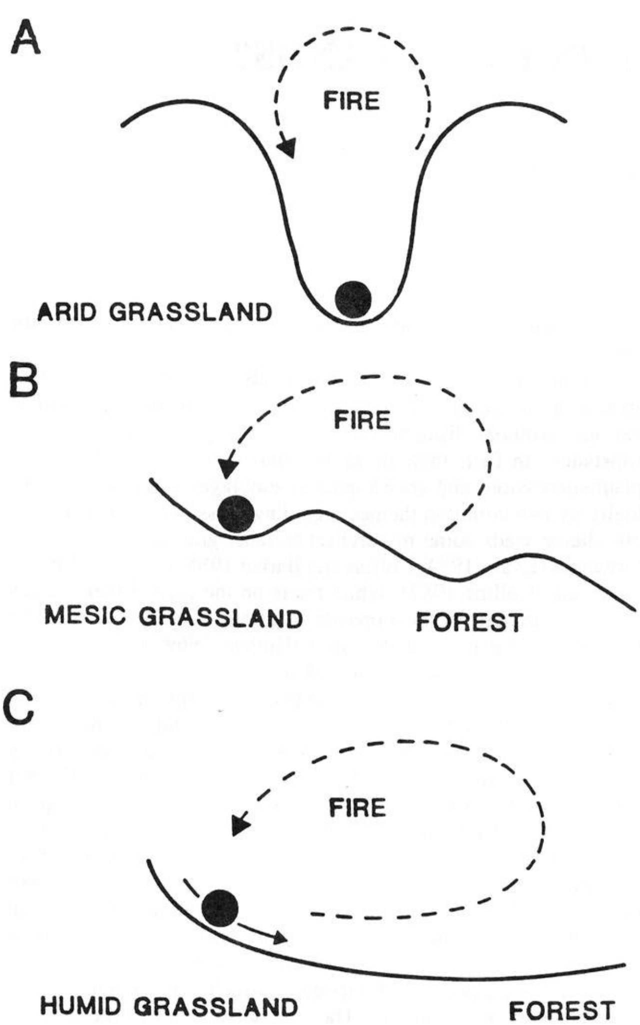


FIG. 2. The influence of fire depends upon the intrinsic properties of the system, as well as other external inputs. In (A) an arid grassland (e.g., shortgrass prairie) remains a grassland regardless of the presence or absence of fire. In (B) a grassland (e.g., mixed grass prairie in some cases) may be invaded by woody species if a seed source is available. The same climatic variables may support either system (a case of multiple stable points), but fire will drive the system to a grassland. In (C) a humid grassland (e.g., tallgrass prairie), with moist climate and woody seed sources present, is converted to forest unless fire intervenes.

Population and community ecologists have emphasized disturbance as a useful concept (Pickett and White 1985) in analyzing how interacting organisms respond to change in the resource bases of ecosystems. Fire is viewed as a naturally-occurring, interactive component of the complex of processes that characterize both grasslands (Loucks *et al.* 1985, Collins 1987, Evans 1988a and 1988b) and communities in general (Sousa 1984, Pickett and White 1985).

These schools of thought have encountered difficulty addressing the diversity of organism and system responses and the attendant problems of scale in deriving a robust operational definition of disturbance/perturbation. Allen and Wyleto (1983) demonstrate, for example, how analyses of different aspects of a single data base can lead to opposing conclusions regarding how fire affects an ecosystem. Both Allen and Starr (1982) and O'Neill *et al.* (1986) emphasize that whether or not fire will be considered a disturbance depends not only on one's definition of disturbance but also on the spatial and temporal scales on which one chooses to focus. These difficulties compound those of joining the frames of reference of diverse ecological perspectives to derive a single, all-encompassing definition of disturbance and perturbation.

Misunderstanding surrounding use of the terms disturbance and perturbation arises because many individuals carry with them some firmly held "psychological baggage." The root of the problem probably lies in a cultural and philosophical predisposition to attach negative connotations to the term disturbance. In a scientific tradition that has generally embraced a gradualist view of change in the earth's geological and biological processes (e.g., continuous evolution *vs.* punctuated equilibria), a disturbance is something outside of the proper train of events. We speak of some individuals as "mentally disturbed;" riots are referred to as "disturbances." Thus, to label an integral ("natural") aspect of an ecosystem, such as fire in grasslands, a "disturbance" may be disquieting, since a disturbance should be something "unnatural." From this viewpoint, labeling a fire as a "natural disturbance" only confuses the issue, as the phrase seemingly is a contradiction in terms. Certainly most would reject the idea that their thoughts were so subjective, but can anyone be sure that years of conditioning do not color one's thought (Mayr 1982)? Perhaps ecologists of a culture with a more revolutionary or cyclical world-view might not have negative associations with labels used for recurrent catastrophes. However, recent developments in evolution and ecology such as the theory of punctuated equilibria (Eldredge 1985), chaos theory (May and Seger 1986), and increased interest in analysis of non-equilibrium situations (Houston 1979), are evidence that ways of thought are changing.

Given these various considerations, it is not surprising that a useful definition of ecological disturbance rising above semantic difficulties has proved elusive (White 1979, Bazzaz 1983, Godron and Forman 1983, Sousa 1984, Pickett and White 1985, Rykiel 1985, van Andel and van den Bergh 1987). Neither is it surprising that there is lack of agreement regarding inclusion/exclusion of grassland fires in particular as disturbances. Good semantic arguments can be made either for or against grassland fire as a natural disturbance. It would be most useful if the debate were simply dropped and investigators focused on the impacts of fire, resisting the temptation to label either grassland fire or its continued absence as a disturbance. A potentially less inflammatory (but also much less inspired) substitute for "disturbance" in highlighting the effects of fire on grassland ecosystems might simply be "disrupting influence." In any case, our studies of a tallgrass prairie ecosystem illustrate the diversity of biotic responses to fire and support the position that facile use of the terms "disturbance" and "perturbation" should be avoided. These words need to be defined and used carefully in any discussion of grassland fires.

ACKNOWLEDGEMENTS

Support was provided by NSF Grants DEB 80-12166 and BSR 85-14327 for Long-Term Ecological Research to Kansas State University. We thank T. B. Bragg and an anonymous reviewer for commenting on the manuscript. The address of the senior author is Department of Biology, UMC 5305, Utah State University, Logan, Utah 84322.

LITERATURE CITED

Abrams, M.D., and L.C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. American Midland Naturalist 117:442-445.

Allen, T.F.H., and T.B. Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago.

Allen, T.F.H., and E.P. Wyleto. 1983. A hierarchical model for the complexity of plant communities. Journal of Theoretical Biology 101:529-540.

Anderson, R.C. 1982. An evolutionary model summarizing roles of fire, climate, and grazing animals in the origin and maintenance of grasslands: an end paper. Pages 297-308. *In* J.R. Estes, R.J. Tyrl and J.N. Brinken (eds.). Grasses and grasslands: systematics and evolution. Oklahoma University Press, Norman.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. Botanical Review 51:163-201.

Bazzaz, F.A. 1983. Characteristics of populations in relation to disturbance in natural and man-modified ecosystems. Pages 259-275. *In* H.A. Mooney and M. Godron (eds). Disturbance and ecosystems. Components of response. Springer-Verlag, Berlin.

Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19-24.

Collins, S.L. 1987. Interaction of disturbance in tallgrass prairie: a field experiment. Ecology 68:1243-1250.

Collins, S.L., and S.C. Barber. 1985. Effects of disturbance in mixed-grass prairie. Vegetatio 64:87-94.

Eldredge, N. 1985. Unfinished synthesis: biological hierarchies and modern evolutionary thought. Oxford University Press, New York.

Evans, E.W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. Oikos 43:9-16.

Evans, E.W. 1988a. Community dynamics of prairie grasshoppers subjected to periodic fire: predictable trajectories or random walks in time? Oikos 52:283-292.

Evans, E.W. 1988b. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie: influences of fire frequency, topography, and vegetation. Canadian Journal of Zoology 66:1495-1501.

Gibson, D.J., and L.C. Hulbert. 1987. Effects of fire, topography, and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72:175-185.

Godron, M., and R.T.T. Forman. 1983. Landscape modification and changing ecological characteristics. Pages 12-28. *In* H.A. Mooney and M. Godron (eds.). Disturbance and ecosystems. Components of response. Springer-Verlag, Berlin.

Houston, M. 1979. A general hypothesis of species diversity. American Naturalist 133:81-101.

Hulbert, L.C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. Ecology 50:874-877.

James, S.W. 1988. The post-fire environment and earthworm populations in tallgrass prairie. Ecology 69:476-483.

Kaufman, D.W., G.A. Kaufman, and E.J. Finck. 1983. Effects of fire on rodents in tallgrass prairie of the Flint Hills Region of eastern Kansas. Prairie Naturalist 15:49-56.

Knapp, A.K. 1986. Postfire water relations, production, and biomass allocation in the shrub, *Rhus glabra,* in tallgrass prairie. Botanical Gazette 147:90-97.

Kucera, C.L. 1981. Grassland and fire. Pages 90-111. *In* H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners (eds.). Fire regimes and ecosystem properties. U.S. Forest Service, Washington, D.C. Technical Report Wo-26.

Lamotte, M. 1983. Research on the characteristics of energy flows within natural and man-altered ecosystems. Pages 48-70. *In* H.A. Mooney and M. Godron (eds.). Disturbance and ecosystems. Components of response. Springer-Verlag, Berlin.

Lewis, J.K. 1969. Range management viewed in the ecosystem framework. Pages 97-187. *In* G.M. Van Dyne (ed.). The ecosystem concept in natural resource management. Academic Press, New York.

Loucks, O.R., M.L. Plum-Mentjes, and D. Rogers. 1985. Gap process and large- scale disturbances in sand prairies. Pages 72-84. *In* S.T.A. Pickett and P.S. White (eds.). The ecology of natural disturbance and patch dynamics. Academic Press, New York.

May, R.M., and J. Seger. 1986. Ideas in ecology. American Scientist 74:256- 267.

Mayr, E. 1982. The growth of biological thought: diversity, evolution and inheritance. Belknap Press, Cambridge, Massachusetts.

Mooney, H.A., T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners, (eds.). 1981. Fire regimes and ecosystem properties. U.S. Forest Service Technical Report Wo-26.

O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. A hierarchical concept of ecosystems. Monographs in Population Biology, 23, Princeton University Press, Princeton, New Jersey.

Pickett, S.T.A., and P.S. White (eds.). 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Rykiel, E.J. 1985. Toward a definition of ecological disturbance. Australian Journal of Ecology 10:361-365.

Seastedt, T.R. 1984a. Belowground macroarthropods of annually burned and unburned tallgrass prairie. American Midland Naturalist 111:405-408.

Seastedt, T.R. 1984b. Microarthropods of burned and unburned tallgrass prairie. Journal of the Kansas Entomological Society 57:468-476.

Seastedt, T.R. 1988. Mass, nitrogen and phosphorus dynamics in foliage and root detritus of annually burned and unburned tallgrass prairie. Ecology 69:59-65.

Sousa, W.P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353-391.

Swank, W.T., and J.B. Waide. 1980. Interpretation of nutrient cycling research in a management context: evaluating potential effects of alternative management strategies on site productivity. Pages 137-158. *In* R.W. Waring (ed.). Forests: fresh perspective from ecosystem analysis. Oregon State University Press, Corvallis.

Towne, G., and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. Journal of Range Management 37:392-397.

van Andel, J., and J. P. van den Bergh. 1987. Disturbance of grasslands. Outline of the theme. Pages 3-13. *In* J. van Andel, J.P. Bakker, and R.W. Snaydon (eds.). Disturbance in grasslands. Dr. W. Junk, Netherlands.

Vogl, R. 1974. Effects of fire on grasslands. Pages 139-194. *In* T.T. Kozlowski and C.E. Algren (eds.). Fire and ecosystems. Academic Press, New York.

Webster, J.R., J.B. Waide, and B.C. Patten. 1975. Nutrient cycling and the stability of ecosystems. Pages 1-27. *In* F.G. Howell, J.B. Gentry, and M.H. Smith (eds.). Mineral cycling in southeastern ecosystems. Energy Research and Development Administration Symposium Series (Conf-740SB), National Technical Information Service, Springfield, Virginia.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review 45:229-299.

White, P.S. 1987. Natural disturbance, patch dynamics and landscape pattern in natural areas. Natural Areas Journal 7:14-22.

Wright, H.A., and A.W. Bailey. 1982. Fire ecology. Wiley-Interscience, New York.

FIVE YEARS OF ANNUAL PRAIRIE BURNS

Donald A. Becker
U. S. Army Corps of Engineers, Environmental Analysis Branch, 215 N. 17th St., Omaha, Nebraska 68102-4978

Abstract. A prairie site at Pipestone National Monument in southwestern Minnesota was burned each spring from 1983-1987. During the past century of use, much of the site had been invaded by various, non-native, cool-season grasses and broadleaf weeds. Also, various woody species have invaded parts of the site. Annual burns generally induced positive changes in native remnants, primarily with big bluestem (*Andropogon gerardii* Vitman) and prairie dropseed (*Sporobolus heterolepis* A. Gray) increasing cover from 6.4 to 21.0%. Cover of native forbs also increased, from 6.5 to 12.8%, due to increased vigor of existing plants and establishment of new individuals. While some tree and shrub species were permanently damaged, wild plum (*Prunus americana* Marsh), chokecherry (*Prunus virginiana* L.), and smooth sumac (*Rhus glabra* L.) re-sprouted from underground parts each year and were able to maintain or slightly increase pre-burn cover levels, although stature was reduced. Dense stands of quackgrass (*Agropyron repens* Beauv.) were reduced in height and vigor, but, unlike stands dominated by other species, were not open to establishment of prairie species. In general, while prescribed burning triggered increases of diversity, cover, and vigor of native prairie species, this was not a uniform effect across the site as most changes occurred within and along the edges of existing prairie remnants. Essentially no changes were observed within the large stands of quackgrass in which additional suppression of the sod is required, which could be accomplished by delay of spring burning, summer mowing, and plantings of native plant materials.

Key Words. prairie restoration, prescribed burning, Pipestone National Monument, Minnesota

INTRODUCTION

The value of fire in prairie management has been recognized at Pipestone National Monument since 1971 when a wildfire induced positive effects on a native prairie tract. Later, a prairie management plan was developed by the U.S. National Park Service (Landers 1975) in order to restore prairie vegetation in parts of the Park which had been subject to various disturbances, including alien plant invasions. Spring burns, varying in frequency from one in three years to one in four years, were considered to be an integral part of the plan. Due to various constraints and concerns, however, the restoration work was not accomplished, and the National Park Service later funded a more extensive prairie investigation from 1982-1985. As part of this effort, prescribed burning trials were conducted on a small, degraded prairie tract from 1983-1987. The purpose was to determine if annual, long-term spring burns could be used as a measure to accomplish the objectives of (1) controlling alien woody and herbaceous plants; and (2) improving native plant diversity, abundance and cover on the site (Becker *et al.* 1986).

STUDY AREA

Pipestone National Monument is located in southwestern Minnesota within a hilly, elevated region known as the Prairie Coteau. The Park consists of about 114 ha located within a glacially-formed valley just north of the city of Pipestone. A wide variety of vegetation types occur on the Park landscapes including dry, mesic, and wet grassland, shrubland, and woodland. A quartzite escarpment bisects the area in a northwest-southeast direction, and is a topographically prominent feature. The study was conducted on 5.1 ha contained within the Circle Trail (Figure 1). This area is bounded by the escarpment on the east and the visitor center on the west. Lake Hiawatha, a shallow impoundment, and Pipestone Creek are located within the area, and a small drainageway (woody draw) crosses the area about 90 m downslope and west of the escarpment. There are no records of the site being burned since the time of settlement. Original prairie vegetation upslope of the draw developed on shallow and rocky soils and was dominated by short and mid grasses while the deeper soils downslope of the draw supported tallgrass prairie. The site has been managed for various recreational activities during the past century by local and Federal interests. Both upslope and downslope prairie types have been extensively degraded by the invasion of numerous non-native cool-season grasses leaving only isolated remnants of native prairie sod. These remnants occupied less than 25% percent of the area prior to initiation of the study. Invading grasses were Kentucky bluegrass (*Poa pratensis* L.), smooth brome (*Bromus inermis* Leyss.), and quackgrass (*Agropyron repens* Beauv.). Also, closed stands of snowberry (*Symphoricarpos occidentalis* Hook.) developed on deeper soils. Small patches of Canada thistle [*Cirsium arvense* (L.) Scop.] and field bindweed (*Convolvulus sepium* L.) were occasionally found within the snowberry stands. In the woody draw, mixed stands of buckthorn (*Rhamnus cathartica* L.), tatarian honeysuckle (*Lonicera tatarica* L.), green ash (*Fraxinus pennsylvanica* Marsh), and other woody species had developed, overtopping and suppressing prairie species. In other parts of the prairie, only isolated green ash trees or small patches of chokecherry (*Prunus virginiana* L.), smooth sumac (*Rhus glabra* L.), wild plum (*Prunus americana* Marsh), or buckthorn had established.

Most native cover within the prairie remnants prior to the study was composed of prairie dropseed (*Sporobolus heterolepis* A. Gray) and big bluestem (*Andropogon gerardii* Vitman). The former was most abundant in the rock outcrop prairie, while the latter was confined to the deeper soil prairie downslope of the woody draw. Native forb cover was sparse in both prairie types, especially spring and early summer forms. Late summer and fall forb flora was more abundant but consisted mostly of goldenrods (*Solidago spp.*).

METHODS

Prescribed spring burns were conducted annually from 1983 through 1987, generally from mid to late April when the cool-season grasses had initiated good growth and were 10-15 cm or less in height. In 1987, however, the growing season arrived earlier and burning was delayed until early May. At that time the cool-season grasses were 15-25 cm in height, and woody plants had considerable foliage. Fire intensity during the study was generally considered to be low to moderate, except during the first year when high fuel levels were present.

Annual pre and post-burn qualitative floristic surveys were conducted to determine site-wide responses, while a quantitative sampling procedure was developed to assess changes in plant communities and to determine the individual responses of each species. The quantitative procedure included use of line transect, quadrat and point methods. A transect, 275 m long, formed the alignment for all methods. It extended from the high quartzite ledge on the east to a lowland area near the visitor center on the west. The transect was divided into nine segments, each 30 m in length. The positions and extent of major plant communities (stands of smooth brome, quackgrass, Kentucky bluegrass, snowberry, big bluestem, prairie dropseed, etc.) were recorded along the transect. Also, percent foliage cover of all bunch-forming grasses and forb species encountered along the transect was determined. For

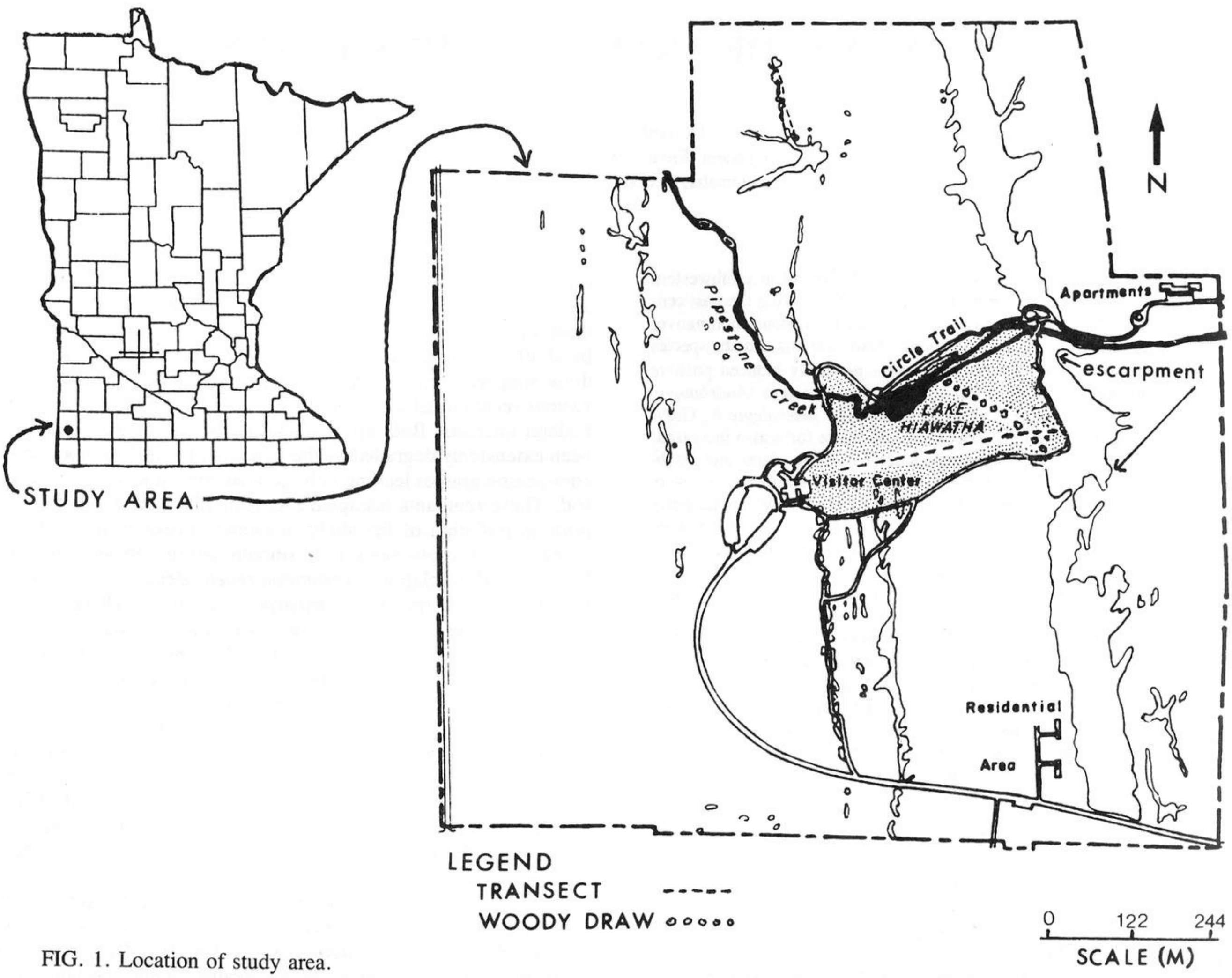


FIG. 1. Location of study area.

single-stalked, cool-season grasses such as Kentucky bluegrass, quackgrass, and smooth brome, 450 uniformly spaced points (0.6 m) along the transect were used to assess percent foliage cover. Each point was projected to the ground from the survey tape and the percent of foliage "hits" was recorded. Ten rectangular quadrats, each 0.10 m², were placed at 30-m intervals along the transect, and foliage cover in each plot was estimated by the class interval method of Daubenmire (1959). Heights of the major community dominants were determined within the quadrats. Frequency was determined from presence data obtained within the quadrat and transect microplots.

Within the line transect and quadrat microplots, foliage cover was obtained twice in both early and late season during 1983 and 1984, but only once during 1985 and 1987. Point foliage cover data for the cool-season grasses were taken only in early season during three years (1984, 1985, and 1987). Additional sampling details and a list of plant taxa found is reported in Becker *et al.* (1986). Agradient and soil depth survey was made along the transect in order to define vegetation-soil-slope relationships and is published elsewhere (Becker *et al.* 1986).

RESULTS

Most native remnant stands remained relatively stable during the treatment period, with the exception of those containing snowberry and big bluestem as major or minor components. Big bluestem expanded along the westerly or lower 150 m of the transect (Table 1), invading either 1) adjacent, nearly closed stands of snowberry having only a sparse understory of Kentucky bluegrass, or 2) adjacent, herbaceous stands where smooth brome, Kentucky bluegrass or quackgrass were dominant and formed the canopy. From transect community position and cover data, it was estimated that about 70% of the expansion of big bluestem cover (24.4 m) resulted from invasion of previously open or closed snowberry stands. Dense, monotypic stands of quackgrass, however, remained very persistent despite the annual fires and reduction of vigor. Stand location and limited frequency and foliage cover data indicated that quackgrass even expanded slightly into adjacent stands of snowberry, Kentucky bluegrass, and smooth brome where big bluestem was absent. Patches of broadleaf aliens, such as Canada thistle, decreased over time, while hedge bindweed disappeared (Table 2). Stand location data also suggested that smooth sumac and wild plum invaded slightly into fire-stressed cool-season grass sod. A stand of bur oak (*Quercus macrocarpa* Michx.) also resisted fire, but green ash and tatarian honeysuckle were susceptible to the burns. A few isolated individuals of buckthorn also exhibited sensitivity, but buckthorn thickets in the draw were not exposed to fire.

One of the most striking changes in the prairie was the reduction in shoot and foliage height of both snowberry and the cool-season grasses. Snowberry height decreased from 1 to 0.5 m, Kentucky bluegrass from 0.6 to 0.3 m, quackgrass from 0.6 to 0.3 m, and smooth brome from 0.6 to 0.4 m (Figure 2). Another obvious change was lack of flowering and seed production in the cool-season grasses during this period. Native grass species on the other hand, including big bluestem, prairie dropseed, and Scribner's

Table 1. Increases in linear extent (m) of big bluestem stands during the study period (1983-1987).

Transect Segment (m)	*1983*	*1984*		*1985*	*1987*	*Change*
	Summer	*Spring*	*Summer*	*Spring*	*Summer*	
	m					
0-122	Shallow soil mid-grass prairie and woody draw; big bluestem stands absent.					
122-153	0	0	0	0	0.5	+0.5
153-183	4.7	6.2	12.4	11.5	13.6	+8.9
183-214	0.6	0.6	0.6	0.6	8.4	+7.8
214-244	1.9	5.0	3.1	5.0	6.8	+4.9
244-275	3.3	10.2	5.3	12.4	12.1	+8.8
Total by year	10.5	22.0	21.4	29.5	41.4	+30.9

Table 2. Transect foliage cover (%) in the study area. Nomenclature from Great Plains Flora Association (1986). Dashed lines (——) indicate that this species was not evaluated on the date listed. Trace levels (tr) refer to values less than 0.1% cover.

	Cover					
	1983		*1984*		*1985*	*1987*
Species	*Spring*	*Summer*	*Spring*	*Summer*	*Spring*	*Summer*
	%					
Grasses:						
Agropyron repens	——	——	9.1	——	10.7	26.4[1]
Andropogon gerardii	2.1	2.2	4.8	3.7	8.7	10.7
Andropogon scoparius	0.0	0.1	0.0	0.1	0.0	0.0
Bouteloua curtipendula	tr	0.2	tr	0.3	0.0	0.7
Bouteloua gracilis	0.7	0.2	0.2	0.2	0.8	0.4
Bromus inermis	——	——	21.3	——	22.4	26.4[1]
Dichanthelium oligosanthes	tr	——	0.4	0.2	0.7	1.3
Muhlenbergia cuspidata	0.0	0.0	0.0	0.0	0.0	0.1
Panicum virgatum	0.0	0.0	0.0	0.0	0.0	0.1
Poa pratensis	——	——	32.2	——	15.6	22.0
Spartina pectinata	0.1	0.1	0.1	0.6	0.4	0.4
Sporobolus heterolepis	3.6	3.9	4.3	4.1	6.3	6.8
Stipa spartea	tr	tr	0.6	0.6	0.9	0.3
Forbs:						
Achillea millefolium	tr	tr	tr	tr	0.0	tr
Ambrosia psilostachya	1.6	3.1	4.9	4.0	0.9	5.3
Anenome canadensis	0.1	0.0	0.0	0.0	0.0	0.0
Apocynum sp.	tr	0.0	0.1	0.0	0.0	0.0
Artemisia ludoviciana	0.1	0.2	0.1	0.3	0.4	0.9
Asclepias sp.	0.0	0.1	0.1	0.0	0.0	0.0
Asparagus officinale	0.1	0.1	0.2	0.1	0.0	0.0
Aster ericoides	0.5	0.9	1.3	2.3	1.4	1.9
Aster oblongifolius	0.0	tr	0.0	0.2	0.0	tr
Cirsium arvense	0.1	0.2	0.2	0.1	0.1	0.1
Convolvulus sepium	0.1	0.2	0.1	0.1	0.2	0.0
Conyza canadensis	tr	0.0	0.0	0.0	0.0	0.0
Erigeron sp.	0.1	0.0	0.3	tr	tr	tr
Glycyrrhiza lepidota	0.3	tr	0.1	0.2	0.3	0.4
Helianthus maximiliani	0.0	0.0	0.0	0.0	0.0	0.1
Helianthus rigidus	0.6	1.0	0.8	1.1	1.6	1.0
Heuchera richardsonii	0.1	tr	0.0	0.0	tr	0.0
Lithospermum sp.	0.1	0.0	0.0	0.0	tr	0.0
Medicago lupulina	0.0	0.0	0.1	0.0	0.0	0.0
Monarda fistulosa	0.2	0.1	0.0	0.2	tr	0.2
Physalis sp.	tr	0.0	0.0	0.0	0.0	0.0
Potentilla arguta	0.2	0.1	0.1	0.0	0.3	0.4
Polygonum coccineum	0.1	0.1	0.2	tr	0.2	0.1
Psoralea argophylla	0.1	tr	0.0	0.0	0.2	0.0
Ratibida pinnata	0.0	tr	0.0	0.0	0.0	0.1
Silene antirrhina	0.0	0.0	tr	0.0	0.0	0.0
Solidago canadensis	1.0	1.3	0.9	0.4	[2]	0.2
Solidago missouriensis	1.0	2.4	0.4	1.6	3.3	1.9
Solidago rigida	0.4	0.3	0.2	0.4	[2]	0.4
Thalictrium dasycarpum	0.1	0.0	tr	0.0	0.0	0.0
Tradescantia bracteata	tr	0.0	0.0	0.0	0.2	0.0
Veronicastrum virginicum	0.0	0.1	0.0	tr	0.1	0.1
Vicia americana	0.0	0.0	0.2	0.0	0.0	0.0

Woody Plants:						
Amorpha canescens	2.0	2.5	3.1	2.8	4.1	1.7
Amorpha fruticosa	0.1	0.2	0.1	0.1	0.1	0.1
Fraxinus pennsylvanica	2.8	4.9	1.6	3.0	1.3	2.4
Lonicera tatarica	1.2	1.9	1.2	0.8	0.1	0.0
Parthenocissus inserta	0.4	0.7	——	——	——	——
Prunus americana	0.5	0.4	0.7	1.4	0.6	1.3
Prunus pumila var. *besseyi*	0.3	0.7	0.2	0.7	0.8	0.4
Prunus virginiana	3.5	1.0	3.5	2.7	0.9	1.8
Quercus macrocarpa	2.0	0.9	2.0	0.9	0.9	2.4
Rhamnus cathartica	1.4	2.0	0.9	3.0	2.6	2.4
Rhus glabra	1.7	1.6	1.7	1.4	2.4	3.0
Ribes missouriense	0.2	0.2	0.2	0.2	0.2	——
Rosa arkansana	1.3	2.2	1.4	1.8	2.9	1.6
Rubus occidentalis	tr	0.2	0.1	0.2	0.1	——
Spiraea alba	0.0	0.0	0.0	0.0	0.0	tr
Symphoricarpos occidentalis	3.7	10.0	6.3	9.6	9.5	5.2
Toxicodendron rydbergii	1.6	0.1	0.4	——	0.7	——
Ulmus americana	0.0	0.2	0.6	0.2	0.2	0.0

Other prairie plants (in study area but not sampled):

Aster novae-angliae, Anenome caroliniana, Antennaria neglecta, Galium boreale, Helianthus tuberosus, Liatris punctata, Mentha arvensis var *villosus, Penstemon gracilis, Silphium perfoliatum, Stellaria longifolia, Solidago gigantea, Talinium parviflorum, Taraxacum officinale, Verbena stricta, Verbena hastata, Viola pedatifida*

[1]Data for smooth brome and quackgrass pooled in 1987, as plants in low vigor condition were difficult to differentiate.
[2]Data not collected separately for three species of goldenrods in 1985.

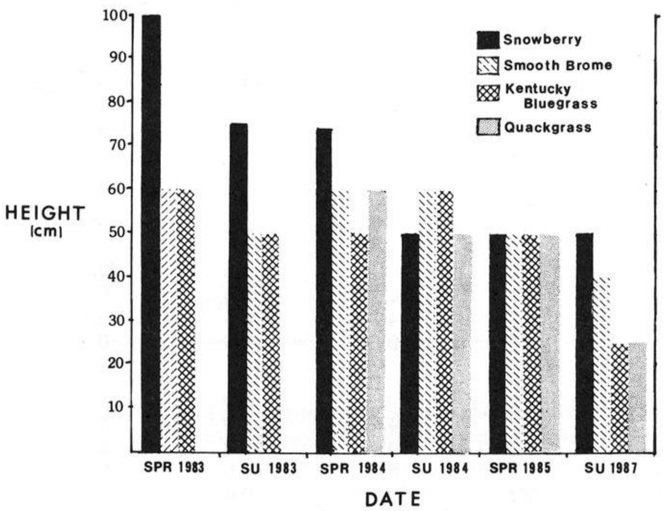


FIG. 2. Height changes of snowberry and some cool-season grasses.

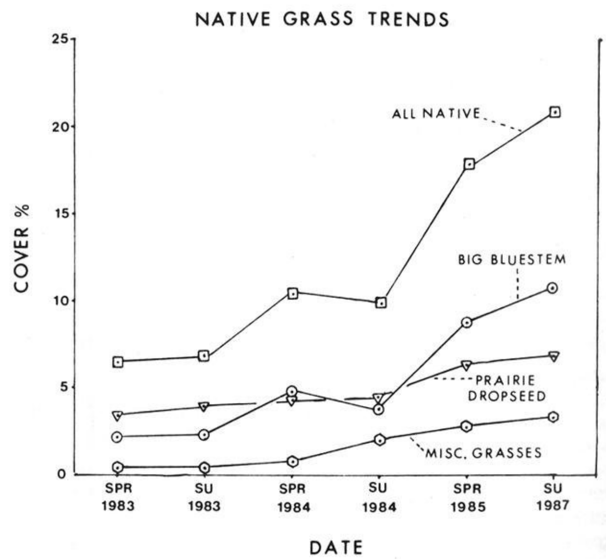


FIG. 3. Native grass cover changes (1983-1987). Miscellaneous grasses referred to include sideoats grama, blue grama, Scribner's panicgrass, porcupine grass, little bluestem, and plains muhly.

panicgrass [*Dichanthelium oligosanthes* (Schult.) Gould var. *scriberianum* (Nash) Gould] exhibited vigorous growth each year, producing numerous flowering culms and apparently viable seed.

Native grass cover increased from 6.4 to 21.0% (Figure 3). Much of this expansion is attributed to spread of the big bluestem community as previously described. Prairie dropseed was the major increaser in the shallow soil prairie, but Scribner's panicgrass, prairie cordgrass (*Spartina pectinata Trin.),* and sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] also increased. Limited coverage of blue grama [*Bouteloua gracilis* (H.B.K.) Lag. *ex* Griffiths], porcupine grass (*Stipa spartea* Trin.), and little bluestem [*Andropogon scoparius* (Michx.) Nash] were present but no change was apparent (Table 2). All native grasses were in reproductive condition each year, which is considered a favorable response to fire. In 1987 switchgrass (*Panicum virgatum* L.) first appeared on lower slopes along the edge of the woody draw, while plains muhly [*Muhlenbergia cuspidata* (Torr.) Rydb.] was first observed along the upper slopes near the escarpment.

Foliage cover of cool-season grasses decreased only about 10%. This is attributed largely to reduction of Kentucky bluegrass and possibly that of smooth brome (Table 2). Quackgrass increased slightly in cover even though aerial parts exhibited low vigor.

Species richness of prairie forbs increased as a result of the annual fire treatments. Additional species encountered during post burn surveys were Culver's root [*Veronicastrum virginicum* (L.) Farw.], slender penstemon (*Penstemon gracilis* Nutt.), New England aster (*Aster novae-angliae* L.), wild bergamot (*Monarda fistulosa* L.), cup plant (*Silphium perfoliatum* L.), blazing star (*Liatris punctata* Hook.), and fringed loosestrife (*Lysimachia ciliata* L.). Of these species, only Culver's root and wild bergamot were located within the microplots.

Large increases in foliage cover along the transect segments were noted for many late summer flowering composites (Table 2), including western ragweed (*Ambrosia psilostachya* D.C.), prairie sagewort (*Artemisia ludoviciana* Nutt.), and white prairie aster (*Aster ericoides* L.). Other species which increased in cover were wild licorice [*Glycyrrhiza lepidota* (Nutt.) Pursh], prairie cinquefoil (*Potentilla arguta* Pursh), tall coneflower [*Ratibida pinnata* (Vent.) Barnh.], and Maximilian's sunflower (*Helianthus maximilianii* Schrad.). Silver leaf psoralea (*Psoralea argophylla* Pursh), a mid-summer flowering forb, also increased in cover and vigor but was not regularly sampled in late summer, since it is a tumbleweed and blows away. Spring-flowering forbs were nearly absent on the site, except for Carolina anenome (*Anenome caroliniana* Walt.) which flowered profusely two weeks after the late April 1984 burn. It apparently was not harmed by the back-to-back 1983 and 1984 burns.

Forb responses in the quadrat plots were similar to responses observed in the transect plots. Western ragweed increased in two plots where it was encountered in 1983, and later became established in three other plots. Stiff goldenrod (*Solidago rigida* L.), stiff sunflower [*Helianthus rigidus* (Cass.) Desf.], prairie sagewort, and white prairie aster became established in at least one plot and increased in cover as well. Increases in forb cover were generally found in quadrats dominated initially by Kentucky bluegrass or snowberry. Plots dominated by taller grasses such as big bluestem or quackgrass exhibited little change. Forb and shrub seedlings of several species were observed in a quackgrass plot in the wet spring of 1984, but were not observed in either 1985 or 1987. Shading from a nearby green ash tree may have reduced growth capability, and they may also have been affected by a period of dry weather from July-September of 1984. Canada thistle seedlings were first observed within a quadrat dominated by snowberry in spring, 1984. These persisted until 1985, but were absent in 1987. These may have been suppressed or eliminated through the expansion of goldenrod and stiff sunflower cover within the plot.

Total foliage cover of woody species in the prairie remained stable during the period, but seasonal and species specific changes were noted. Smooth sumac cover increased each year, but adverse effects of fire on tatarian honeysuckle, green ash, and buckthorn were noted. Several native prairie shrubs of short stature increased each year until the late 1987 sampling, when a slight drop of foliage cover was recorded. These included lead plant (*Amorpha canescens* Pursh), sand cherry (*Prunus pumilia* L. var. *besseyi* Bailey), and prairie rose (*Rosa arkansana* Porter). It is believed, however, that these lower values reflect drought conditions prior to leaf drop. Snowberry cover fluctuated greatly each year as it was initially set back by the spring burns, but typically recovered well by late summer. Lower cover values in the late summer of 1987 may also be a result of premature leaf drop. The extensive stands of buckthorn and honeysuckle in the woody draw were not subjected to fire during the study due to inadequate levels of herbaceous fuel.

By 1987, site aesthetics had improved greatly, as compared to an adjacent degraded prairie which was managed on a one year in four burn frequency plan. The annually burned prairie became more open each year with the reduction in dominance of snowberry and the tall cool-season grasses, and a concomitant increase in dominance of native grasses and forbs. The flowering shoots of the native plants emerged into the canopy, providing many different hues and textures in a formerly rather drab prairie. Several of the native, broadleaf forbs also had attractive, silvery foliage extending into the canopy.

While the annual rainfall varied considerably both annually and seasonally on the site (Table 3), annual burning had a much greater effect on growth and expansion of native plant cover than did differences in precipitation. As noted above, an adjacent prairie having a low fire frequency did not noticeably change during the five-year period. Details on responses of prairie vegetation to seasonal and yearly differences in precipitation were reported in a previous study (Becker *et al.* 1986).

After 1983, lack of fuel likely reduced the heat intensity of the prescribed burns. This was particularly evident in areas dominated by cool-season grasses or woody plants where herbage production was reduced. This effect may have reduced damage to woody species on site, especially to plant parts located near to the surface.

DISCUSSION

Several studies in the central prairies and plains region of North America have expressed concerns about the undesirable effects of high fire frequency. Increases in weedy forbs and reduction of grass cover have been reported (Aldous 1934, Hopkins *et al.* 1948, Weaver and Rowland 1952). Development of grassland monotypes has also been reported (Kucera and Koelling 1964, Vogl 1974). Kucera (1970) suggested a fire frequency of one in four years to maintain grass dominance and species diversity typical of native tall grass prairies. High frequency burning (annual or biennial) for extended periods of time, however, created favorable results in several studies of northern prairies, including restoration work in Wisconsin (Curtis and Partsch 1948, Anderson 1972, Henderson *et al.* (1982), and maintenance studies of aspen-prairie savannas in northwestern Minnesota (Svedarsky *et al.* 1986) and central Alberta (Anderson and Bailey 1980). Changes observed in the Pipestone study closely paralled those found in the Wisconsin, Minnesota, and Canadian studies in that increases in both native species richness and foliage cover were observed. Species responding similarly included big bluestem, side oats grama, snowberry, prairie sagewort, white prairie aster, wild bergamot, and various goldenrods.

All species responses at Pipestone, however, were not considered desirable: the increase of western ragweed, the resistance of quackgrass sod to native plant establishment, and the increase and

Table 3. Precipitation (cm) during the 1983-1987 study period[1].

Year	*Jan-Apr.*	*May*	*June*	*July*	*Aug.*	*Sept-Dec.*	*Annual*
				cm			
1983	16.1	6.3	16.7	8.2	6.1	25.4	78.8
1984	21.2	7.8	24.3	7.6	3.0	2.4	66.3
1985	17.3	12.1	4.2	4.0	11.4	21.0	70.0
1986	19.1	9.2	12.9	9.9	7.2	30.8	89.1
1987	10.7	9.8	4.3	10.1	3.3	17.4	55.6
Average (period-of-record)	——	8.8	10.5	7.5	8.6	——	62.0

[1]Data taken from the U.S. Weather Bureau Reporting Station at the city of Pipestone (U.S. Dept. of Commerce, 1983-87). Long term averages for the January-April and September-December periods were not computed.

persistence of native woody species (smooth sumac) are still major concerns. Western ragweed, a native but sometimes weedy perennial, either invaded or increased in five of the quadrats dominated prior to burning by cool-season grasses (smooth brome and Kentucky bluegrass), snowberry, or prairie dropseed. In this respect, western ragweed responded similarly to its behavior under moderate to heavy grazing. Dense quackgrass stands, although curtailed in terms of aerial growth and flowering, were resistent to change and actually expanded slightly into adjacent areas of smooth brome or Kentucky bluegrass sod. This is in contrast with findings in Wisconsin (Curtis and Partch 1948, Anderson 1972), where quackgrass cover was reduced. Because the phenology of this species is somewhat later than for either Kentucky bluegrass or smooth brome, it is likely that prescribed burns at Pipestone were not timed for optimum control. Although shoots of smooth sumac were damaged or killed each year, numerous suckers emerged within the area of the old plant, resulting in slight increases in stand area. This finding is consistent with findings in the Kansas tallgrass prairie (Owensby and Smith 1972). In that study the success of smooth sumac under late spring burning was attributed to its later phenology which paralled that of the warm-season grasses. Control of smooth sumac at Pipestone might be more effective through mowing or cutting of the shoots during its flowering period when carbohydrate reserves of the roots are lower.

The opening of dense, tall stands of snowberry, but not reduction in its areal extent, was previously reported in a three-year study of central Alberta aspen savanna (Anderson and Bailey 1979). The increase of species diversity was attributed to the reduction in competition from shrubs, higher light intensity at the soil surface, warmer soil temperatures, favorable seed bed, and release of nutrients.

At Pipestone no long-term adverse effects on early spring forbs was documented, although more observations are needed since this floral component was poorly represented on the site. Continued monitoring of the prairie is needed. Of particular interest and concern are the responses of quackgrass, woody plants, and early spring forbs over the entire seven-year period. While any specific recommendations are tentative at present, continuation of prescribed burning on a delayed and less frequent basis may be needed, complemented with other restorative measures within the quackgrass stands.

In conclusion, five years of repetitive spring burns significantly improved the structure, composition, and diversity of a severely degraded native prairie site. The procedure may be most effective on sites where native prairie inclusions are large and well-dispersed within a large matrix of degraded sod dominated by brush or alien, cool-season grasses. If dispersion and quality of the inclusions are poor, as at the study site, interplantings of native materials may greatly promote the recovery process.

ACKNOWLEDGEMENTS

Appreciation is extended to the Midwest Region of the U.S. National Park Service for providing financial and technical assistance during conduct of the study. Park personnel conducted the burns each year. Individuals from the National Park Service who were particularly helpful were Chuck Derby, Denise Boudreau, Vince Halvorson, and Gary Willson.

LITERATURE CITED

Aldous, A.E. 1934. Effect of burning on Kansas bluestem pastures. Kansas Agricultural Experiment Station Technical Bulletin 38:1-65.

Anderson, K.L., E.F. Smith, and C.E. Owensby. 1970. Burning bluestem range. Journal of Range Management 23:81-92.

Anderson, H.G., and A.W. Bailey. 1979. Effect of fire on a *Symphoricarpos occidentalis* shrub community in central Alberta. Canadian Journal of Botany 57:2819-2823.

Anderson, H.G., and A.W. Bailey. 1980. Effects of annual burning on grassland in the aspen parkland of east-central Alberta. Canadian Journal of Botany 8:985-996.

Anderson, R.C. 1972. The use of fire as a management tool on the Curtis Prairie. Proceedings of Tall Timber Ecology Conference 12:23-35.

Becker, D.A., T.B. Bragg, and D.M. Sutherland. 1986. Vegetation Survey and Prairie Management Plan. Ecosystems Management, Elkhorn, Nebraska.

Curtis, J.T., and M.L. Partch. 1948. Effects of fire on competition between bluegrass and certain prairie plants. American Midland Naturalist 39: 437-443.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Scientist 33:43-64.

Great Plains Flora Association. 1986. Flora of the Great Plains. University of Kansas Press, Lawrence.

Henderson, R.A., D.L. Lovell, and E.A. Howell. 1982. The flowering responses of 7 grasses to seasonal timing of prescribed burns in remnant Wisconsin prairie. Pages 7-10. *In* R. Brewer (ed.). Proceedings of the North American Prairie Conference, Western Michigan University, Kalamazoo, Michigan.

Hopkins, H.H., F.W. Albertson, and A. Riegel. 1948. Some effects of burning upon a prairie in west-central Kansas. Kansas Academy Science Transactions 51:131-141.

Kucera, C.L. 1970. Ecological effects of fire on tallgrass. Page 12. *In* P. Schramm (ed.). Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College, Galesburg, Illinois.

Kucera, C.L., and M. Koelling. 1964. The influence of fire on composition of central Missouri prairie. American Midland Naturalist 72:142-147.

Landers, R.Q., Jr. 1975. A report of management of native prairie areas, Pipestone National Monument. Iowa State University, Ames.

Owensby, C.E., and E.F. Smith. 1972. Burning true prairie. Pages 1-14. *In* L.C. Hulbert (ed.). Proceedings of the Third Midwest Prairie Conference. Kansas State University, Manhattan.

Svedarsky, W.D., P.E. Buckley, and T.A. Feiro. 1986. The effects of 13 years of annual burning on aspen-prairie ecotone in northwestern Minnesota. Pages 118-122. *In* G. Clambey and R. Pemble (eds.). Proceedings of the Ninth North American Prairie Conference. Tri-College University Center for Environmental Studies, Moorhead, Minnesota.

U.S. Department of Commerce. 1982-87. Climatological Data-Minnesota. Volumes 89, 90, 91, 92, 93. National Oceanic and Atmospheric Administration, Asheville, North Carolina.

Weaver, J.E., and N.W. Rowland. 1952. Effects of excessive natural mulch on development, yield and structure of native grassland. Botanical Gazette ll4:1-19.

Vogl, R.J. 1974. Effects of fire on grassland. Pages 139-193. *In* T.T. Kozlowski and C.E. Ahlgren (eds.). Fire and ecosystems. Academic Press, New York.

EFFECT OF BURNING ON GERMINATION OF TALLGRASS PRAIRIE PLANT SPECIES

Sherry R. Rohn and Thomas B. Bragg
Department of Biology, University of Nebraska-Omaha, Omaha, Nebraska 68182

Abstract. Seeds from 10 prairie plant species of burned and unburned portions of three tallgrass prairies were collected and tested for germinability. Germination of big bluestem (*Andropogon gerardii* Vitman) consistently averaged higher with burning. Indiangrass (*Sorghastrum nutans* L.) and sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] averaged 5% higher with burning on two of the three sites, although for indiangrass average germination for all three sites was 7% lower. Species for which germination declined with burning were false sunflower [*Heliopsis helianthoides* (L.) Sweet var. *scabra* (Dun.) Fern.], -13%; wholeleaf rosinweed (*Silphium integrifolium* Michx.), -10%; and white prairieclover (*Dalea candida* Michx. *ex* Willd.), -4%. For all species combined, burning also delayed peak germination and extended the length of time of germination.

Key Words. fire, germination, tallgrass prairie, Nebraska

INTRODUCTION

Fire, a natural component of the tallgrass prairie ecosystem, has been found both to increase seed production in some species, such as big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Andropogon scoparius* Michx.), and indiangrass (*Sorghastrum nutans* L.) (Risser *et al.* 1981), and to decrease it in others, such as western ironweed (*Vernonia baldwinii* Torr. var. *baldwinii*) (Knapp 1984). In addition, percent germination has been found to be higher for seeds produced from burned areas for big bluestem, little bluestem, and Canada wild rye (*Elymus canadensis* L.) (Ehrenreich and Aikman 1957). Went *et al.* (1952) indicate that increased *in situ* germination in burned areas was due largely to better conditions created by the fire, but Daubenmire (1970) suggests that increased germination reflects the greater vigor and vitality of the burned plant itself. Other than these studies, little has been done to evaluate the effects of burning on seed germination of prairie species. The purpose of this study, therefore, was to expand this information with the specific focus being to evaluate the effect of burning on germination of several prairie species. This study was intended only as a limited, single-year, study to provide preliminary information for further, more detailed research. The study was not designed as a full, statistical evaluation of all aspects of fire effects on germination.

METHODS AND MATERIALS

Seeds of ten prairie plant species (Table 1) were collected in September 1985 from burned and unburned areas of three grass-

Table 1. Germination (%) of ten prairie species in burned and unburned sites. Species ordered from most positive to most negative response to burning based on averages for all sites. n = 30/treatment area/site. Emergence data are for combined sites. BU = Unburned; B = Burned; — = no data available. Species nomenclature is from the Great Plains Flora Association (1986).

	Hover Prairie		*Stolley Prairie*		*Allwine Prairie*		*Days to First Emergence*	
	UB	*B*	*UB*	*B*	*UB*	*B*	*UB*	*B*
	%						days	
Big bluestem (*Andropogon gerardii* Vitman)	—	—	3	13	7	20	32	16
Leadplant (*Amorpha canescens* Pursh)	20	33	3	3	—	—	40	14
Side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.]	30	13	10	20	20	43	22	10
Canada wild rye (*Elymus canadensis* L.)	100	100	100	100	—	—	10	8
Finger coreopsis (*Coreopsis palmata* Nutt.)	20	23	20	17	—	—	9	10
Switchgrass (*Panicum virgatum* L.)	10	0	0	10	13	13	17	24
White prairie clover (*Dalea candida* Michx. *ex* Willd.)	13	13	17	10	—	—	14	14
Indiangrass (*Sorghastrum nutans* L.)	50	3	0	17	7	17	18	37
Wholeleaf rosinweed (*Silphium integrifolium* Michx.)	37	17	47	47	—	—	10	14
False sunflower [*Heliopsis helianthoides* (L.) Sweet var. *scabra* (Dun.) Fern.]	37	13	33	30	—	—	14	11

lands: Hover Prairie and Stolley Prairie, two native grasslands, and Allwine Prairie Preserve, a reestablished grassland. All sites were situated in east central Nebraska within 15 km of Omaha. Selection of different study areas was designed to allow the results to be more generally applicable to the tallgrass prairie region. Prescribed burns were conducted during late April 1985; unburned areas were last burned in Spring 1982. The species selected were determined by seed availability and by the intent to consider a variety of grasses and forbs. Due to low species diversity at Allwine Prairie, only indiangrass, big bluestem, switchgrass (*Panicum virgatum* L.), and sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] were collected. Plants at this site were from seed provided by the Soil Conservation Service and were probably of Kansas origin.

Seeds were collected from at least ten individuals of each species at each site and for each treatment (burned or unburned). All seeds from a single species/site/treatment were combined in a single paper sack. Samples at each site were not replicated. All awns, hairs, and glumes were left on seeds. The seeds were stored at room temperature for six weeks. During this time, filled seeds, presumably viable, were visually separated from chaff and from unfilled seeds using a dissecting microscope. The principal means used to separate filled from unfilled seeds was to use gentle pressure of a finger nail against the caryopsis. This procedure was especially important for those species with loose lemmae and paleae such as indiangrass, big bluestem, and sideoats grama. For species with hard lemmae and paleae, such as switchgrass, selection of viable seeds was slightly more subjective being based on general fullness of appearance of seeds. In addition to these criteria, seeds with apparent damage by herbivores were also excluded.

From each species/site/treatment sample, 30 seeds were randomly selected and stratified by placing them on moist filter paper in petri dishes and storing them at 0 C for four weeks. During this time, the filter paper was regularly checked and moistened with distilled water when found dry. After stratification, the seeds were planted in flats in a greenhouse. The flats contained a sterile mixture of 1:1:1 sand, peat, and clay loam soil. Burned and unburned samples were planted side by side in rows that were separated by dividers. Planting depth was approximately 0.1 cm. Flats were kept moist and rotated weekly to reduce any effects of location. No attempt was made to adjust photoperiod. Maximum greenhouse temperatures during this time varied from 16-19 C.

Seedling emergence was used as the indicator of seed germination success. The flats were checked daily for the first two weeks after planting, every other day during the third week, and only weekly for the fourth and subsequent weeks. The study was terminated after 13 weeks. At each observation, the occurrence of new seedlings was recorded and each individual marked with a toothpick.

RESULTS AND DISCUSSION

Total germination averaged 25% for combined seeds from the burned area and 23% for the unburned area. Canada wild rye germination was 100% for both treatments. The second highest total germination was for wholeleaf rosinweed (*Silphium integrifolium* Michx.) which averaged 47% in both the burned and unburned portions of one site (Table 1). The lowest average germination was 7% for switchgrass, although no germination occurred in two samples of this species as well as in one sample of indiangrass.

Big bluestem was the only species for which germination consistently increased with burning. Despite a spring burn, flowering of this species at one site was unexplainably low during 1985 suggesting between-site differences which could explain some of the variability of results obtained. The 10% average increase in germination of big bluestem with burning was similar to the 7% increase reported by Ehrenreich and Aikman (1957). While the response of germination to burning varied by site for other species, average germination for combined sites showed slight increases with burning for leadplant (*Amorpha canescens* Pursh) and sideoats grama. Germination of sideoats grama increased with burning in two sites but declined in the third. Germination of indiangrass is

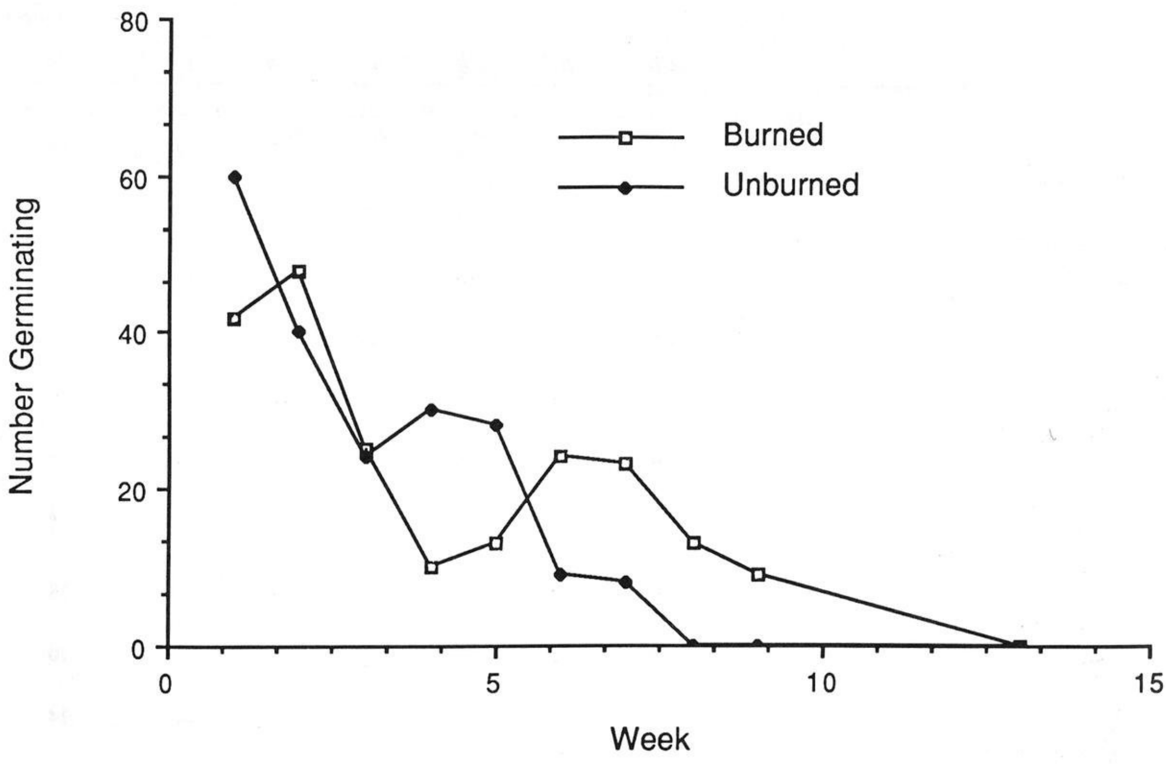


FIG. 1. Germination of combined seeds of 10 prairie species collected from burned and unburned sites in 1985.

also likely to increase with burning. While the average value for combined sites showed a 7% decline in germination of indiangrass, two sites showed increases (+14%) and only one decreased (-47%). Decreases in sideoats grama and indiangrass were both recorded for the same prairie (Hover Prairie) although no explanation for this difference in response is apparent. An increase in germination of indiangrass with burning is consistent with the results reported by Ehrenreich and Aikman (1957) although the increase they noted was only 2%.

Of species for which germination declined with burning, only false sunflower [*Heliopsis helianthoides* (L.) Sweet var. *scabra* (Dun.) Fern.] showed this response at all sites. For combined sites, however, average germination decline for wholeleaf rosin weed (-7%). Ehrenreich and Aikman (1957) indicated a substantial (36%) decline in germination of Canada wild rye with burning but, in this study, germination of this species was unaffected with all seeds germinating regardless of treatment.

The number of days before germination of the first seedling of a species was also quite variable (Table 1). For burned areas, these dates varied from as early as 8 days for Canada wild rye to as late as 37 days for indiangrass. Unburned areas varied from 9 days for finger coreopsis (*Coreopsis palmata* Nutt.) to 40 days for leadplant.

Germination over time for all species combined provides a general perspective of post-burn germination in grasslands. The results of this study indicated first, that two peaks occurred in germination; and second, that these peaks differed somewhat for burned and unburned areas. The highest germination, for both burned and unburned areas, occurred within the first 1-2 weeks of planting (Fig. 1). For seeds from the unburned area, this initial flush of germination occurred within the first week. For burned area seeds, the peak occurred during the second week. The subsequent peak occurred from weeks 4-5 for the unburned areas and weeks 6-7 for burned areas. Germination of seed continued for at least a week longer in the burned area than in the unburned area. Burning, thus, appears to both delay and extend germination.

The combined results of this study suggest that burning has the potential to affect the germination of seeds of prairie plants in various ways including increasing germination in some species and decreasing it in others and also altering the time and duration of overall germination. The variability of the results between sites, however, suggests that burning alone may not explain the germination responses observed. It is likely, for example, that different burning conditions occurred at each site or at each plant within a site and that these differently affected individuals. Moreover, it seems clear that there is some physiological response of prairie plants to burning that yet needs to be identified. Studies on physiological effects of fire on prairie plants, therefore, will be necessary to further explain the observed responses. From the results obtained, it is clear that a larger and more detailed sampling is needed to further refine our understanding of this aspect of prairie fire ecology.

ACKNOWLEDGEMENTS

The authors wish to thank Dr. David M. Sutherland, Department of Biology, University of Nebraska-Omaha, for his assistance in field collections and seedling identification.

LITERATURE CITED

Daubenmire R. 1968. Ecology of fire in grasslands. Pages 209-266. *In* J. B. Cragg (ed.) Advances in Ecological Research, Volume 5. Academic Press, New York.

Ehrenreich, J.H., and J.M. Aikman. 1957. Effect of burning on seedstalk production of native prairie grasses. Proceedings of the Iowa Academy of Science 64:205-212.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Knapp, A. 1984. Effect of fire in tallgrass prairie on seed production of *Vernonia baldwinii* Torr. (Compositae). Southwestern Naturalist 29:242-243.

Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.S. Parton, and J.A. Weins. 1981. The True Prairie ecosystem. Hutchinson Ross Publishers, Stroudsburg, Pennsylvania.

Went, F.W., G. Juhren, and M.C. Juhren. 1952. Fire and biotic factors affecting germination. Ecology 33:351-364.

RODENTS AND SHREWS IN UNGRAZED TALLGRASS PRAIRIE MANIPULATED BY FIRE

Donald W. Kaufman, Glennis A. Kaufman, and Elmer J. Finck
Division of Biology, Kansas State University, Manhattan, Kansas 66506

Abstract. Natural prairie was a mosaic of patches of depths of plant litter due to topoedaphic conditions and to spatial-temporal variation in fire and grazing. Such variation in litter depth undoubtedly influenced the distribution and abundance of small mammals. To examine this issue, small mammals were censused and plant litter depth was measured during autumn from 1981 to 1984 on the Konza Prairie Research Natural Area near Manhattan, Kansas. Five to 11 sites subjected to fire at different times from 1967 to 1984 were sampled during each of the four years of the study. Relative densities of deer mice (*Peromyscus maniculatus*) were negatively correlated to litter depth, whereas relative densities of Elliot's short-tailed shrews (*Blarina hylophaga*) and western harvest mice (*Reithrodontomys megalotis*) were positively correlated to the depth of plant litter. White-footed mice (*Peromyscus leucopus*), typically found in wooded and brushy habitats, were captured in prairie sites, but no significant association with plant litter was evident. Although prairie voles (*Microtus ochrogaster*) were expected to be positively associated with litter, no significant relationship was found for 1982 (the only year with sufficiently high densities to test for a possible pattern).

Key Words. small mammals, plant litter, tallgrass prairie, fire, rodents, shrews, Kansas

INTRODUCTION

General observations in tallgrass and mixed grass prairies reveal dramatic spatial and temporal variation in plant litter depth as the result of grazing by large ungulates, occurrence of fire, and topoedaphic conditions. Presettlement prairie would have been a mosaic of habitat patches with different depths of litter brought about by spatial variation in grazing by bison (*Bison bison*), occurrence and intensity of natural and anthropogenic fires, and topoedaphic conditions. For many species of grassland animals, suitability of a habitat patch undoubtedly would have been influenced by the depth of the litter layer. For example, Henslow's sparrows (*Ammodramus henslowii*) require a well-developed layer of standing dead vegetation in their territories (Zimmerman 1988). Further, use of local areas of prairie by deer mice (*Peromyscus maniculatus*), as censused by use of individual trap stations, is negatively related to the depth of litter (Kaufman *et al.* 1988).

To examine possible relationships between litter architecture and use of prairie by rodents and shrews, small mammals were censused and plant litter depth was measured in watersheds with different fire histories on the Konza Prairie Research Natural Area. Based on general habitat associations, negative relationships were expected between density and plant litter depth for some species of small mammals (e.g., the deer mouse), and positive relationships were expected for others (e.g., the prairie vole, *Microtus ochrogaster*; western harvest mouse, *Reithrodontomys megalotis*; and Elliot's short-tailed shrew, *Blarina hylophaga*).

The objective of this research was to test these predictions as well as examine the relationships of plant litter depth to species richness and diversity of the assemblages of small mammals found in different habitats in the tallgrass prairie of the Flint Hills region of eastern Kansas. An additional objective was to test for a possible relationship between litter and use of prairie by the white-footed mouse (*Peromyscus leucopus*), which is typically a woodland rodent that is caught only infrequently in prairie sites.

STUDY AREA AND METHODS

This study was conducted on the Konza Prairie Research Natural Area which is located south of Manhattan in Riley and Geary counties, Kansas. This 3,487-ha site is characterized by steep-sided hills with flat-topped ridges dissected by ravines that create lowland prairie. The area was grazed by domestic livestock for over 100 years before establishment of the Konza Prairie Research Natural Area in 1971-1977, but no cattle have been grazed on these research sites since 1977. Vegetation is typical of tallgrass prairie of the Flint Hills which is dominated by big bluestem (*Andropogon gerardii* Vitman), indiangrass [*Sorghastrum nutans* (L.) Nash], and little bluestem (*Andropogon scoparius* Michx). Several other grasses, numerous forbs, and some shrubs occur commonly in prairie habitats on Konza Prairie (Freeman and Hulbert 1985). Additional information on habitat types as well as mammals found on the Konza Prairie is given in Finck *et al.* (1986) and Kaufman *et al.* (1988).

Small mammals and litter conditions were studied along permanent trap lines in 10 watersheds in 1981, 11 in 1982, 5 in 1983, and 10 in 1984. Time since last fire for each watershed in each year is summarized in Table 1. The first year after fire indicates that the watershed was sampled in autumn after a spring fire approximately six months earlier, the second year in autumn approximately 18 months after fire, and so forth.

Table 1. Years since last fire for each watershed sampled in each year.

Watershed	*1981*	*1982*	*1983*	*1984*
	years			
1D	1	1	—	1
10A	1	2	3	4
4F	1	2	—	4
4G	2	3	—	1
4B	3	4	1	2
4D	4	1	2	3
20B	9	10	11	12
NUD	14	15	—	—
N1B	14	15	—	17
N4D	14	15	16	17
NUB	—	3	—	5

Small mammals were sampled in each watershed in each year using two permanent 20-station census lines with a 15 m interstation distance. These lines were placed so that similar mixtures of upland, hillside, and lowland prairie were trapped in each watershed. Traps were set and checked on each line for four consecutive days during October in each of the four years. Two large Sherman live traps (7.6 X 8.9 X 22.9 cm) were set within 1 m of each station marker. Bait was a mixture of peanut butter and rolled oats molded into a small ball and suspended in weighing paper from the back door of the trap. Polyester fiberfill was used as nesting material in each trap. Small mammals were toe-clipped and released at the point of capture. Relative densities of small mammals were calculated as the average number of unique individuals caught per trap line in each watershed in each year.

Litter depth was indexed at 20 points around each trap station during November of each year. This was done by placing a 2-m length of metal conduit (18 mm in diameter) straight down through the vegetation and recording the presence of litter touching the pole at a height of 0-1 cm (height class 1), 1-10 cm (height class 2), and above 10 cm (height class 3). The 20 points around each station were on four transects radiating out from the station marker at approximately 45° from the axis of the trap line. The sampling points along each of the four transects were chosen by stepping from the station marker to a point approximately 1.5 m from the station marker and placing the conduit directly down through the vegetation. Point 2 was chosen by stepping about 1.5 m from point 1; this procedure was repeated for the remaining points along each transect. Data from the 20 points around each station along the two trap lines in each watershed (a total of 40 stations) were used to calculate the average percent occurrence of plant litter in the three height classes for each watershed in each year. A summary index of litter depth was created by adding the percent occurrences for all three height classes; this is the litter index used for tests of relationships of small mammals to litter reported in this paper.

In addition to litter height, the presence of vegetation or litter under the conduit was also recorded. Subtraction of the percent occurrence of both litter and vegetation from 100% yielded an index to the percent of bare surface in each watershed.

Table 2. Relative density of small mammals (numbers/trap line) during 1981-1984.

Species	*1981*[1]	*1982*[1]	*1983*[1]	*1984*[1]
	numbers/trap line			
Deer mouse	6.1	5.0	3.2	4.6
Elliot's short-tailed shrew	2.9	5.8	3.4	3.9
Western harvst mouse	5.2	6.3	0.7	0.1
White-footed mouse	3.3	2.3	0.4	1.8
Prairie vole	1.2	5.9	0.2	0.6
Thirteen-lined ground squirrel	0.3	0.6	2.0	0.6
Cotton rat	3.8	0.5	0.2	0.0
Hispid pocket mouse	0.1	0.1	0.4	0.0
Plains harvest mouse	0.6	0.3	0.0	0.0
House mouse	0.3	0.1	0.0	0.0
Meadow jumping mouse	0.1	0.0	0.0	0.0
Southern bog lemming	0.0	0.8	0.0	0.0
Least shrew	0.0	0.2	0.0	0.0

[1]Numbers of trap lines/year 2343 20 in 1981, 22 in 1982, 10 in 1983, and 20 in 1984.

RESULTS

Thirteen species of small mammals (11 of rodents and 2 of shrews) were recorded during the four years of the study with 11 species caught in 1981, 12 in 1982, 8 in 1983, and 6 in 1984. The average number of small mammals caught per trap line was 19.1 in 1981, 22.5 in 1982, 8.9 in 1983, and 10.0 in 1984. The thirteen species caught were the deer mouse, Elliot's short-tailed shrew, western harvest mouse, white-footed mouse, prairie vole,

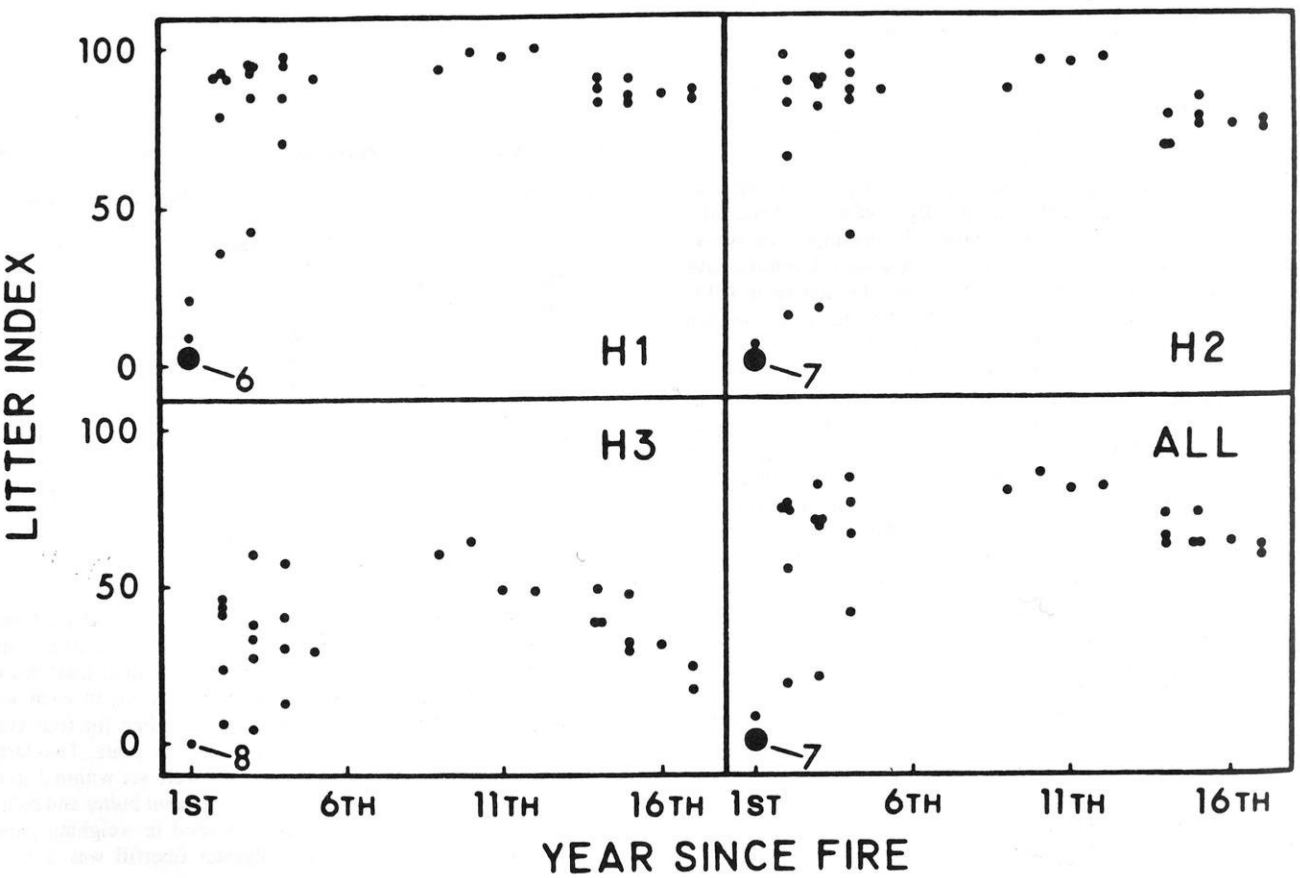


FIG. 1. Relationships between percent occurrence of litter and year since fire for height classes of 0-1 cm (H1), 1-10 cm (H2), above 10 cm (H3), and sum of H1, H2, and H3 (ALL; y-axis values should be multiplied by three for ALL). Values plotted for first year (1st) are for autumn during the first year after an experimental spring fire and so forth. Numbers associated with small and large dots indicate the number of sample points that are encompassed by the area of the dot.

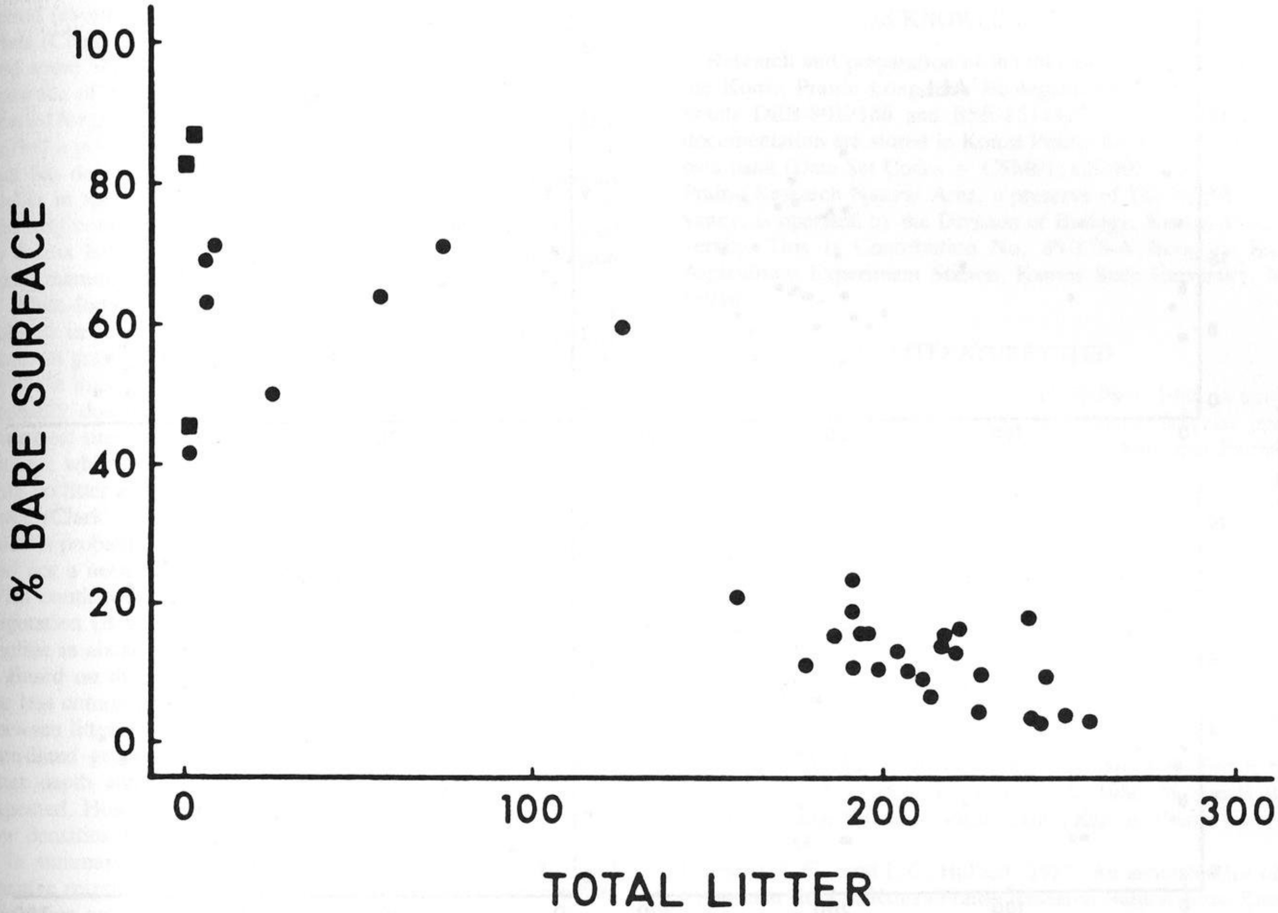


FIG. 2. Relationship between percent bare surface and total litter. Squares are for the annually burned treatment (same site sampled in 1981, 1982, and 1984).

thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), cotton rat (*Sigmodon hispidus*), hispid pocket mouse (*Chaetodipus hispidus*), plains harvest mouse (*Reithrodontomys montanus*), house mouse (*Mus musculus*), meadow jumping mouse (*Zapus hudsonius*), southern bog lemming (*Synaptomys cooperi*), and least shrew (*Cryptotis parva*). Relative densities of each of these species are summarized by year in Table 2.

Changes in percent occurrence of plant litter with time since fire are summarized in Figure 1. The lowest values for each index occurred during the first autumn after experimental spring fires with the major change between the first and second year following a fire. The lowest values for the second, third, and fourth years after fire were all recorded during 1981 and were probably due to a small amount of new litter added following the low production of plant biomass in 1980 (Abrams *et al.* 1986). As expected, the amount of bare soil surface decreased as the amount of litter increased ($r = -0.92$, d.f. = 34, $P < 0.001$; Figure 2).

No significant pattern was evident between numbers of small mammals caught per trap line and litter depth ($r = -0.23$, d.f. = 34, $P > 0.10$; Figure 3). This lack of a significant relationship remained when all sites in the first year after fire were excluded from the analysis ($r = -0.01$, d.f. = 26, $P > 0.10$). As with assemblage abundance, no other assemblage characteristic was correlated with litter depth [species richness (number of species): $r = -0.04$, d.f. = 34, $P > 0.10$; species diversity (Shannon-Wiener H'): $r = -0.01$, d.f. = 34, $P > 0.10$; evenness (Shannon-Wiener J): $r = -0.06$, d.f. = 34, $P > 0.10$]. Exclusion of all sites in the first year after fire (the eight sites with the lowest litter depth) did not alter the lack of relationships of species richness, diversity, and evenness to litter depth ($P > 0.10$ in all cases).

Relative densities of deer mice were negatively related to plant litter ($r = -0.70$, d.f. = 34, $P < 0.001$; Figure 3). This general relationship remained after exclusion of the eight samples taken from watersheds in the first year after fire ($r = -0.45$, d.f. = 26, $P < 0.05$).

In contrast to the deer mice, autumnal densities of Elliot's short-tailed shrews were positively correlated to the depth of plant litter ($r = 0.42$, d.f. = 34, $P < 0.01$; Figure 3). The positive relationship was strengthened by exclusion of all samples collected from watersheds in the first year after experimental spring fire ($r = 0.62$, d.f. = 26, $P < 0.01$).

Western harvest mice were abundant in 1981 and 1982, but densities in 1983 and 1984 were too low for analysis. For 1981 and 1982, relative densities were positively correlated with litter depth ($r = 0.48$, d.f. = 19, $P < 0.05$; Figure 3). With removal from the analysis of samples from watersheds in the first year after fire, no significant relationship remained between relative density of western harvest mice and litter depth ($r = 0.14$, d.f. = 14, $P > 0.10$).

Although prairie voles were moderately abundant in 1982, density was not correlated to litter depth ($r = -0.33$, d.f. = 9, $P > 0.10$). Removal of the sites in the first year after fire did not alter this basic finding ($r = -0.40$, d.f. = 7, $P > 0.10$). The relationship between relative density of prairie voles and depth of plant litter could not be tested using data from 1981, 1983, and 1984 due to the low density of voles.

Density of white-footed mice was highly variable among watersheds and years, but density was not correlated to depth of plant litter ($r = -0.21$, d.f. = 29, $P > 0.10$ with 1983 data excluded due to low densities). When the sites in the first year after fire

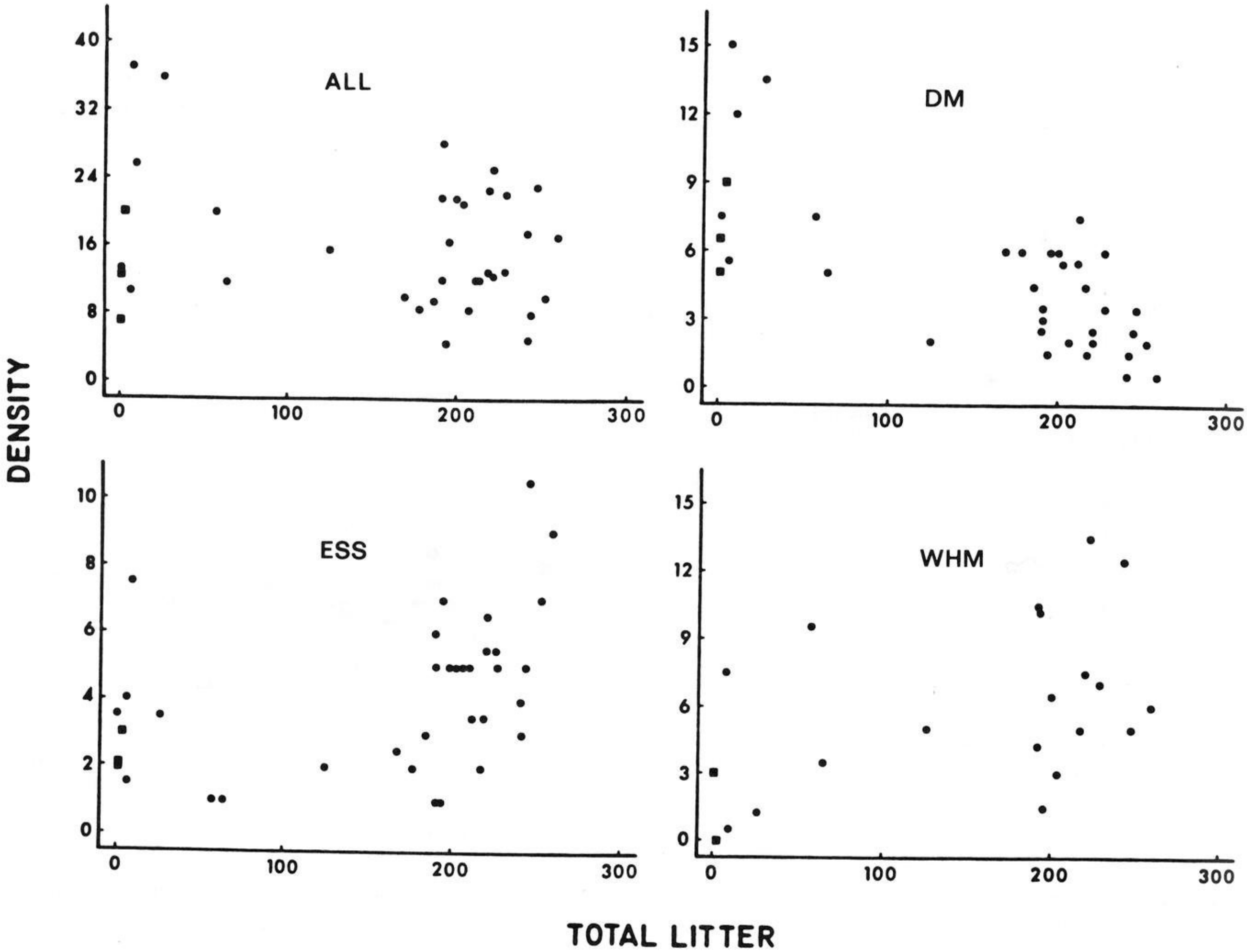


FIG. 3. Relationships between relative density (individuals/trap line) and litter depth for all species of small mammals combined (ALL), deer mice (DM), Elliot's short-tailed shrews (ESS), and western harvest mice (WHM, only 1981 and 1982). Squares are for the annually burned watershed.

were excluded, however, the negative relationship between relative density and litter depth approached significance ($r = -0.35$, d.f. $= 22$, $0.10 > P > 0.05$).

DISCUSSION

None of the characteristics of assemblages of small mammals (abundance, richness, diversity, and evenness) changed in any predictable manner with changes in litter depth. However, species composition changed with litter depth as indicated by the patterns of change observed for the three common grassland mammals (deer mouse, Elliot's short-tailed shrew, and western harvest mouse).

Densities of deer mice in tallgrass prairie decreased as the litter layer increased from nearly absent to more than 10 cm deep. This pattern was consistent with the high abundance of deer mice in open grasslands of the mixed grass prairie (Kaufman and Fleharty 1974). Also, use of small patches (represented by individual live trap stations) by deer mice was negatively associated with the amount of litter and positively associated with amount of bare ground and grass (Kaufman *et al.* 1988). Although these patterns were only correlative ones, laboratory studies indicated that deer mice selectively forage in areas with low litter (Clark 1989).

Elliot's short-tailed shrews, insectivores that forage in the litter layer, were positively associated with litter depth. These data do not suggest an upper bound to this litter depth association, but other observations suggest that the compaction of litter may have a negative effect on this species. Additionally, density values during the first year after fire were unexpectedly high given both the positive pattern and the relative density values for treatments with deep litter. The high values during the first autumn after a spring fire may be due to the availability of invertebrate prey even though the litter architecture is probably less than optimal for short-tailed shrews.

The western harvest mouse, a species that commonly nests aboveground (Webster and Jones 1982), showed a positive correlation with litter depth. However, no significant correlation remained when samples for treatments in the first year after fire were removed from the analysis. This suggests that this small rodent (10-15 g) requires some threshold depth of litter, but is little influenced by even deeper layers of plant litter. In agreement with our general observation of densities being higher in areas with litter versus those with essentially no litter, experimental studies demonstrated that western harvest mice foraged proportionately more often in microhabitats with litter relative to microhabitats without litter than did deer mice (Clark 1989). In contrast to the positive effect of litter on densities of western harvest mice, use of the area of individual trap stations was not directly related to the depth of litter surrounding the trap stations (Kaufman *et al.* 1988).

Based on these limited data, prairie voles did not show the expected positive response to litter depth, although they did respond favorably to the presence of litter in experimental foraging trials (Clark 1989). As a species that constructs surface runways and some aboveground nests (Tamarin 1985), perhaps, it is the presence of some minimal amount of vegetation and litter that is needed for protection and, in some cases, nest building. The failure to find a positive relationship is possibly due to the heavy foliage that has developed by autumn in areas burned about six months earlier in spring; this heavy foliage provides food and protection and may compensate for the lack of litter. Further study is needed to assess habitat requirements of this unexpectedly uncommon small mammal on Konza Prairie.

White-footed mice are typically associated with woody or brushy habitats in Kansas (Kaufman *et al.* 1983), and only infrequently occur in grasslands (Clark *et al.* 1987). Use of grassland habitats by these mice usually occurs in areas near trees or shrubs and is probably due to nocturnal foraging movements into the prairie from nest sites in wooded microhabitats. Under experimental conditions, white-footed mice foraged preferentially in microhabitats with no litter as compared to those with a moderate to heavy litter layer (Clark 1989). Therefore, the distribution of white-footed mice is probably related to the presence of tree and shrub patches and not a need for a deep layer of litter in the adjacent prairie. With continued frequent fire and subsequent removal of woody vegetation (Bragg and Hulbert 1976), white-footed mice should decline in abundance in grassland habitats on Konza Prairie.

Based on these findings and natural history characteristics of the less common rodents on Konza Prairie, negative relationships between litter depth and numbers of hispid pocket mice and thirteen-lined ground squirrels and a positive relationship between litter depth and numbers of southern bog lemmings would be expected. However, these patterns could not be examined due to low densities during these censuses.

In summary, the negative response of deer mice to litter and positive responses of Elliot's short-tailed shrews and western harvest mice were generally as expected from known habitat associations. In contrast to short-tailed shrews, however, harvest mice demonstrated no further increase in abundance after the first year's litter was in place, i.e., no relationship between density and litter with the first year after fire excluded. Laboratory studies of foraging behavior in patches with different depths of litter by deer mice and western harvest mice lend support to these correlative findings (Clark 1989). In addition, experimental work by Clark (1989) indicated a positive response of prairie voles to litter. This failure to find such an association between abundance and litter demonstrates the need for further study of the interaction of the architecture of live vegetation, standing dead vegetation, and litter in influencing habitat use by prairie voles. Fire-positive and fire-negative responses of small mammals to a spring fire in ungrazed tallgrass prairie are probably determined in large part by the removal of the litter layer. Because of the low amount of variance in autumnal density accounted for by litter depth, experimental manipulations (e.g., addition of litter to burned sites and mechanical removal of litter from unburned sites) need to be done to confirm the direct impact of litter on population levels reached by the end of the growing season in burned and unburned prairie.

ACKNOWLEDGEMENTS

Research and preparation of the manuscript were supported by the Konza Prairie Long-term Ecological Research project (NSF grants DEB-8012166 and BSR-8514327). Data and supporting documentation are stored in Konza Prairie Research Natural Area data bank (Data Set Codes = CSM01, CSM02, CSM04). Konza Prairie Research Natural Area, a preserve of The Nature Conservancy, is operated by the Division of Biology, Kansas State University. This is Contribution No. 89-126-A from the Kansas Agricultural Experiment Station, Kansas State University, Manhattan.

LITERATURE CITED

Abrams, M.D., A.K. Knapp, and L.C. Hulbert. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position. American Journal of Botany 73:1509-1515.

Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19-24.

Clark, B.K. 1989. Influence of litter and habitat structure on small mammal assemblages: experimental manipulations and field observations. Doctor of Philosophy Dissertation, Kansas State University, Manhattan.

Clark, B.K., D.W. Kaufman, G.A. Kaufman, and E.J. Finck. 1987. Use of tallgrass prairie by *Peromyscus leucopus*. Journal of Mammalogy 68:158-160.

Finck, E.J., D.W. Kaufman, G.A. Kaufman, S.K. Gurtz, B.K. Clark, L.J. McLellan, and B.S. Clark. 1986. Mammals of the Konza Prairie Research Natural Area, Kansas. Prairie Naturalist 18:153-166.

Freeman, C.C., and L.C. Hulbert. 1985. An annotated list of the vascular flora of Konza Prairie Research Natural Area, Kansas. Transactions of the Kansas Academy of Science 88:84-115.

Kaufman, D.W., and E.D. Fleharty. 1974. Habitat selection by nine species of rodents in north-central Kansas. Southwestern Naturalist 18:443-452.

Kaufman, D.W., S.K. Peterson, R. Fristik, and G.A. Kaufman. 1983. Effects of microhabitat features on habitat use by *Peromyscus leucopus*. American Midland Naturalist 110:177-185.

Kaufman, G.A., D.W. Kaufman, and E.J. Finck. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in ungrazed tallgrass prairie. Journal of Mammalogy 69:476-483.

Tamarin, R.H. (ed.) 1985. Biology of new world *Microtus*. Special Publication No. 8, American Society of Mammalogists.

Webster, W.D., and J.K. Jones, Jr. 1982. *Reithrodontomys megalotis*. Mammalian Species 167:1-5.

Zimmerman, J.L. 1988. Breeding season habitat selection by the Henslow's sparrow (*Ammodramus henslowii*) in Kansas. Wilson Bulletin 100:17-24.

EFFECTS OF PRESCRIBED FIRE ON SMALL MAMMALS IN ASPEN PARKLAND

Garry C. Trottier, Ludwig N. Carbyn, and George W. Scotter
Canadian Wildlife Service, Room 210, 4999-98 Avenue, Edmonton, Alberta T6B 2X3

Abstract. Relative abundance of small mammals was monitored in an area of aspen parkland burned periodically in spring or fall over eight years to control trembling aspen (*Populus tremuloides* Michx.) encroachment into grassland meadows. Seven small mammal species were trapped on the burned and control areas. Meadow voles (*Microtus pennsylvanicus* Ord) and red-backed voles (*Clethrionomys gapperi* Vigors) dominated the captures prior to burning. Meadow voles were the most abundant species trapped throughout the study, but abundance was affected by frequency of burning and habitat. After three vegetative growing seasons, meadow voles had not recovered to pre-burn abundance in burned grasslands. Red-backed voles declined in burned areas while deer mice (*Peromyscus maniculatus* Wagner) and meadow jumping mice (*Zapus hudsonius* Zimmermann) were more prevalent. No differences were observed in small mammal abundance related to spring versus fall burns.

Key Words. prescribed fire, small mammals, aspen parkland, Prince Albert National Park, Saskatchewan

INTRODUCTION

In 1975, the Canadian Parks Service initiated a study in Prince Albert National Park to examine the role of fire as a management tool to maintain grassland communities. The objectives were to determine the optimal burn frequency and season to control trembling aspen (*Populus tremuloides* Michx.) encroachment into grassland areas and to monitor wildlife responses to a severe regime of burn treatments involving annual and biennial burns.

METHODS

Description of the Study Area

Prince Albert National Park (2,407 km²) is located in central Saskatchewan. The northern two-thirds of the park is covered by dense coniferous and mixedwood forests. Although the whole area is included in the Mixedwood Forest zone (Rowe 1959), the southern one-third of the park more closely resembles the aspen parkland, which is the transition zone between northern coniferous forests and the grasslands of the mixed prairie and fescue prairie (Rowe and Coupland 1984). Trembling aspen and balsam poplar (*Populus balsamifera* L.) form groves which are interspersed with patches of open to semi-open rough fescue [*Festuca hallii* (Vasey) Piper] grasslands (Carbyn 1971). Scattered jack pine (*Pinus banksiana* Lamb.) are present. Most of the large grasslands are located on gently undulating glacial outwash deposits in the southwest corner of the park at about 53° 30″ N latitude.

The burn treatments were conducted at Westrom Flats, a rough fescue grassland surrounded by predominantly trembling aspen forest. Aspen bluffs and isolated jack pine trees were scattered throughout the grassland. Soils were very well-drained, stony Brown Chernozems.

Plowed fire guards divided the central portion of the grassland into three adjacent burn treatment areas. Two unburned control areas were left at the east and west ends of the grassland, respectively. Over the period 1975 through 1982, spring and fall burns were conducted as weather permitted. Treatment Area A (16.2 ha) was burned five times in the fall. Area B (16.0 ha) was burned three times in the fall, and Area C (33.6 ha) was burned four times in the spring.

Patches of ecotone habitat (trembling aspen trees and suckers) scattered throughout the grassland were variably stocked with aspen suckers up to 1.5 m tall in 1983 following the burn treatments. In general, spring-burned ecotone experienced 24-92% tree mortality and increased sucker density compared with 60-96% tree mortality and reduced sucker density with fall burning. Sucker density averaged 5.6 stems/m² in the former and 2.3 stems/m² in the latter.

Small Mammal Trapping Studies

The three small mammal trapping studies conducted over the term of the management burns employed different procedures and timing. A pre-burn study was conducted from 11 June through 21 August 1975 on four grids each consisting of 206 unbaited Sherman live traps set for five consecutive nights. Two grids were placed in grassland habitat and two in ecotone habitat. Information on locations of these grids was not available to the authors, therefore, it was not possible to assign 1975 captures to the specific burn treatment areas. All 1975 captures were reported as unburned control rather than as pre-burn data points for the various treatments.

The 1976 study, which followed the first burn sequence, employed lines of museum special snap traps baited with peanut butter. Three traps were set at each of ten stations at 20 m intervals along two lines in each treatment and the controls. Habitat type for each cluster was recorded. Sampling was conducted for three nights per trap line from 21 May through 9 June.

Fire effects of different burn frequencies and seasons were evaluated by comparing residual small mammal communities on the treatment areas and controls using snap trap lines set during August, 1983. Trap lines consisted of 40 museum special traps baited with peanut butter and set in pairs at approximately 10 m intervals. Traps were set for three consecutive nights within homogeneous habitat. Different burn treatments were trapped simultaneously for each habitat type (e.g. three nights in grassland cover, then three nights in ecotone cover). This served to control the effects of varying weather conditions.

In 1983 the cover of accumulated organic matter (litter) and exposed soil in each treatment and control area were estimated within a grid of 25 1 m² microplots by the canopy-coverage method of Daubenmire (1959). Two vegetation grids were established in ecotone and grassland habitat in each burn treatment and one in an unburned control area.

Where sufficient captures of small mammals were obtained, the data were evaluated using a Chi-square test to assess the effect of burn frequency and habitat on small mammals inhabiting post-burn vegetation. Vegetation litter and soil variables for grassland and ecotone habitat on the study area were compared using the two-sample Mann-Whitney U test.

RESULTS

The number and timing of prescribed burns dictated the number of vegetation growing seasons that had elapsed prior to the final small mammal trapping survey conducted on the treatment areas during August 1983 (Table 1). Fall burn Area A, which was burned more frequently than fall burn Area B, had three growing seasons for recovery. Area B and spring burn Area C had two growing seasons for recovery. n nSeven small mammal species were captured on the study area over the term of the study. They were, in order of relative abundance, meadow vole (*Microtus pennsylvanicus* Ord), red-backed vole (*Clethrionomys gapperi* Vigors), deer mouse (*Peromyscus maniculatus* Wagner), meadow jumping mouse (*Zapus hudsonius* Zimmermann), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus* Mitchell), northern pocket gopher (*Thomomys talpoides* Richardson), and least chipmunk (*Eutamias minimus* Bachman). Only the four most frequently captured species (Table 2) are discussed further in this paper.

Meadow voles were the most abundant on the study area in contrast to the other species whose relative status changed following the burns (Table 2). Red-backed voles, which were quite abundant in unburned ecotone areas prior to burning, had not recovered to pre-burn abundance after three post-burn vegetative growing seasons. Conversely, deer mice and meadow jumping mice responded positively to burning, particularly in the ecotone areas, although the small number of captures precluded a statistical test of the trend.

Captures of meadow voles in spring 1976 were almost none as compared with 1975 (Table 2). Little vegetation recovery would have occurred at that time nor would there have been sufficient time for displaced populations to reoccupy and repopulate the burn areas. However, the capture rate in unburned control areas was also extremely low suggesting that other factors, perhaps population cycle or season of trapping, had an effect.

Burn frequency had a pronounced residual impact on meadow vole numbers in grassland habitat but not in ecotone habitat (Table 2). Four spring and five fall burns significantly reduced meadow voles compared with unburned grassland and the area burned three times (Chi-square = 58.28, d.f. = 3, $P < 0.005$). In contrast, meadow vole captures were the same in burned and unburned ecotone and for the different burn frequencies (Chi-square = 1.758, d.f. = 3, $P = 0.624$). This latter observation was not expected because ground cover of vegetation litter in the burned grasslands was either greater or not significantly different from that in the burned ecotone areas (Table 3).

The interaction of habitat had an influence on small mammal numbers in the burn treatment areas. More meadow voles (Chi-square = 30.7, d.f. = 3, $P < 0.005$), red-backed voles, deer mice, and meadow jumping mice were captured in ecotone than in grassland habitat.

Visual examination of the capture results indicated no difference in the effect of burn season on small mammals (Table 2). Lack of a spring burn treatment area with low burn frequency and the low capture rates precluded any evaluation of burn season effects.

DISCUSSION

The major effect of burning on small mammals is related to vegetation modification which, in turn, affects food resources and cover. Vegetation modification also alters microclimate (moisture

Table 1. Prescribed burns at Westrom Flats, Prince Albert National Park, Saskatchewan.

Burn study area	Burn season	Number of burns	75	76	77	78	79	80	81	82
			Burn years: 1975-1982							
A	Fall	5	X	X			X	X	X	
B	Fall	3	X				X	X		
C	Spring	4		X	X				X	X

Table 2. Small mammal captures for three different years on burn treatment sites and unburned controls at Westrom Flats, Prince Albert National Park, Saskatchewan ("—" = not evaluated).

Species and year	Grassland habitat				Ecotone habitat			
		Burn area[1]				Burn area[1]		
	Control	A	B	C	Control	A	B	C
Meadow vole								
1975	65	—	—	—	50	—	—	—
1976	5	0	0	—	1	0	0	—
1983	25	1	9	—	33	30	26	33
Red-backed vole								
1975	0	—	—	—	38	—	—	—
1976	0	0	0	—	0	0	3	—
1983	0	0	0	0	0	0	0	0
Deer mouse								
1975	0	—	—	—	1	—	—	—
1976	0	0	0	—	0	0	2	—
1983	0	0	0	0	0	6	2	0
Meadow jumping mouse								
1975	0	—	—	—	2	—	—	—
1976	0	0	0	—	0	0	0	—
1983	1	0	0	0	2	6	0	0

[1]Area A five fall burns.
Area B three fall burns.
Area C four spring burns.

Table 3. End-of-study litter (%) and bare ground (%) measured in 1983 at Westrom Flats, Prince Albert National Park, Saskatchewan.

Treatment	Growing[1] seasons	Litter		Soil	
		Grassland	Ecotone	Grassland	Ecotone
		% cover			
Control	N/A	94[2]	38[2]	2	6
3 fall burns	3	69[2]	44[2]	19[2]	33[2]
4 spring burns	2	27	28	67	51
5 fall burns	2	20	22	67[2]	50[2]

[1]Number of growing seasons since the last prescribed burn.
[2]Grassland and ecotone values differed significantly different (Mann-Whitney U test, $P < 0.001$).

regime and temperature) at ground level (Ream 1981, Wright and Bailey 1982). Over the short term, burning results in loss of cover and food, injury and death to some individuals, and increased exposure to predation. Over the long term, some species increase following burns due to the surge in herbage growth, increased seed production, and increased density of certain insect populations.

The depressed capture rate of meadow voles on the more frequently burned grassland areas in this study was probably due to loss of litter. Litter decreased and exposed soil increased as fire frequency increased (Table 3). This effect was tempered by the fact that the area with the lowest burn frequency also experienced one more year of vegetation recovery than the more frequently burned areas. However, the area burned five times had less litter cover than the area burned four times, with the same recovery time.

In contrast to the burned grassland areas, meadow vole captures in the ecotones were unaffected by burning. Litter cover did not appear to be a factor limiting the presence of small mammals in ecotones, because even in unburned ecotones, the ground cover of litter was less than one-half that of unburned grassland and was considerably less than in grassland burned three times (Table 3). Perhaps the abundance of trembling aspen suckers and the large amount of dead and downed woody material provided sufficient cover, particularly for protection from predators. Cover was an important habitat factor affecting site occupancy by meadow voles (Cook 1959, Ream 1981). Vacanti and Geluso (1985) also observed that meadow voles were not killed by fire and emigrated to better cover when disturbed.

Two vegetative growing seasons following fire disturbance appeared to be sufficient time for meadow voles to reoccupy burned ecotone in the aspen parkland. It appeared to take more than three growing seasons for populations to recover in burned grassland habitat. Meadow voles have been observed to be severely depleted for up to two years following prescribed burning in grasslands and then to recover as organic matter accumulates at ground level (Cook 1959, Vacanti and Geluso 1985, Driver 1987). Chance (1986), however, found that meadow voles recovered to pre-burn numbers in grassland ten months after a fall burn.

Ahlgren (1966) and Viereck (1979) found that red-backed voles were sensitive to burning and that populations remained low for at least two years following a burn. Three red-backed voles were captured in burned ecotone three growing seasons after the last burn, but the numbers were much depressed compared to the pre-burn trapping study in 1975. Since no red-backed voles were captured in unburned ecotone during 1983, it is possible that some other factor was affecting overall presence of this species in the study area. Tester (1965) postulated that the post-burn flush of herbs attracted the red-backed voles that were captured in burned areas, because this species traditionally occupies a variety of habitats within its home range.

Deer mice and meadow jumping mice were expected to occur more frequently in areas that had been recently burned. Although insufficient numbers of these species were captured for confirmation, an increase did occur in capture of these species compared with pre-burn conditions in 1975 and with the unburned control areas in 1983. The immediate invasion of burned areas by deer mice has been reported in a variety of habitats (Tester 1965, Ahlgren 1966, Sims and Buckner 1973, Kaufman *et al.* 1983, Vacanti and Geluso 1985, Driver 1987).

The evidence for viable mouse-vole populations in burned ecotone areas in Prince Albert National Park indicated that refuges were maintained from which adjacent burned grassland could be repopulated when habitat conditions recovered. The treatment areas together sustained a diverse small mammal prey base under a burn management regime.

ACKNOWLEDGEMENTS

The authors wish to thank the following technicians and contract employees who participated in the field work during the three small mammal trapping studies: Duane Sept, Howard Samoil, Anne Gunn, Robert Hutchison, Tom Peart, and Alan Arsenault. Statistical analyses were prepared by Sam Barry. The manuscript was ably reviewed by Andrew Radvanyi, Ed Driver, Thomas Bragg, and an anonymous reviewer. Financial support for this project was provided by the Canadian Parks Service and the Canadian Wildlife Service, both part of Environment Canada.

LITERATURE CITED

Ahlgren, C.E. 1966. Small mammals and reforestation following prescribed burning. Journal of Forestry 64:614-618.

Carbyn, L.N. 1971. Description of the *Festuca scabrella* association in Prince Albert National Park, Saskatchewan. Canadian Field-Naturalist 85:25-30.

Chance, R.L. 1986. The effect of fall burning on small mammals in Blue Mounds State Park, Luverne, Minnesota. Pages 157-159. *In* G.K. Clambey and R.H. Pemble (eds.). Proceedings of the Ninth North American Prairie Conference, Tri-College University Center for Environmental Studies, Moorhead, Minnesota.

Cook, S.F. 1959. The effects of fire on a population of small rodents. Ecology 40:102-108.

Daubenmire, R.F. 1959. A canopy coverage method of vegetation analysis. Northwest Science 33:43-61.

Driver, E.A. 1987. Fire on grasslands - friend or foe? Blue Jay 45:217-225.

Kaufman, D.W., Kaufman, G.A., and E.J. Finck. 1983. Effects of fire on rodents in tallgrass prairie of the Flint Hills region of eastern Kansas. Prairie Naturalist 15:49-56.

Ream, C.H. 1981. The effects of fire and other disturbances on small mammals and their predators; an annotated bibliography. United States Department of Agriculture Forest Service General Technical Report INT-106.

Rowe, J.S. 1959. Forest regions of Canada. Department of Northern Affairs and Natural Resources, Ottawa. Bulletin 123.

Rowe, J.S., and R.T. Coupland. 1984. Vegetation of the Canadian Plains. Prairie Forum 9:231-248.

Sims, H.P., and C.H. Buckner. 1973. The effects of clearcutting and burning of *Pinus banksiana* forests on populations of small mammals in southeastern Manitoba. American Midland Naturalist 90:228-231.

Tester, J.R. 1965. Effects of a controlled burn on small mammals in a Minnesota oak-savanna. American Midland Naturalist 74:240-243.

Vacanti, P.L., and K.N. Geluso 1985. Recolonization of a burned prairie by meadow voles (*Microtus pennsylvanicus*). Prairie Naturalist 17:15-22.

Viereck, L.A. 1979. Ecological effects of the Wickersham Dome fire near Fairbanks, Alaska. United States Department of Agriculture Forest Service General Technical Report.

Wright, H.A., and A.W. Bailey. 1982. Fire ecology, United States and southern Canada. John Wiley & Sons. New York.

FUNGUS DISEASE IN RELATION TO MANAGING PRAIRIE PLANTS WITH FIRE

Judy F. Shearer and Lois H. Tiffany
Department of Botany, Iowa State University, Ames, Iowa 50011

Abstract. Specific fungal foliar diseases were assessed on selected prairie plant species in relation to fire as a management practice on Hayden Prairie Preserve, Iowa. Selected plant species in burned and unburned areas were visually inspected and rated for presence and severity of specific fungal diseases at three sampling times in July and September 1987 and in June 1988. Less disease and lower disease severity ratings were recorded on plants in burned areas except for powdery mildew on Canada tickclover [*Desmodium canadense* (L.) DC.]. Increasing amounts of disease developed on plants in the areas unburned for one and two years.

Key Words. fungi, fire, prairie, disease, Iowa

INTRODUCTION

The effect of disease on plants in natural communities is poorly documented. Research with fungal pathogens of agriculturally important crop plants has established that these fungi affect their host species not only by reducing leaf area or root volume, but by altering processes of photosynthesis, respiration, nitrogen metabolism, ion uptake and transport, and water relations. Severely infected plants may eventually die from stunting and reduction in vigor (Burdon 1987).

Fire may play an important role in the reduction and severity of disease in grassland ecosystems. Burning destroys fungus propagules present on diseased plant parts in the litter layer. Changes in the microclimate of burned areas may further inhibit the establishment and growth of disease producing fungi due to changes in moisture, humidity, and air circulation. Historically, fire has been shown to be important as a control for brown needle spot disease of longleaf pine (*Pinus palustris* Mill.) and leafspot of blueberry (*Vaccinium* sp.) (Ahlgren 1974). Fire is currently used in Australia to control *Phytophthora cinnamomi* Rands, the fungus causing dieback in *Eucalyptus* (Groves and Burdon 1986).

METHODS

Hayden Prairie is a 240 acre black soil prairie preserve located in Howard County, Iowa. The northern section of the prairie is divided by mowed fire lanes into four units which in recent years have been spring burned on a three year rotation cycle (Christiansen 1969). These large tracts with similar plant species and well documented burn histories make them ideal sites for studying the effects of burning on plant parasitic fungi. Areas I, II, and III chosen as the experimental units were burned in 1985 and 1988, 1986, and 1987, respectively.

Seventy random plots (4 x 10 m), were delineated in each of the three areas. Plant species were selected for disease evaluation based on frequency of occurrence and on susceptibility to common distinctive fungal foliar pathogens. Plots were confined as nearly as possible to ridgetops to insure similar growth situations for the plant species examined for disease development.

Individual plants of each species were visually inspected for presence of the particular disease and then given a disease rating based on percent leaf area destroyed by lesions. Disease assessments and ratings were adapted from Clive (1971). The single individual of each species in each plot was randomly selected by its proximity to the plot center point. Names of vascular plants follow the Great Plains Flora Association (1986). Disease readings were made on two consecutive days during July 1987, September 1987, and June 1988.

RESULTS AND DISCUSSION

When disease readings were made in July 1987, three months after the spring burn, leaf disease incidence on six of the eight host plant species was significantly lower in the spring burn area (Table 1). These six plant species had the same amount of disease or progressively increasing numbers of diseased individuals in the areas unburned for one and two years respectively. On *Baptisia*, *Marsonnina* leaf spot development was not affected by burning and was equally common in all areas. On *Desmodium canadense*, powdery mildew (*Microsphaeria diffusa* Cke. & Pk.) was apparently stimulated by burning for it had higher incidence and disease ratings on plants in recently burned areas.

Table 1. Percent incidence of foliar pathogens on selected prairie plant species on Hayden Prairie July, 1987.

Host	Disease[1]	Areas I (Burned 1985)	II (Burned 1986)	III (Burned 1987)
		%		
Anemone cylindrica A. Gray	Rust	83	86	0
Rosa sp.	LS	88	34	3
Eryngium yuccifolium Michx.	LS	72	65	3
Desmodium canadense (L.) DC.	ALS	100	79	6
Aster oolentangiensis Ridd.	LS	92	58	13
Calamagrostis canadensis (Michx.) Beauv.	LS	97	84	46
Desmodium canadense (L.) DC.	PM	26	98	93
Baptisia bracteata Muhl. *ex.* Ell. var. *glabrescens* (Larisey) Isely	LS	100	100	98

[1]Disease abbreviations: LS = leaf spot; ALS = angular leaf spot; PM = powdery mildew.

Ahlgren (1974) reported powdery mildew disease increase on blueberry following fire. A myriad of factors including inoculum levels, nitrogen availability to the host plant and microclimate all contribute to disease development in the field. Powdery mildews, unlike most other fungi, can thrive in the absence of free water (Butt 1978). Conditions in the burned area and the area one year out of the burn rotation must have been ideal for disease development during the early summer of 1987.

Insect transmission of *Marsonnina* spores may account for high incidence of *Marsonnina* leaf spot on *Baptisia* in all areas. *Baptisia*, a vernal prairie species, develops and flowers early in the growing season. Soon after *Marsonnina* leaf spot has developed on plants in unburned areas, spores are produced in a moist mass on the diseased tissue and could easily have been transported from plant to plant by insects. Although leaf spot incidence was high, severity was very low in areas which had been burned (Table 2).

Seven of eight plant species sampled in July 1987 had reduced severity of disease on plants in burned areas as compared to plants from unburned areas (Table 2). Disease severity increased on these species as the number of years since burning increased. On *Desmodium*, disease severity of powdery mildew was much higher in burned and one year unburned areas than in the two year unburned area. Microclimatic conditions were in all probability responsible for the high incidence and severity ratings of this disease. However the possibility for fungal interactions as a factor in disease development should be considered. Increases of angular leaf spot on *Desmodium* were coincident with decreases in powdery mildew. More research in fungus-host interactions is needed.

Table 2. Average disease rating for foliar pathogens on selected prairie plant species on Hayden Prairie July, 1987.

Host	Disease[1]	Areas I (Burned 1985)	Areas II (Burned 1986)	Areas III (Burned 1987)
Anemone cylindrica A. Gray	Rust	2.66	2.29	.00
Desmodium canadense (L.) DC.	ALS	2.96	2.15	.01
Rosa sp.	LS	2.09	.47	.03
Eryngium yuccifolium Michx.	LS	1.68	1.30	.05
Aster oolentangiensis Ridd.	LS	2.05	.90	.14
Calamagrostis canadensis (Michx.) Beauv.	LS	2.38	2.29	.39
Baptisia bracteata Muhl. *ex* Ell. var. *glabrescens* (Larisey) Isely	LS	2.97	3.47	1.52
Desmodium canadense (L.) DC.	PM	.65	2.64	2.96

[1]Disease abbreviations: LS = leaf spot; ALS = angular leaf spot; PM = powdery mildew.

Disease readings of the same leaf spot fungi were made on the same eight host plant species in September 1987 (Table 3). Disease readings on *Baptisia* were attempted but abandoned because plants were dead and accurate disease readings were impossible.

Disease assessment on individual plants was difficult in the fall sampling period. During a growing season, more than one disease may develop on a host plant and attributing necrotic lesions to a specific fungus requires careful inspection. Since only attached leaves were considered for disease reading, severely infected leaves which had already dropped from the plant were not evaluated and some disease percentages are less than in the July 1987 sampling period.

In general, numbers of diseased individuals increased as the growing season progressed both in burned and in unburned areas. During this same time period, severity of disease also increased substantially on individual plants (Tables 3 and 4).

Area 1 became the burned tract in April 1988. Seven of the eight host species examined for disease in 1987 were included in the June 1988 sampling (Table 5). *Comandra umbellata* (L.) Nutt. was added because aecial stages of the*Comandra* -big bluestem

Table 3. Percent incidence of foliar pathogens on selected prairie plant species on Hayden Prairie September, 1987.

Host	Disease[1]	Areas I (Burned 1985)	Areas II (Burned 1986)	Areas III (Burned 1987)
			%	
Desmodium canadense (L.) DC.	ALS	100	—[2]	—[2]
Anemone cylindrica A. Gray	Rust	78	97	0
Aster oolentangiensis Ridd.	LS	93	72	33
Fragaria virginiana Dunch.	LS	93	90	40
Calamagrostis canadensis (Michx.) Beauv.	LS	100	100	70
Desmodium canadense (L.) DC.	PM	—[2]	—[2]	86
Eryngium yuccifolium Michx.	LS	100	100	90
Rosa sp.	LS	98	100	9

[1]Disease abbreviations: LS = leaf spot; ALS = angular leaf spot; PM = powdery mildew.
[2]Complete plants not available for evaluation.

Table 4. Average disease rating for foliar pathogens on selected prairie plant species on Hayden Prairie September, 1987.

Host	Disease[1]	Areas I (Burned 1985)	Areas II (Burned 1986)	Areas III (Burned 1987)
Desmodium canadense (L.) DC.	LS	5.00	—[2]	—[2]
Anemone cylindrica A. Gray	Rust	3.31	4.00	.00
Aster oolentangiensis Ridd.	LS	2.85	1.84	.56
Eryngium yuccifolium Michx.	LS	4.29	3.82	1.27
Calamagrostis canadensis Michx. Beauv.	LS	5.93	6.00	1.40
Rosa sp.	LS	3.55	3.19	2.34
Desmodium canadense (L.) DC.	PM	—[2]	—[2]	4.02

[1]Disease abbreviations: LS = leaf spot; ALS = angular leaf spot; PM = powdery mildew.
[2]Complete plants not available for evaluation.

(*Andropogon gerardii*) rust are present during late spring on *Comandra*. Diseased *Comandra* plants soon die, thus they are not evident later in the growing season. From past personal observation, the aecial spore stage on *Comandra* is usually lacking in areas which are spring burned. At the time disease readings were made in June, several portions of the burned area still had substantial litter remaining on the ground. The incomplete burn in the area apparently allowed survival of overwintering rust spores on big bluestem residues and in June an unusually high level of disease development on *Comandra* in the burned area.

Table 5. Percent incidence of foliar pathogens on selected prairie plant species on Hayden Prairie June, 1988.

Host	Disease[1]	I (Burned 1988)	II (Burned 1986)	III (Burned 1987)
			%	
Baptisia bracteata Muhl. *ex.* Ell. *glabrescens* (Larisey) Isely	LS	0	0	0
Desmodium canadense (L.) DC.	ALS	0	0	0
Desmodium canadense (L.) DC.	PM	0	0	0
Eryngium yuccifolium Michx.	LS	0	0	3
Calamagrostis canadensis (Michx.) Beauv.	LS	0	1	8
Anemone cylindrica A. Gray	Rust	0	60	10
Rosa sp.	LS	0	29	13
Comandra umbellata (L.) Nutt.	Rust	56	93	89

[1]Disease abbreviations: LS = leaf spot; ALS = angular leaf spot; PM = powdery mildew.

Disease severity and incidence readings were low for all species except *Comandra* (Tables 5 and 6). Disease development on the other hosts, would normally be at low levels early in the growing season and become progressively higher later. Absence of diseases such as angular leaf spot and powdery mildew on *Desmodium* was unexpected, particularly after the high levels recorded in 1987. The unusually dry spring and higher than normal temperatures may have resulted in unfavorable conditions for spore germination and subsequent disease development.

Table 6. Average disease rating for foliar pathogens on selected prairie plant species on Hayden Prairie June, 1988.

Host	Disease[1]	I (Burned 1988)	II (Burned 1986)	III (Burned 1987)
Baptisia bracteata Muhl. *ex.* Ell. var. *glabrescens* (Larisey) Isely	LS	.00	.00	.00
Desmodium canadense (L.) DC.	ALS	.00	.00	.00
Desmodium canadense (L.) DC.	PM	.00	.00	.00
Eryngium yuccifolium Michx.	LS	.00	.00	.05
Calamagrostis canadensis (Michx.) Beauv.	LS	.00	.01	.15
Rosa sp.	LS	.00	.21	.19
Anemone cylindrica A. Gray	Rust	.00	.52	.23
Comandra umbellata (L.) Nutt.	Rust	.65	3.75	2.62

[1]Disease abbreviations: LS = leaf spot; ALS = angular leaf spot; PM = powdery mildew.

In addition to the numerous effects commonly attributed to fire in grassland ecosystems, an additional benefit is documented by the data from this field research. Both the incidence and severity of most diseases were reduced in areas which had been recently burned. Removal of the litter layer destroyed fungus spores and any other survival structures which had developed on weathered plant parts. Therefore, young plants did not become immediately diseased as a result of colonization from fungal spores present on debris surrounding them. Rather infection must occur from spores produced on infected plants in surrounding areas as the spores are moved by wind and rains.

Although plant parasitic fungi and the diseases resulting from their growth on plants of the prairie are often inconspicuous, they may have significant effects in native prairie ecosystem dynamics. Plants killed or limited in reproductive capability will be replaced, often by individuals of a different species. Over time, a plant species may be eliminated from the prairie, especially if it has no resistance to a fungal parasite. Natural reintroduction of resistant strains of the species might never occur at the present time because of the isolation of our prairie remnants.

Fire interrupts the plant disease cycles by destroying the over-wintering fungus propagules on plant debris. Disease development in burned areas may be greatly modified during the season immediately following a spring burn and also for the next one or two years.

LITERATURE CITED

Ahlgren, I.F. 1974. The effect of fire on soil organisms. Pages 47-72. *In* T.T. Kozlowski and C.E. Ahlgren (eds.). Fire and ecosystems. Academic Press, New York.

Burdon, J.J. 1987. Diseases and plant population biology. Cambridge University Press, Cambridge.

Butt, D.J. 1978. Epidemiology of powdery mildews. Pages 51-81. *In* D.M. Spencer (ed.). The powdery mildews. Academic Press, New York.

Christiansen, P.A. 1969. A management master plan for Hayden Prairie, Howard County, Iowa. Report to the State Preserves Advisory Board.

Clive, J. 1971. A manual of assessment keys for plant diseases. APS Press, St. Paul, Minnesota.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Groves, R. H., and J.J. Burdon. 1986. Ecology of biological invasions. Cambridge University Press, Cambridge.

ECOLOGY OF MEAD'S MILKWEED (*ASCLEPIAS MEADII* TORREY)

Robert F. Betz
Northeastern Illinois University, 5500 N. St. Louis Avenue, Chicago, Illinois 60625

Abstract. Mead's milkweed (*Asclepias meadii* Torrey) is a plant of virgin prairies, whose pre-settlement range included much of the midwest. It is now a rare plant confined to prairie hay meadows, railroad rights-of-way, prairie preserves and pioneer cemeteries. Studies of approximately a hundred individual plants, producing hundreds of flowering and sterile stems, in the wild and in cultivation for seven years (1965-1971) indicated that it was a moderately-sized plant whose stems averaged 56 cm in height with sagittate sessile leaves with a herringbone arrangement of the veins. In late May to early June a mature stem produced a solitary, terminal, nodding umbel with an average of 12 flowers. Pollination was by digger bees (*Anthophora* spp.) and bumble bees (*Bombus* spp.). Approximately 6.4% of the flowering stems produced a long narrow pod averaging 12 cm in length and 1.3 cm in diameter with approximately 60 seeds per pod. Seed germination was relatively low (47.6%). Some plants in virgin prairies and in cultivation were over a quarter century old, and indications are they may live for a century or longer. In contrast to most milkweeds, the seedlings were difficult to grow. Four or more years were usually required to reach maturity. Like most milkweeds, a number of insects were associated with the plant. Most damaging were the larvae of the milkweed beetles (*Tetraopes* spp.) and milkweed weevils (*Rhyssematus* spp.) that fed on the roots and the adult weevils that girdled the peduncle causing the eventual collapse of the terminal umbel.

Key Words: Mead's milkweed, *Asclepias meadii*, prairie plant ecology, threatened species, tallgrass ecology, Illinois, Kansas, Missouri, Iowa

INTRODUCTION

Mead's milkweed (*Asclepias meadii* Torrey) was first collected by Dr. Samuel Barnum Mead, a physician-botanist, in western Illinois in 1843, as shown by herbarium specimens at the Chicago Natural History Museum. It was first reported in print in a list of plants of Hancock County published in the Prairie Farmer under the name of "Asclepias cordata non Walt?" (Mead 1846). A specimen of the plant was subsequently sent to John Torrey who recognized it as a new species and named it *Asclepias meadii* (Torrey 1856). This published description of the plant appeared in 1856 as a addendum to the second edition of Gray's Manual of Botany. However, from correspondence between Torrey and Mead and from the herbarium specimens at the Chicago Natural History Museum, it is probable that the plant was recognized as a new species and given the new name by Torrey sometime between 1846 and 1848.

In pre-settlement times Mead's milkweed appears to have had a wide distribution through the tallgrass region from northwestern Indiana (Deam 1940); southern Wisconsin (Greene 1880 and 1898), and northern Iowa (Fitzpatrick 1899, Greene 1907), to southern Illinois (Mead 1846, Lapham 1857, Patterson 1876, Brendel 1887, Huett 1897, McDonald 1899, Jones 1963), southern Missouri (Tracy 1886, Woodson 1954, Steyermark 1963), and northeastern Kansas (Carruth 1877, Gates 1940, McGregor 1948). With the plowing and cultivation of the prairies, the plant quickly disappeared. On December 15, 1871, Mead wrote to H. N. Patterson, a naturalist and plant collector from neighboring Henderson County: "My *Asclepias Meadii* is reduced very low. If possible will send at some other time with other plants which you may want. It grows 10-15 inches high, on high, rolling prairies, or did years ago. I have seen it in Missouri, and it has been found near Davenport, Iowa, . . . but perhaps the plough has destroyed it". On April 1, 1872, Mead wrote: "*Asclepias Meadii*. This I have not met with for several years and my duplicates are reduced low, as many of my rare plants". In July 1879, Mead wrote: "*Asclepias Meadii*. I tried years ago to cultivate it. Rev. Green . . . ought to protect and preserve the plant for cultivation". The only specimen remaining in Hancock County at present, is a framed specimen hanging in the College Museum (Kibbe 1952).

Now, over a century after Mead wrote these letters, the species is extinct throughout a large part of its original range. It is still found in some of the prairie preserves and hay meadows and along a few railroad rights-of-way in western Missouri (8 counties) and northeastern Kansas (12 counties). Very small populations are found in two or three places in Iowa (2 counties) and Illinois (2 counties). Intensive field searches have failed to rediscover this plant in Indiana and Wisconsin. In September 1988, the United States Fish and Wildlife Service officially listed it as a Federally threatened species (Harrison 1988).

METHODS

Field Studies

Using information obtained from herbarium specimens at the Field Museum of Natural History, Chicago, searches were made to locate Mead's milkweed plants in virgin prairies along railroad rights-of-way in western Missouri-northeastern Kansas and in prairie hay meadows. With practice, the inconspicuous yellow-green umbels growing just below the tops of the grasses could be spotted within a six to ten meter radius of an observer. Additional help in locating the plant on large hay meadows was provided by female monarch butterflies searching for plants on which to lay their eggs. Once a female detected a plant (probably by scent) she would fly in an excited manner in decreasing circles till she was directly over the plant before she dropped down to lay her eggs. A close inspection of the area would reveal the blooming plant.

Because of the incomplete data that would have been obtained from plants annually mowed in mid-growth, a thorough search of prairie hay meadows and mowed prairie preserves for the plant was not undertaken. The few plants in hay meadows that were studied were protected by surrounding them with piles of brush marked with red flags mounted on top of the piles. This was done with the consent of the owner and prevented inadvertent mowing.

Plants were marked with a 30 cm luminescent orange stake placed a few centimeters from each specimen. Careful measurements were then taken of distances to the nearest telephone pole, fence post, etc., so that they could be found again. In prairie hay meadows a Brunton pocket transit-compass mounted on a tripod was used to get azimuths on two or three different distance landmarks (telephone poles, tree trunks, corners of barns, chimneys, etc.) to fix the positions of plants so they could be relocated again for further studies and to collect pods.

During seven years of field observations (1965-1971), stems were checked annually for height, number of nodes, attached leaves, and flowers. This was done from late May into early June. The stems were checked for the presence of pods in early August. Any pods observed were later collected in early September. Subsequently, the total number of seeds produced by all pods and their percentage of germination were determined. In addition, insect pollinators and associates of Mead's milkweed were collected and recorded during all of these three observational periods.

Cultivation Studies

The seeds collected from ripe pods of Mead's milkweed were stored in a cool room during the winter months. At the end of February the seeds were placed on wet filter paper in petri plates and put in a refrigerator set at 5 C. After ten weeks of this cold moist treatment, the seeds were planted individually, using blunt tongs, into pots filled with soil that was one-third sand and two-thirds loam. A well-drained soil was necessary to prevent the damping off of the seedlings.

Germination usually occurred within two weeks. The seedlings were difficult to raise because of their soft stems and of the presence of buds which were subject to injury from sucking insects. In the greenhouse they were attacked by thrips which caused spotting of leaves by destroying the chlorophyll-bearing cells. Outside the greenhouse, aphids injured and caused distorting of the terminal buds and leaves. To prevent this extensive thrip and aphid damage, it was necessary to clean the young seedlings each day with a wet camel's hair brush.

After the first killing frost, the seedlings were placed in a cold room kept at 5 C for the winter. When allowed to winter outdoors they were subject to winter kills which caused considerable losses.

During the second growing season, the young plants were stronger and could stand erect unsupported, but they still had to be cleaned and freed of insect pests. By the beginning of the third growing season, the seedlings were mature enough to be transplanted in the early spring into a prairie being restored at the Morton Arboretum, Lisle, Illinois. To insure their survival, they were not allowed to dry out during the first two weeks after transplanting.

In addition, 14 plants were grown in pots from seed to flowering stage, a process requiring from five to seven years. These potted plants: 1) facilitated the study of the rootstocks without harming the plants to any great extent, 2) allowed blooming plants to be placed in areas having high densities of potential pollinators, and 3) made flowers more accessible in efforts to hand-pollinate them.

RESULTS

Morphology

While a large portion of Mead's milkweed stems represent single isolated rockstocks, some rootstocks produce multiple stems. Because of this, the unit of observation used in these results is the stem rather than the plant. The data collected were on approximately 100 plants, producing hundreds of both flowering and sterile stems, over a period of seven years.

Height.

The heights of 604 blooming Mead's milkweed stems observed varied from 31 to 92 cm. The average height was 56 cm. In general, the plants found in unmowed railroad prairies were markedly taller and more robust than those found in hay meadows and subjected to annual mowing.

Nodes.

Three to seven nodes occurred on flowering stems, with an average of six. Usually the lower nodes were devoid of leaves.

Leaves.

Leaves on a stem ranged in number from three to seven pairs, with an average of four pairs. The sagittate leaves were about 7.5 cm long and 3.3 cm wide, sessile, attached with a slightly upward slant and had a herringbone arrangement of the veins.

Roots.

The plant produced a white rootstock with a long fibrous emergent root penetrating downward into the soil. The rootstock may remain fixed in position for a few years; however, there was a tendency for it to shift in position. Thus, a plant may appear a short distance away from the place it was seen to grow the preceding year.

Umbel and flowers.

The stem produced a solitary, flat, disk-like umbel on an elongated peduncle. This peduncle had a characteristically hooked tip that causes the umbel to nod downward. No other North American milkweed has this unusual characteristic. Unfortunately, this definitive feature has not been used in any of the taxonomic keys. Only 6.4% of the observed stems which flowered produced pods. Generally, one pod was produced per stem, but occasionally two were formed. The flowers were fragrant, and the corolla and lobes varied from green to yellow-green, turning to ivory in older flowers. The umbels had from 1 to 26 flowers, producing 12 on average (Table 1). Depending on latitude and weather conditions, blooming occurred in the period from the last week in May until the third or fourth week in June. The flowers lasted about five or six days.

Table 1. Umbel and flower production in *Asclepias meadii* (1965-1971).

Year	*Stems observed*	*Stems with umbels*	*Total flowers*	*Average flowers/umbel*
	number			
1965	140	114	1520	13.3
1966	131	106	1275	12.0
1967	48	28	265	9.5
1968	103	97	1176	12.1
1969	127	92	1090	11.8
1970	107	71	856	12.1
1971	127	96	1082	11.3
Total	783	604	7,264	
Average				12.0

Pod and seed production.

The pod was long and narrow. It measured 11-12 cm in length and about 1.3 cm in diameter. The number of seeds per pod varied from 42 to 92, and had an average of 60 seeds per pod (Table 2). It took 100 to 110 days for the seeds to mature. If the flowers were pollinated during the first week of June, the pod was ripe by the second week of September.

Germination and Seedling Development

The viability of seed was relatively low; out of 2,429 seeds studied, only 1,156 germinated (47.6%) (Table 3). In germinating, the long petioles of the cotyledons appeared first above ground, followed by the emergence of the cotyledons themselves in a day or two. Within 48 hours after the appearance of the cotyledons, the epicotyl appeared above ground, which is unusual among members of the *Asclepias,* since more typically the epicotyl appears first, followed later by the cotyledons.

The seedlings were spindly and leaned over onto the ground and onto one another. The differed from mature plants in that they had linear leaves. If the terminal bud was injured, there was a tendency for the stem to produce a new shoot from an axillary bud. This was also true for mature plants. However, if the stem was cut off completely without leaving an axillary bud, the rootstock usually did not produce another stem that season.

Plant Associates

In remnant populations observed along railroad rights-of-ways and growing on deep silt loam soils, Mead's milkweed was found growing with approximately 60 species of prairie plants. Very common species of grass associated with the plant were prairie dropseed (*Sporobolus heterolepis* Gray), indiangrass [*Sorghastrum nutans* (L.) Nash], and big bluestem (*Andropogon gerardii* Vitman), growing in such abundance and age as to produce a comparatively low sward 60-90 cm high with few flowering culms. Prairie forbs commonly found with Mead's milkweed were white prairie clover [*Petalostemum candidum* (Willd.) Michx.], purple prairie clover [*Petalostemum purpureum* (Vent.) Rydb.], prairie gentian (*Gentiana puberula* Michx.), and prairie compass plant (*Silphium laciniatum* L.).

Table 2. Pod and seed production in *Asclepias meadii* (1965-1971).

Year	Total pods produced	Total seeds appearing viable	Total seeds appearing non-viable	Total seeds produced	Average pods/stem	Average seeds/pod
	-------	-------	-------	number	-------	-------
1965	16	949	44	993	0.14	62
1966	6	337	12	349	0.06	58
1967	1	10	45	55	0.04	55
1968	—	—	—	—	—	
1969	4	204	43	247	0.04	62
1970	9	430	84	514	0.13	57
1971	4	233	38	271	0.04	68
Total	40	2,163	266	2,429		
Average					0.06	61

Table 3. Germination in *Asclepias meadii* (1965-1971).

Year	*Total seeds produced*	*Total seeds germinating*	*Percent germination*
	------ number	------	----- % -----
1965	993	487	49.1
1966	349	162	46.4
1967	55	26	47.3
1968	—	—	—
1969	247	95	38.5
1970	514	249	48.4
1971	271	137	50.6
Total	2,429	1,166	
Average			47.6

Insect Associates

Plant feeders.

Relatively few insects were collected on Mead's milkweed. The milkweed bug (*Oncopeltus fasciatus* Dallus) and the lesser milkweed bug (*Lygaeus kalmii* Stal) were occasionally found feeding in or on pods and appeared to do little harm to the plants. The same is true of the monarch butterfly (*Danaus plexippus* L.) whose caterpillars were only rarely found feeding on the leaves.

More damaging, however, was the cerambycid milkweed beetle (*Tetraopes femoratus* LeConte) which was occasionally found chewing on the flowers. Its larva is a borer in stems and roots of *Asclepias* species, and the appearance of the adult on Mead's milkweed would seem to indicate that it is also a borer in it. The common milkweed beetle (*Tetraopes tetraophthalamus* Forster) was never found on Mead's milkweed even though it was commonly found on plants of the common milkweed (*Asclepias syriaca* L.), growing in disturbed areas near Mead's milkweed plants.

Potentially damaging were the milkweed weevils (*Rhyssematus annectans* Casey and *Rhyssematus lineaticollis* Say), whose adults girdled the peduncle of flowering stems and caused the umbel to collapse and fall downward. Although it was reported in the literature that their larvae were found in the pods of milkweeds (Smith 1899, Blatchley and Leng 1916, Leonard 1928, Kissinger 1964), these have never been seen on or in the pods of any of the 18 species of *Asclepias* studied over a period of 25 years. However, the adults of *Rhyssematus lineaticollis* were seen emerging after dark from holes in the ground adjacent to the stems of *Asclepias* plants. Like the milkweed beetle, the milkweed weevil larvae feeding on the roots of Mead's milkweed plants presumably could seriously injure and possible kill them.

Pollinators.

Few potential insect pollinators were observed on Mead's milkweed. However, two bumble bee queens were collected on it. The one queen, *Bombus affinis* Gresson, carried two pairs of pollinia on its right-front leg. The other, *Bombus griseocollis* (Degeer), had a pair of pollinia on the right-hind leg. In addition, two males and three female digger bees (*Anthophora raui* Rohwer) also were collected. Of these, one male had a pair of pollinia on its right-middle leg and a pair on its proboscis, and one female had a pair of pollinia on its right-front leg. It should be noted that the insects were still carrying intact pairs of pollinia. Thus, neither the *Bombus* queens nor the *Anthophora* bees had transferred pollinia to any stigmatic chambers. Nevertheless, it is possible that the *Anthophora* bees could be one of the most important pollinators of the species because of the larger populations of these bees found to be present at the time the plants are in flower. This is in contrast to the rather low populations of *Bombus* occurring at that time.

DISCUSSION

Mead's milkweed is a slow growing plant and requires at least four or more years after seed germination to reach flowering stage. Once established in a prairie, it can live for decades. Plants that were raised from seed in 1966 and planted in the restored prairie at the Morton Arboretum are still healthy and producing flowers in 1988. The same is true for fully mature plants first observed in 1965 on railroad prairies in western Missouri and northeastern Kansas.

Most rootstocks produced one stem, but others produced multiple stems, both flowering and sterile. Some formed clusters or clones with a flowering stem surrounded by a half-dozen sterile stems varying in size from those that equaled a flowering stem down to some that resembled two-year-old seedlings. A more uncommon clone was one in which three or four stems, both flowering and sterile, would be aligned in a row and separated from each other by a few centimeters. It would appear that these clones or small colonies were derived from the same rootstock.

In some cases stems suddenly wilted and died back in the middle of the growing season (12.5% in plants observed in 1965). In other instances, rootstocks produced flowering stems for a number of years and then stopped producing stems for a year or two before stems became evident again. During the years that stems were not readily seen where plants had previously been observed, a close examination usually disclosed a single small seedling-like stem or a few small stems. In both instances, it would appear that the plants were being or had been attacked by borers (*Tetraopes* or *Physemmatus*) and had been stunted. If over a period of a few years a stem did not appear again, it was presumed that the rootstock was dead.

Pod production in Mead's milkweed was extremely low, and the pods contained relatively large numbers of aborted seed (11.1%). The germination of seed was also comparatively low (47.6%). This low production both of pods and viable seed would appear to be due in part to: 1) the low populations of insect pollinators, 2) the low populations of Mead's milkweed available to attract potential pollinators and thus enhance cross-pollination which is necessary to set viable seed (Woodson 1947), and 3) the incompatibility between the closely related plants found within the isolated clones and colonies.

In pre-settlement prairies, Mead's milkweed presumably had healthy reproducing populations with many plants producing pods. Since the species lived in a relatively stable plant community and was long-lived, it could produce small numbers of flowers and pods with relatively few seeds and still survive. During pre-settlement times, there were large numbers of pollinating bees on the virgin prairies utilizing a large diversity of prairie forbs blooming in a continuous spectrum throughout the growing season. This assured that Mead's milkweed flowers had adequate numbers of pollinators available to them. The occasional loss of individual plants to borers and other disease organisms would easily be offset by the production of new seedlings from seeds which were continually being produced.

However, with the coming of the settlers all of this changed. The populations of Mead's milkweed on the silt-loam prairies of Illinois, Iowa, and northern Missouri were plowed under along with the rest of the other prairie plants. The populations of the plant in western Missouri and northeastern Kansas fared much better since they were growing on poorer soils which were never immediately cultivated. Some of these were eventually turned into hay meadows. Mead's milkweed plants, still found in these hay meadows and in the prairie preserves derived from hay meadows probably represent survivors of larger populations originally found on those areas of the prairie which became hay meadows over a century ago. Annual mowing has prevented these plants surviving in the hay meadows from reproducing and maturing seed. Inasmuch as prairies originally surrounding the hay meadows were destroyed by plowing, no new seeds of Mead's milkweed are now available from the outside to increase their numbers within these old hay meadow populations. With a continuing loss of individual plants to borers, disease organisms and mowing stress, it is probable that the populations in the hay meadows will continue to decline and eventually become extinct.

Even unmowed railroad prairies have declining populations of Mead's milkweed because of constant herbicide application, shading of encroaching woody plants which are spreading due to lack of fires and digging and trenching done in laying television and telephone cables. The laying of cable along the Missouri Pacific Railroad west of Sedalia, Missouri, in the early 1980s resulted in the destruction of more than 70 Mead's milkweed plants growing in prairies along that right-of-way.

Because of the slow continuing destruction of the hay meadows by plowing and of the elimination of the railroad prairies by spraying, shading, and trenching, Mead's milkweed eventually will survive mainly in prairie preserves. In order to enhance survival of this plant in these sanctuaries, it is imperative to manage the prairie preserves so that they can be returned as closely as possible to their pre-settlement condition. This means the discontinuance of mowing as a management tool. Mowing stresses the plants, not only by preventing the production of ripened pods, but also by weakening them through shortening their growing season. The low level of food reserves in plants that have been mowed the previous season is reflected in the reduced viable seed production the following season. Even seeds which do germinate often produce seedlings that are weak and fail to survive. Mowing probably also has a detrimental effect on populations of potential pollinators. Along with the cessation of mowing, prescribed burns should be a part of management of the preserves in order to envigorate the growth and reproduction of Mead's milkweed.

To increase the genetic variability of the present small populations in these preserves, both seeds and seedlings should be introduced from neighboring preserves. In addition, seedlings derived from plants growing in the northern remnant prairies (Illinois and Iowa) should be grown in greenhouses for reintroducing Mead's milkweed into prairie preserves in Iowa, Illinois, Indiana, southern Wisconsin, and northern Missouri where this species has been eliminated.

However, cultivating and establishing Mead's milkweed in preserves is a difficult task. More than 800 two-year old seedlings were grown and transplanted into a restored prairie (600 seedlings), a virgin sandy-loam prairie (50 seedlings) and an old settler cemetery without prairie vegetation but having a deep prairie soil (150 seedlings). Only 2 plants were ever established. A major reason for this failure may have been genetic; the plants were grown from seed collected in western Missouri-northeastern Kansas and may not have had the ability to withstand the winter conditions of northern Illinois. For that reason, the remnant populations in Iowa and Illinois are very important in being reservoirs of an ecotype(s) adapted to a more northerly climatic regimen which could be very important in the re-establishment of Mead's milkweed in the northern prairie preserves. If these measures are undertaken, there is reason to believe that Mead's milkweed could again become a self-sustaining member of the tallgrass prairie ecosystem and remain so for centuries to come.

LITERATURE CITED

Blatchley, W.S., and C.W. Leng. 1916. Rhynchophora or weevils of North Eastern America. The Nature Publishing Company, Indianapolis.

Brendel, F. 1887. Flora Peoriana: The vegetation in the climate of middle Illinois. J.W. Franks and Sons, Peoria, Illinois.

Carruth, J.H. 1877. Centennial catalogue of the plants of Kansas. Transactions of the Kansas Academy of Science 5:54.

Deam, C.C. 1940. Flora of Indiana. Department of Conservation, Division of Forestry, Indianapolis.

Fitzpatrick, T.J. 1899. Manual of flowering plants of Iowa. A thesis. Privately published.

Gates, F.C. 1940. Annotated list of the plants of Kansas: ferns and flowering plants. Kansas State College of Agriculture and Applied Science, Manhattan.

Greene, E.L. 1880. Notes of certain silkweeds. Botanical Gazette 5:64-65.

Greene, E.L. 1898. Wisconsin field notes. Plant World 2:37-38.

Greene, W. 1907. Plants of Iowa. Bulletin of the State Horticultural Society, Des Moines.

Harrison, W.F. 1988. Endangered and threatened wildlife and plants: determination of threatened status for *Asclepias meadii* (Mead's milkweed). Federal Register 53:33992-33995.

Huett, J.W. 1897. Essay toward a natural history of LaSalle County, Illinois. Part 1. Flora La Sallensis. Fair-Dealer Printers. Ottawa.

Jones, G.N. 1963. Flora of Illinois. American Midland Naturalist Monograph. University of Notre Dame Press, Notre Dame, Indiana.

Kibbe, A.L. 1952. A botanical study and survey of a typical midwestern county (Hancock County, Illinois). Privately published. Carthage, Illinois.

Kissinger, D.G. 1964. Curculionidae of American North of Mexico. A key to the genera. Taxonomic Publications. South Lancaster, Massachusetts.

Lapham, I.A. 1857. Catalogue of the plants of the state of Illinois. Transactions of the Illinois State Agricultural Society 2:531.

Leonard, M.D. 1928. A list of insects of New York. Cornell University Agricultural Experiment Station Memoir 101.

McDonald, F.E. 1899. Geographic range of *Asclepias meadii* and *Hypericum kalmianum*. Plant World 2:126-127.

McGregor, R.L. 1948. The flora of Douglas County, Kansas. Transactions of the Kansas Academy of Science 51:77-186.

Mead, S.B. 1846. Catalogue of plants growing spontaneously in the state of Illinois, the principal part near Augusta, Hancock County. Prairie Farmer 6:35-36, 60, 93, 119-122.

Patterson, H.N. 1876. Catalogue of the phaenogamous and vascular cryptogamous plants of Illinois. Oquawka.

Smith, J.B. 1899. Insects of New Jersey. McCrellish and Quigley, State Printers. Trenton.

Steyermark, J.A. 1963. Flora of Missouri. Iowa Station University Press, Ames.

Tracy, S.M. 1886. Catalogue of the phaenogamous and vascular cryptogamous plants of Missouri. Tribune Printing Company, Jefferson City.

Torrey, J. 1856. *Asclepias meadii* in Asa Gray, Manual of Botany. G.P. Putnam and Company, New York.

Woodson, R.E., Jr. 1954. The North American species of *Asclepias*. Annals of the Missouri Botanical Garden 41:109-110.

DISTRIBUTION OF FLODMAN'S THISTLE AND ITS RESPONSE TO DIFFERENT DISTURBANCES

Charles E. Umbanhowar Jr.
Department of Botany, University of Wisconsin-Madison,
Madison, Wisconsin 53706

Abstract. The importance of disturbance in prairie has long been recognized. Increasingly interest and research have focused on the action and interaction of multiple disturbances. The distribution of Flodman's thistle [*Cirsium flodmanii* (Rydb.) Arthur] on ant mounds, badger mounds, buffalo wallows, and potholes and in a lightly and a moderately grazed pasture was compared at the Nature Conservancy's S. H. Ordway Jr. Memorial Prairie in northcentral South Dakota. In the lightly grazed pasture, Flodman's thistle occurred most frequently on hilltops and ridges, but in the moderately grazed pasture it occurred with equal frequency on hilltops and ridges, and low areas surrounding potholes. Flodman's thistle was common on earthen mammal mounds and was less abundant on thatching ant mounds and buffalo wallows. No thistles were sampled in potholes. Relative availability of light may explain the thistle's distribution. Implications of observed patterns are discussed for the evolution of life history traits and the management of prairie remnants.

Key Words. Flodman's thistle, *Cirsium flodmanii*, northern mixed prairie, disturbance, patches, grazing, South Dakota

INTRODUCTION

Historically, many different disturbances have affected and continue to influence North American grasslands. In this paper, disturbance is narrowly defined as the destruction of biomass (Grime 1979), although of equal importance are the past and present temporal and spatial patterns of disturbance (Allen and Starr 1982). Ecologists have long been interested in the effect of disturbance on prairie, studying fire (Higgins 1986, Steuter 1987, Collins 1987, Hulbert 1988), drought (Albertson and Weaver 1946, Albertson *et al*. 1957, Coupland 1958), grazing of bison or cattle (Dix 1959, Ellison 1960, England and DeVos 1969, Collins 1987), prairie dog towns (Bonham and Lerwick 1976, Coppock *et al*. 1983, Archer *et al*. 1987), buffalo wallows (Polley and Collins 1984), and badger mounds (Platt 1975, Platt and Weis 1977). Recent discussions of grasslands and disturbance have emphasized the interaction of disturbances with each other (Collins and Barber 1985, Collins 1987) and with the physical environment (Platt and Weis 1977, Gibson and Hulbert 1987).

Flodman's thistle [*Cirsium flodmanii* (Rydb.) Arthur] is a rosette forming perennial. It is rhizomatous, spreading rapidly in open, bare areas (Wilson and McCarty 1984). In eastern South Dakota, Beebe and Hoffman (1968) found that this species increased in abundance when under moderate to heavy grazing pressure by cattle.

As part of work in progress at the Nature Conservancy's Samuel H. Ordway Jr. Memorial Prairie, the distribution of Flodman's thistle in slightly and moderately grazed stands of three major upland plant communities was compared. The response of Flodman's thistle to different disturbances was examined by recording its presence or absence on the mounds of the western thatching ant (*Formica obscuripes* Forel) (Weber 1935), earthen mounds built by burrowing mammals, and buffalo wallows. While not disturbances in the sense of Grime (1979), ephemeral prairie potholes provide bare areas suitable for colonization and were included.

METHODS

Site Description

The Nature Conservancy's Samuel H. Ordway Jr. Memorial Prairie is a 3,156 ha prairie, located in McPherson County in northcentral South Dakota. It is of the northern mixed prairie type (Singh *et al*. 1983) and has been previously described by Barnes *et al*. (1983). Soils are mostly loams and annual precipitation is about 490 mm (Soil Conservation Service 1981). Since its purchase in 1975, the preserve has been grazed primarily with cattle.

Community Sampling

All community sampling was done in July, 1987 and was divided between a moderately and a lightly grazed pasture. The moderately grazed pasture had been grazed at 1.24-1.98 AUM/ha by cattle as part of a three pasture deferred rotation for 11 of the previous 13 years. The lightly grazed pasture was grazed by cattle for two years (1977 and 1981 at 1.48 AUM/ha) and by bison for the past six years in the fall and winter. The former pasture was burned in April, 1985, and the latter May, 1984.

In each pasture, eight stands of low, mid, and high prairie (Barnes *et al*. 1983) were delineated for a total of 48 stands. Stands were selected to cover a range of soil types and slope aspects and angles. Four 0.5 m^2 quadrats were placed in the center of each stand, using characteristic species for each community to determine stand boundaries. Low prairie was dominated by big bluestem (*Andropogon gerardii* Vitman) and found near potholes. Mid prairie was dominated by bluegrasses (*Poa* spp. L.), green needlegrass (*Stipa viridula* Trin.), and western wheatgrass (*Agropyron smithii* Rydb.) and covered most of the preserve. High prairie was dominated by little bluestem (*Andropogon scoparius* Michx.), plains muhly [*Muhlenbergia cuspidata* (Torr.) Rydb.], and porcupine grass (*Stipa spartea* Trin.) and was found on dry hilltops and ridges. Quadrats were separated by 1 m and placed along a line perpendicular to the slope. Presence of Flodman's thistle (rosettes and flowering adults combined) was recorded for each quadrat and calculated as a percentage (0%, 25%, 50%, or 100%) for each stand.

Visual estimates of aerial cover were made for all species, using a Daubenmire cover class system (Mueller-Dumbois and Ellenberg 1974), slightly modified with the two largest cover classes combined. Designation of a stand as high, mid, or low prairie was verified by group membership in a Bray-Curtis ordination (Beals 1984), using cover data for all species at each stand. Some stands were reclassified.

Patch Sampling

Mounds of burrowing mammals and western thatching ant were selected from a list of mounds compiled from walking surveys of one 22 ha plot in each pasture. Mound size, age, and location were all criteria in selection. A total of 63 earthen mammal mounds (37 in the lightly grazed pasture and 26 in the moderately grazed pasture) and 65 ant mounds (46 in the lightly grazed pasture and 19 in the moderately grazed pasture) were selected. No more than four mounds were located in low prairie in either pasture. Quadrats, 0.5 m^2, were placed 1 m on either side of most mounds. Presence or absence of Flodman's thistle was recorded for mounds and adjacent off mound quadrats. The larger number of mounds sampled in the moderately grazed pasture reflected their greater abundance in that pasture. Mounds were similar in size (mammal mounds mean diameter = 92 cm, s.d. = 19 cm; thatching ant mounds mean diameter = 87 cm, s.d. = 20 cm).

Buffalo wallows were not present in either the lightly or moderately grazed pasture, because these were not grazed by bison during the summer months. Wallows were present in a pasture adjacent to the lightly grazed pasture. This pasture was grazed alternately by cattle and bison at 1.24-1.48 AUM/ha from 1985 to 1987 and at 0.30-1.90 AUM/ha during the previous nine years, primarily by bison. Twelve wallows (mean size = 240 cm, s.d. = 45 cm) were selected for sampling, and all had at least a 10% vegetative cover (visually estimated) and had not been used by bison since the previous year. Each wallow was sampled with two to four 0.5 m^2 quadrats placed along a north-south or east-west transect in each wallow. Quadrats were also placed 1 m on either side of each wallow on the same transect. Presence or absence of Flodman's thistle was recorded for the quadrats in and adjacent to wallows.

Six small openings (4-15 m in diameter) in five small potholes were sampled with 0.5 m 2 quadrats placed on north-south transects through the center of each. At the time of sampling, the openings were dry and contained relatively little (less than 50% live cover, visually estimated) emergent vegetation (*Eleochoris* spp, *Carex* spp). Twenty-four quadrats were sampled for the presence of the thistle.

RESULTS

Prairie Communities

In the lightly grazed pasture, Flodman's thistle was most abundant in high prairie stands; but in the moderately grazed pasture, it occurred with equal frequency in low and high prairie (Figure 1). The thistle was much more abundant in the moderately grazed pasture. Grazing treatments were not replicated, but the increased abundance of Flodman's thistle in the moderately grazed pasture agrees with earlier work by Beebe and Hoffman (1968).

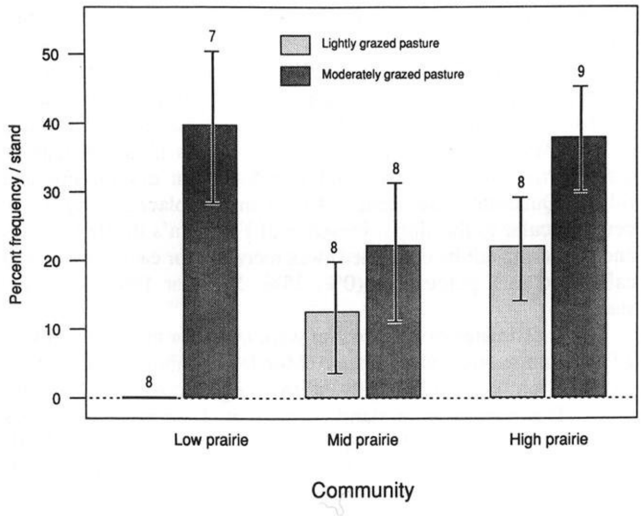


FIG. 1. Mean percent frequency of Flodman's thistle in lightly and moderately grazed stands of three upland communities at the S. H. Ordway Jr. Memorial Prairie. Number of samples is given above each histogram. Vertical bars are plus and minus one standard error of the mean.

Patches

Flodman's thistle occurred on all of the upland patches but was not found in any of the small potholes (Figure 2). Individual plants were observed in dry potholes in 1988. Where it did occur, percent frequency was lowest on the mounds of the thatching ant. Percent frequency was similar for mounds in both the moderately and lightly grazed pastures, despite a doubling in frequency in the adjacent area. Areas next to the earthen mammal mounds showed a similar trend. One-half of the earthen mounds in the moderately grazed pasture had Flodman's thistle, compared to 11% in the lightly grazed pasture. Frequency data for the wallows are best compared with results from the grazed pasture. Thistle abundance adjacent to wallows was most like the grazed pasture. Flodman's thistle was present in only 15% of the samples taken from wallows.

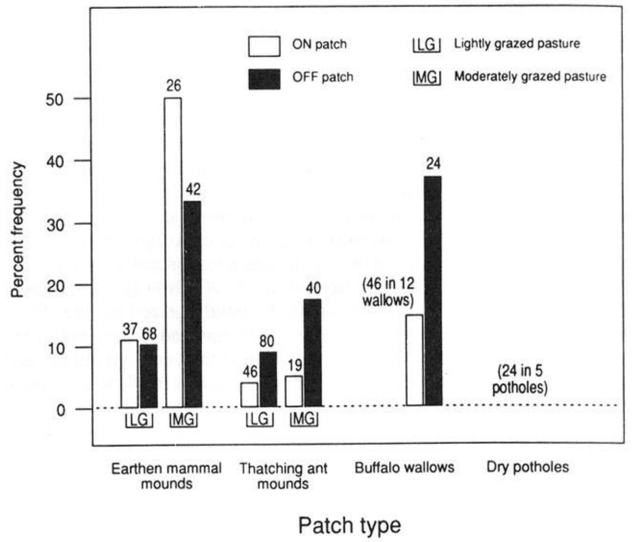


FIG. 2. Percent frequency of Flodman's thistle on and adjacent to different patches in a lightly and moderately grazed pasture at the S. H. Ordway Jr. Memorial Prairie. Number of samples is given above each histogram.

DISCUSSION

Flodman's thistle, in the three upland communities at the Samuel H. Ordway Jr. Memorial Prairie, was present in greatest abundance in the moderately grazed pasture. Its pattern of occurrence on patches suggested a major influence of light. The step-wise decrease in percent frequency of Flodman's thistle from lightly grazed high to low prairie may correspond to a decreasing availability of light. Ungrazed low prairie has a tall, almost continuous canopy and a much greater above-ground biomass than do either mid or high prairies (Barnes *et al.* 1983, Steuter 1987). The vegetation is shorter in ungrazed high prairie and does not form a continuous canopy. Grazing in the moderately grazed pasture reduced live cover, especially in low prairie where cattle reduced the canopy to a height of 1 to 2 cm. Mounds of the thatching ant had a dense cover of grasses, such as western wheatgrass, prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], or green needlegrass, that shaded most of the surface of the mound. Vegetative cover on the earthen mammal mounds, wallows, and potholes was much sparser, although a thick layer of litter occurred in the potholes. Actual measurements of vegetation cover, canopy height, and light availability are needed to confirm these qualitative observations.

Because Flodman's thistle forms rosettes, it may be especially susceptible to shading even though leaves range from prostrate to erect. For example, Givnish (1982) found a positive correlation between forest herb leaf height and vegetative cover in an eastern deciduous forest and discussed the importance of light. Wilson and McCarty (1984) found reduced germination in Flodman's thistle under low light conditions. Shading of young ramets may be equally or more important. Several earthen mounds were excavated, and it was found that the thistles on them originated from rhizomes located below the original ground level.

Factors other than light are critical to the success of this species. Its absence in potholes may reflect an inability of the seeds to survive submersion. Van Der Valk (1981) presented a general discussion of plant colonization and establishment in potholes and marshes. Ants may directly attack or bury (King 1977) young seedlings or ramets. In creating wallows. bison appeared to remove most roots and rhizomes in the wallow and compact the soil, likely reducing the rate of vegetative colonization. Bison probably destroy young plants in active wallows.

Studies of a single patch type or single disturbance at a single site may not accurately estimate the relative importance of that patch or disturbance to the reproductive success of a species. Percent frequency of Flodman's thistle varied greatly between the different patch types, communities, and pastures examined in this study. This is shown in the difference between on and off patch frequencies for the thistles on earthen mounds (Figure 2). If vegetative colonization is important, higher frequency of Flodman's thistle on earthen mounds in the moderately grazed pasture could be the direct result of higher off patch frequencies. In contrast, thistle frequency on ant mounds was the same in the two pastures despite a two-fold difference in frequency adjacent to mounds. Life history traits such as seed dispersal and rhizomatous growth need to be considered in relation to the range of both the disturbance and environmental factors encountered by individuals of a species before their significance and possibly evolutionary history are to be understood.

While Flodman's thistle is not rare, its distribution raises several important issues for the management of prairies, especially small remnants. Of particular importance may be an understanding of 1) the dependence of plants on disturbance for regeneration and the similarity of different disturbances, 2) how the presence of one type of disturbance affects the probability or abundance of other disturbances, and 3) the need to supplement burn management of prairies with grazing or mowing or creation of artificial mounds and other openings or the importation ants and small mammals.

ACKNOWLEDGEMENTS

This work was supported in part by the Nature Conservancy and grants from University of Wisconsin Department of Botany Davis Fund. Thanks go to the Nature Conservancy and the Ordway Prairie managers for their cooperation and permission to work at Ordway, and to Ed Beals and anonymous reviewers whose comments greatly improved this paper.

LITERATURE CITED

Albertson, F.W., G.W. Tomanek, and A. Riegel. 1957. Ecology of drought cycles and grazing intensity on grasslands of central Great Plains. Ecological Monographs 27:27-44.

Albertson, F.W., and J.E. Weaver. 1946. Reduction of ungrazed mixed prairie to short grass as a result of drought and dust. Ecological Monographs 16:451-463.

Allen, T.F.H., and T.B. Starr. 1982. Hierarchy: Perspectives for ecological complexity. University of Chicago Press. Chicago.

Archer, S.A., M.G. Garrett, and J.K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio 72:159-166.

Barnes, P.W., L.L. Tieszen, and D.J. Ode. 1983. Distribution, production and diversity of C_3- and C_4-dominated communities in mixed prairie. Canadian Journal of Botany 61:741-751.

Beals, E.W. 1984. Bray-Curtis ordination: An effective strategy for analysis of multivariate ecological data. Advances in Ecological Research 14:1-55.

Beebe, J.B., and G.R. Hoffman. 1968. Effects of grazing on vegetation and soils in southeastern South Dakota. American Midland Naturalist 80:96-110.

Bonham, C.D., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. Journal of Range Management 29:221-225.

Collins, S.L. 1987. Interactions of disturbance in tallgrass prairie: a field experiment. Ecology 68:1243-1250.

Collins, S.L., and S.C. Barber. 1985. Effects of disturbance on mixed-grass prairie. Vegetatio 64:87-94.

Coppock, D.L., J.K. Detling, J.E. Ellis, and M.I. Dyer. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia 56:1-9.

Coupland, R.T. 1958. The effects of fluctuations in weather upon the grasslands of the great plains. Botanical Review 24:274-317.

Dix, R.L. 1959. The influence of grazing on the thin-soil prairies of Wisconsin. Ecology 40:36-49.

Ellison, L. 1960. Influence of grazing on plant succession of rangelands. Botanical Review 26:1-78.

England, R.E., and A. DeVos. 1969. Influence of animals on pristine conditions on the Canadian grasslands. Journal of Range Management 22:87-94.

Gibson, D.J., and L.C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. Vegetatio 72:175-185.

Givnish, T.J. 1982. On the adaptive significance of leaf height in forest herbs. American Naturalist 120:353-381.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley and Sons. New York.

Higgins, K.F. 1986. Interpretation and compendium of historical fire accounts in the northern great plains. U.S. Department of Interior Fish and Wildlife Service Resource Publication 161.

Hulbert, L.C. 1988. Causes of fire effects in tallgrass prairie. Ecology 69:46-58.

King, T.J. 1977. The plant ecology of ant-hills in calcareous grasslands. III. Patterns of species in relation to ant-hills in southern England. Journal of Ecology 65:235-256.

Mueller-Dumbois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons. New York.

Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. Ecological Monographs 45:285-305.

Platt, W.J., and I.M. Weis. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. American Naturalist 111:479-513.

Polley, H.W., and S.L. Collins. 1984. Relationships of vegetation and nenvironment in buffalo wallows. American Midland Naturalist 112:178-186.

Singh, J.S., W.K. Lauenroth, R.K. Heitschmidt, and J.L. Dodd. 1983. Structural and functional attributes of the vegetation of Northern Mixed Prairie of North America. Botanical Review 49:117-149.

Soil Conservation Service. 1981. Soil survey of McPherson County, South Dakota. U.S. Department of Agriculture, Washington D.C.

Steuter, A.A. 1987. C_3/C_4 production shift on seasonal burns - northern mixed prairie. Journal of Range Management 40:27-31.

Van Der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. Ecology 62:688-696.

Weber, N.A. 1935. The biology of the thatching ant, *Formica rufa obscuripes* Forel, in North Dakota. Ecological Monographs 5:166-206.

Wilson, R.G., and M.K. McCarty. 1984. Germination, and seedling and rosette development of flodman thistle (*Cirsium flodmanii*). Weed Science 32:768-773.

THE WESTERN PRAIRIE FRINGED ORCHID (*PLATANTHERA PRAECLARA*): MONITORING AND RESEARCH

Ardell J. Bjugstad
USDA Forest Service, Rocky Mountain Forest and Range Experiment Station,
Rapid City, South Dakota 57701

and

William Fortune
USDA Forest Service, Custer National Forest, Sheyenne National Grassland,
Lisbon, North Dakota 58054

Abstract. Western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles) populations at one time extended from southwestern Missouri north to northwestern Minnesota, and from eastern Iowa to the Sandhills of north central Nebraska. It is listed as endangered in Iowa and Minnesota and candidate for threatened or endangered status in Kansas, Missouri, Nebraska, North Dakota, Oklahoma, and South Dakota. The questions are, "Why has it declined in numbers?" How have uses such as mowing for hay or grazing by cattle or no use (control) affected the numbers? In 1987, permanently located individual plants were counted on the Sheyenne National Grasslands of southeastern North Dakota. Population trends of this orchid were compared regarding effects of mowing, grazing, and fire. The evaluation of the permanently located individual plants, and data on total counts per area in 1988 showed a difference between years and significant difference among grazed, mowed, or no use treatments. The western prairie fringed orchid appears very resilient, but more data will be needed to test this prognosis.

Key Words. western prairie fringed orchid, *Platanthera praeclara*, orchid, wet meadow, Sheyenne National Grasslands, North Dakota

INTRODUCTION

The western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles) is one of the few characteristic North American tallgrass prairie orchids and appears restricted to the tallgrass habitat (Bowles and Duxbury 1986). It occurs in wet areas of the tallgrass vegetation type, often referred to as sedge meadows. Eastern prairie fringed orchid [*Platanthera leucophaea* (Nutt.) Lindl.], closely resembling western prairie fringed orchid, also occurs in wet meadows, but its distribution is more easterly. Western prairie fringed orchid has larger flowers and a longer nectar spur than eastern prairie fringed orchid (Sheviak and Bowles 1986). Western prairie fringed orchid occurs mainly west of the Mississippi River in the tallgrass prairie region, while eastern prairie fringed orchid extends primarily eastward from the Mississippi River.

Western prairie fringed orchid reaches its northern range limit in the Red River Valley of northern Minnesota. It ranges south through the eastern Dakotas, central Nebraska, eastern Kansas, and northeastern Oklahoma (Dusk and Fletcher 1943, Magrath 1973, Magrath and Taylor 1978). Its distribution extends eastward in a narrowing pattern through southern Minnesota, Iowa, and northern Missouri, and it is known to be present at this time in these various locations at varying densities. Many subpopulations appear extant, with others very limited in numbers. The western prairie fringed orchid has been proposed for listing as threatened and endangered. Presently the greatest number of plants appear to be in southeastern North Dakota and northwestern Minnesota. Bowles and Duxbury (1986) reported western prairie fringed orchid was dispersed across several thousand hectares of the southeastern North Dakota area, and it comprised several indistinct subpopulations and isolated outliers. Precise delineation of these was difficult because of the irregular terrain.

In North Dakota, the western prairie fringed orchid has been found in Ransom and Richland counties, mainly on the Glacial Sheyenne Delta. It occurs as widely scattered plants probably as viable populations or subpopulations in wet meadows, also known as sedge meadows or as interdunal sedge meadows (Bowles and Duxbury 1986). The Glacial Sheyenne Delta was formed near the end of the Wisconsin Glaciation where glacial meltwater of the glacial Sheyenne River emptied into Glacial Lake Agassiz and deposited sands, clays, and gravels. A layer of nearly impervious lake sediments is below the delta formation. This layer is responsible for the relatively high water table of the area (Manske and Barker 1988).

Vegetation on the Glacial Sheyenne Delta consists of native forest, woodland and grassland communities and nonnative (cropland) replacement communities with associated cultivated and introduced plant species. The Delta has been divided into 11 habitat types on the basis of similar plant species composition, soil type, and topography (Manske and Barker 1988). Eight habitat types consist of native vegetation and three of replacement (cropland) vegetation. The habitat types with closely related characteristics and distribution were grouped into four habitat associations. The Hummocky Sandhills Habitat Association consists of 26,516 ha, 50% of the Sheyenne National Grasslands. The topography is gently rolling and undulating hummocks (small hills) with relief usually of 1.7 to 3 m and slope of 5 to 10%. Soils are primarily loamy fine sand which have typically moderate to low water holding capacity but with high moisture due to a high water table. This habitat association is divided into four habitat types. The Lowland Grassland Habitat Type exists on the foot and toe slopes and has an area of 5,157 ha (10%). Soils are fine sandy loams with moderate to low available water holding capacity but with high soil moisture because of a high water table. The vegetation is the wooly sedge-northern reedgrass-Baltic rush (*Carex lanuginosa - Calamagrostis inexpansa - Juncus balticus*) sedge meadow community. This sedge meadow plant community appears to be the habitat type where the western prairie fringed orchid is located. This plant community covers a total of 7,338 ha (14%) (Manske and Barker 1988).

The Deltaic Plain Habitat Association consists of 15,693 ha, 30% of the Glacial Sheyenne Delta. The topography is nearly level with relief usually 0.3 to 0.6 m and small areas of relief of 0.3 to 1.7 m with slopes mostly less than 2%. Soils are primarily loam with high to moderate available soil moisture. The entire association has a high water table. This habitat association is divided into three habitat types, the Midland Grassland Habitat Type, the Lowland Habitat Type (*Carex lanuginosa - Calamagrostis inexpansa - Carex* spp. sedge meadow community), and the Cropland Habitat Type. The Cropland Habitat Type is a large portion of this association because of the nearly level topography and good fertile soil. This also very likely was occupied by western prairie fringed orchid before conversion to cropland.

During 1984-1985, a systematic mapping effort recorded approximately 2,000 flowering individuals. Most of the population is on the Sheyenne National Grasslands, managed by the USDA Forest Service (Bowles and Duxbury 1986). Population characteristics of this species on the Sheyenne National Grassland, the area where it now is most abundant, remain unknown. Knowledge is lacking on the effects of fire, grazing, or mowing on populations of orchids. Woody vegetation on sedge meadows not properly managed may increase with unknown effects on the orchid populations. On other sites where woody vegetation is greatly reduced or lacking, the population characteristics of the orchid are unknown. The effects of repeated summer mowing for hay with follow-up grazing by cattle and the effects of fire or the lack of fire are also unknown (Barker 1983). Fire has been shown to increase seed stalk production on other species (Ehrenreich and Aikman 1963, Probasco and Bjugstad 1977).

The estimated 100-year decline of the population level throughout North America of the western prairie fringed orchid was mainly due to the conversion of its virgin prairie habitat to intensive agriculture-cropland (Bowles and Duxbury 1986). Decline has been recorded since 1969 in Kansas and Nebraska. Several intact sites remain where it should exist but is sparingly present. The immediate need is to determine why the plants are only sparingly present, what factors may increase the population, and later determine how to expand the population to new sites. The current management practices that may negatively or positively affect the orchid are summer mowing for hay, utilization by cattle, and fire or lack of fire. No data exist indicating whether or not any one or all of these treatments may benefit or threaten the survival of the western prairie fringed orchid.

The purpose of this paper is to describe the stronghold of the western prairie fringed orchid in southeastern North Dakota, the five-year plan to monitor populations levels, and discuss the preliminary (two years) research data.

METHODS

Five-Year Monitoring Plan

To monitor population trends, systematic counting and mapping of the plants during inflorescence will be done when the flowering is at its peak for a five-year period. This will need concentrated efforts on the Lowland Habitat Type. General reconnaissance and close examination of the area for plants will be done to monitor the total population count of all known western prairie fringed orchid locations on the Sheyenne National Grasslands. A person knowledgeable in identification of the western prairie fringed orchid will traverse potential sites on selected grid systems. Travel lines will be 30 m apart, giving a viewing distance of 15 m on each side of the traverse line. These data will be recorded on Forest Service maps on the Sheyenne National Grassland by site, allotment, pasture, and previous treatment.

Study Design

The locations of western prairie fringed orchid plants were permanently recorded starting in 1987 along research transects on five areas of different management treatments. More intensive sampling was initiated in 1988 to determine if individual plants (flowering structures) replace themselves each consecutive year or if they flower biannually or follow some other pattern. The five treatments (and their labels) were: 1) mowed for hay followed by grazing (Olerud); 2) mowed for hay according to grazing sequence (Penberthy 2); 3) grazed season-long (A-Annex); 4) burned followed by grazing (Penberthy 1); 5) burned only without livestock (Penberthy 3); and 6) no burned, mowed, or grazed (Railroad). Three subplots, with 10 plants each, were located within each treatment. Each subplot consisted of a permanently marked belt transect (50 x 2 m). The transect traversed a known community of orchid plants. All orchids within the belt transect were counted and 10 plant locations were permanently recorded. This was done by noting the location on the meter tape and measurements perpendicular to the exact location of the plant. Total percent canopy cover, bare ground, plant litter, and cover by individual plant species by use category was estimated using 50 quadrats (20 x 50 cm) placed 1 m apart along the 50-m permanent transects (Daubenmire 1959).

Two years of data have been collected on all research treatments except the burning treatments. The area was too dry to chance a prescribed burn in the spring of 1988. This will be delayed until 1989.

In 1988 each plant was measured for existence of aboveground parts (dead or alive). Plant height and length of inflorescence were measured as an indicator of vigor. Stages of plant phenology were numerically rated as either 1) vegetative, 2) immature inflorescence, 3) flowering, 4) seed set, and 5) seed dispersal. These estimates were determined during the study of the individual plants. Photo points were located at each end of the tightened tape where steel fenceposts were installed.

RESULTS

During the period of 14 to 16 July 1987, 796 plants were counted by using a 4-wheel-drive all-terrain vehicle (ATV) to grid the wet meadows at 30-m intervals on the study sites. Of the 796 plants, 160 locations were permanently recorded.

Flowering stalks of the species emerged from the same place, at least for 1987 and 1988 for several individual plants. In some cases there were no flower stalks, and sometimes not even a plant, in 1988 where they had been present in 1987. In spite of only 30% of average rainfall during the growing season of 1988, most plants emerged (Table 1). This may be important and will be monitored.

Table 1. Orchid plant numbers by year at monitoring sites over 2-year period.

Sites	*Treatments*	*1987*	*1988*
Railroad	Control	24	13
Olerud	Mowed	173	125
Penberthy	Grazed	236	233
Sagvold[1]	Grazed	87	86

[1]This allotment was included only in monitoring phase.

An inspection of precipitation data may provide some answers (Table 2). The plants may still be responding to the high level of precipitation in 1986. This characteristic is common for this species, i.e., plants may be very showy then seemingly disappear, likely surviving in only the vegetative stage, for several years (Currier 1984). One hypothesis is that the plants or populations are weather oriented, i.e., being showy only following growing seasons of high precipitation levels, being vegetative for long periods of time before flowering, and not being visible for long periods of time (Magrath 1973).

An unexpected number of individually located plants did grow in 1988 in spite of the drought. Fifty-five percent were relocated as alive, 30% had previous year's stem but no growth in 1988 (Table 3). No relocation was possible for 16%. It is too early to conclude anything from this preliminary data, yet snow accumulation associated with brushiness (as in the A-Annex site) could promote growth and seed stalk production not observed on grassy areas. This has been determined in the relations of stubble height, snow accumulation, and growth of forage plants (Ries and Power 1981). However, it is not known whether it was the drought of 1988 or the mowing treatment in 1987 that contributed to the difference in numbers of plants on the Olerud site in 1988. It should be noted that on the Penberthy 2 site, which had similar treatment as the Olerud site, differences were small.

Table 2. Annual precipitation (mm) at Lisbon and McLeod[1], North Dakota, with emphasis on January to July percentage of normal for 1988.

Year		McLeod	Lisbon
		----------mm----------	
1980		670	668
1981		904	650
1982		798	715
1983		709	661
1984		830	744
1985		634	591
1986		1092	993
1987		438	624
	Average	759	705
1988			
Jan		48	19
Feb		5	4
Mar		24	14
Apr		14	0
May		181	50
June		69	70
	Total	342 (60%)[2]	159 (30%)[2]

[1]Lisbon is located 16 km west and McLeod is located 8 km east of the study area.
[2]Percent of 8-year average midyear precipitation.

Table 3. Percent ± S.E. of individual located plants counted in 1988 that were live plants in 1987.

Site	Treatment	Alive	Old stem[1]	No stem[1]
		----------	%	----------
Olerud	Mowed & grazed	42 ± 7.5	20 ± 10.8	38 ± 8.5
A-annex	Grazed-brushy	75 ± 8.6	18 ± 4.8	7 ± 4.8
Railroad	No use	65 ± 15.0	15 ± 5.0	20 ± 10.0
Penberthy				
	Nongrazed 1	50 ± 5.8	43 ± 8.8	7 ± 6.7
	Grazed 2	40 ± 17.3	53 ± 17.6	7 ± 3.3
Average		55	30	16

[1]No living tissue above ground, old stem present or absent.

In the literature, western prairie fringed orchid plant densities have varied from 0.01 to 6 plants per m² for limited localities (Bowles 1983, Bowles and Duxbury 1986). The data collected in 1988 on the Sheyenne National Grasslands show plant densities that varied from 0.02 per m² and less. In most stands, the plants were too infrequent to be measured using 50 quadrats (0.1 m²) on a 50-m transect. Phenology, plant height, and length of inflorescence of the permanently recorded plant locations for the 1988 season show few differences among treatments (Table 4). More continuous data will be needed to compare treatments.

Table 4. Phenology, plant height (cm ± S.E.), and length of inflorescence (cm ± SE) in 1988 by treatment.

Site	Treatment	Phenology[1]	Height	Length of inflorescence
		----------	cm ± S.E.	----------
Olerud	Mowed & grazed	2.3	17.5 ± 1.9	4.2 ± 1.1
A-Annex	Grazed-brushy	2.7	13.6 ± 1.3	3.0 ± 0.4
Railroad	No use	2.0	16.9 ÷ 1.8	None
Penberthy				
	Nongrazed 1	2.0	18.3 ± 1.5	None
	Grazed 2	2.4	25.9 ± 3.5	4.8 ± 0.7

[1]1 = vegetative, 2 = immature inflorescene, 3 = flowering, 4 = seed set, 5 = seed dispersal. Average for each site (treatment) at peak flowering time.

CONCLUSIONS

A monitoring and research plan are in effect for the prairie fringed orchid on the Sheyenne National Grassland. The preliminary data are inconclusive, but early indications suggest the prairie fringed orchid appears resilient, with little to no change in numbers of plants on the monitor sites between years in spite of severe drought (30% of 8-year average) in 1988 compared to 1987. The percent alive in 1988 was highest on a grazed-brushy site (A-Annex), exceeding that on the no-use site (Railroad). The characteristics measured of the western prairie fringed orchid varied considerably neutralizing will be required to determine treatment effects. This is common when working with unknown genetics of a wild plant.

LITERATURE CITED

Barker, W. 1983. Manipulation of plant species composition, animal distribution, and herbage production by burning. Bulletin of the Ecological Society of America 64:110.

Bowles, M.L. 1983. The tallgrass prairie orchids *Platanthera leucophaea* (Nutt.) Lindl. and *Cypripedium candidum* Muhl. *ex* Willd.: Some aspects of their status, biology, and ecology, and implications toward management. Natural Areas Journal 3:14-37.

Bowles, M.L., and A. Duxbury. 1986. Report on the Status of *Platanthera praeclara* Sheviak and Bowles in Oklahoma, Kansas, Nebraska, South Dakota and North Dakota. Report submitted to U.S. Fish and Wildlife Service, Endangered Species, Denver.

Currier, P. 1984. Response of prairie fringed orchid to fire and reduction in grazing. Restoration and Management Notes 2:28.

Daubenmire, R. 1959. A canopy cover method of vegetational analysis. Northwest Science 33:43-65.

Dusk, L.G., and J.B. Fletcher. 1943. A game type map of Oklahoma. Oklahoma Biological Survey, Norman.

Ehrenreich, J.H., and J.M. Aikman. 1963. An ecological study of the effects of certain management practices on native prairie in Iowa. Ecological Monographs 33:113-130.

Magrath, L.K. 1973. The native orchids of the prairies and plains region of North America. Doctor of Philosophy Dissertation. Department of Botany, University of Kansas, Lawrence.

Magrath, L.K., and J. Taylor. 1978. Orchids and other new and interesting plants from Oklahoma. Southeastern Oklahoma State University Herbarium Publication Number 2.

Manske, L.L., and W.T. Barker. 1988. Habit usage by Prairie Grouse on the Sheyenne National Grasslands. Pages 8-20. *In* USDA, Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report RM-159.

Probasco, G.E., and A.J. Bjugstad. 1977. Tall fescue response to fire. USDA Forest Service, North Central Forest Experiment Station Research Note NC-218.

Ries, R.E., and J.F. Power. 1981. Increased soil water storage and herbage production from snow catch in North Dakota. Journal Range Management 34:485-488.

Sheviak, C.J., and M.L. Bowles. 1986. The prairie fringed orchids: a pollinator-isolated species pair. Rhodora 88:267-290.

DO YOU KNOW *PLATANTHERA PRAECLARA*?

Rochelle Bjugstad
Moon Meadows Road, Rapid City, South Dakota 57701
and
Ardell J. Bjugstad
Rocky Mountain Forest and Range Experiment Station, USDA, Forest Service,
Rapid City, South Dakota 57701

Abstract. This is a brief synthesis on the plant, habitat and range of the western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles). This species was once common in the tallgrass prairie, but its numbers have been greatly reduced by improper management and loss of habitat. Comparisons are made to the eastern prairie fringed orchid [*Platanthera leucophaea* (Nutt.) Lindl].

Key Words. western prairie fringed orchid, *Platanthera praeclara*, orchid, wet meadow, rare species

INTRODUCTION

Western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles) is a rare prairie orchid known only to a few people. It has only recently been separated from the eastern prairie fringed orchid [*Platanthera leucophaea* (Nutt.) Lindl.] as a distinct species. Only a few basic facts are known about the species: what it looks like in its floral state, where it lives, where it doesn't live, and some land management practices with which it can survive.

DISCUSSION

The Plant

Western prairie fringed orchid is similar to the eastern prairie fringed orchid, its relative east of the Mississippi River. Both are among the most highly evolved North American *Platanthera*. Each orchid has achieved speciation by adapting to different pollinators through differences in floral anatomy. These differences are morphological which dictate differences in pollinators. The flowers of western prairie fringed orchid are larger than the flowers of eastern prairie fringed orchid. The larger flower size of western prairie fringed orchid also means a longer nectar spur, which is the longest of any northern temperate member of the genus. Therefore, the western prairie fringed orchid requires pollinators (usually a moth, as both orchids display flowers which are nocturnally fragrant) with longer proboscises. The average spur length of western prairie fringed orchid is 1 cm longer than that of the eastern prairie fringed orchid (Sheviak and Bowles 1986). The pollinaria placement is slightly different between these orchids, which also separate effective pollinators and prevents cross-pollination. In general, western prairie fringed orchid produces shorter, denser inflorescences of fewer, larger flowers than eastern prairie fringed orchid. Western prairie fringed orchid has only recently been separated from *Platanthera leucophaea* (Luer 1975). Some taxonomists have placed it in the genus *Habenaria* Willd. (Luer 1975, Great Plains Flora Association 1986).

The western prairie fringed orchid is an herbaceous perennial that grows from a fusiform tuber. The leaves are lance shaped to suborbicular and sheath the lower stem. Basal leaves can be up to 20 cm long, while other leaves are reduced upwards. Flowers are large and showy, arranged in a spiciform raceme with 20 or more flowers. Each hooded flower is creamy white with three larger lower petals that are three-lobed and fringed. A slender nectar spur is included. Total flower length can be up to 15 cm, the nectar tube 3.5- 5 cm, and the main petals 1.5-2.5 cm. Western prairie fringed orchid capsules are produced after flowering and remain in the pod until it drys, cracks, and tiny seeds are dispersed. Little is known about its incubation needs or germination requirements (Sheviak and Bowles 1986).

The Habitat

Western prairie fringed orchid is found mostly in mesic prairie swales. These lowlands usually have sandy soils where the water table is near the surface and is often flooded. Western prairie fringed orchid is one of the few orchids of the tallgrass prairie, appears restricted to this habitat, and is usually an indicator of virgin prairie. Rarely is it found under successional conditions. This orchid is often seen in a sedge-meadow site on soils that are slightly acidic to neutral (5.4 to 7.6 pH), calcareous (1,730 to 6,456 ppm Ca), alluvial, lacustrine over sand, and loess or glacial till (Bowles and Duxbury 1986).

The Range

Western prairie fringed orchid reaches its northern distribution in the Red River Valley of northern Minnesota. Southward, it ranges through the eastern Dakotas, central Nebraska, Kansas, and northeastern Oklahoma (Magrath 1973, Magrath and Taylor 1978). Its distribution extends eastward in a narrowing pattern through southern Minnesota, Iowa and northern Missouri. The Mississippi River is its eastern range boundary. Precise occurrences are located in five states: Oklahoma (treated by Tyrl *et al.* 1978 as eastern prairie fringed orchid), Kansas, Nebraska, South Dakota, and North Dakota.

In the past, western prairie fringed orchid was erroneously noted to have been seen as far west as Wyoming. Many old reports are known to be vague in land description and/or precise location. One such report was from the early explorer Lt. John Fremont. He collected a western prairie fringed orchid specimen and noted its location in the Platte Valley near what is now Casper, Wyoming. According to A. E. Nelson, Herbarium Manager of the Rocky Mountain Herbarium at the University of Wyoming, further research into Fremont's diary of the exploration has shown that the date of collection is unclear, as well as the diary report of that date. Some speculation is that Fremont actually collected the plant in the Nebraska Sandhills, because proper habitat does not exist near Casper, Wyoming.

Populations vary over the entire range of the western prairie fringed orchid from a few plants in some locations to over 2,000 at another. Many potential habitats and populations may exist for this orchid, but may be overlooked because the different life stages are not yet recognized

Land management where western prairie fringed orchid is found varies. The largest population known (over 2,000 plants) is in the Sheyenne National Grassland where cattle grazing is the major use. Many areas where populations exist are hay meadows, which are occasionally mowed. These orchids do not survive plowing or urban development (Bowles and Duxbury 1986).

CONCLUSIONS

Western prairie fringed orchids are beautiful plants that are protected by law in many states. They may again become a part of the common flora of the tallgrass prairie. This species had a wide distribution throughout the tallgrass prairie, but it now exists in a few locations with the largest population in southeastern North Dakota. Little adequate data are available on the habitat needs or effects of various land management practices on this species. More information is needed on its needs and life history.

LITERATURE CITED

Bowles, M.L., and A.V. Duxbury. 1986. Report on the Status of *Platanthera praeclara*. U.S. Fish & Wildlife Service Endangered Species, Denver.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Luer, C.A. 1975. The native orchids of the United States and Canada, excluding Florida. New York Botanical Garden, New York.

Magrath, L.K. 1973. The native orchids of the prairies and plains region of North America. Doctor of Philosophy Dissertation, Department of Botany, University of Kansas, Lawrence.

Magrath, L.K., and J. Taylor. 1978. Orchids and other new and interesting plants from Oklahoma. Southeastern Oklahoma State University, Herbarium Publication Number 2.

Sheviak, C.J., and M.L. Bowles. 1986. The prairie fringed orchids: a pollinator-isolated species pair. Rhodora 88:267-290.

Tyrl, R.J., J.L. Gentry, Jr., P.G. Risser, and J.J. Crockett. 1978. Status report on *Platanthera leucophaea* (Nutt.) Lindl. School of Biological Sciences, Oklahoma State University, Stillwater.

THE FUTURE OF A PROLIFIC VARIANT OF EASTERN GAMAGRASS

Laura Jackson
Department of Ecology and Systematics, Cornell University,
Ithaca, New York 14853

and

Chet Dewald
USDA-ARS Southern Plains Range Research Station, 2000 18th Street,
Woodward, Oklahoma 73801

Abstract. Eastern gamagrass [*Tripsacum dactyloides* (L.) L.] is currently being selected for higher forage yield. A prolific variant which can produce up to 20 times the number and 3 times the weight of seeds of a normal plant was found in a wild population and is now instrumental in the breeding program. Could this prolific type spread in wild populations? Vegetative vigor of mature plants was assessed by clipping plants to a 7 cm height every two weeks throughout the growing season. The two types did not differ in dry weight of regrowth, suggesting that they tolerate defoliation equally. Seed germination was compared by determining the parentage of 1,043 seedlings emerging near a nursery containing 64% normal and 36% prolific plants. Based on counts of inflorescences and seeds in the soil, variant plants contributed up to 90% of the seeds in the area. However, only 29% of the seedlings established in the area came from prolific plants. The prolific variant was equal in vegetative vigor as an adult plant, and equal or at a disadvantage as a maternal parent. Since the condition is recessive, pollen production is extremely low, and high seed fecundity is offset by poor germination success, the prolific type is not expected to spread in the wild.

Key Words. eastern gamagrass, *Tripsacum dactyloides,* seed germination, resource allocation, forage grass breeding, Oklahoma

INTRODUCTION

General agreement is that when establishing or restoring prairie, it is best to use seeds from local sources, if possible. The goal is to preserve the genetic diversity of prairie species for its own sake, not to try to "improve" on the prairie's innate beauty or productivity. However, some prairie species, especially grasses, have considerable economic value as forage for cattle. In the last few decades selection has occurred for strains of native grasses with higher forage yield, palatability, and nutrition (Harlan 1975). Even more recently, researchers at The Land Institute in Salina, Kansas have begun to domesticate prairie grasses and forbs for grain.

Eastern gamagrass [*Tripsacum dactyloides* (L.) L.] is under intensive selection for forage production at the USDA-ARS Southern Plains Range Research Station in Woodward, OK. A recently discovered form of the grass [*Tripsacum dactyloides* (L.) L. forma *prolificum* Dayton et Dewald), which has the potential to produce 20 times the number of seeds and 3 times the weight of seeds of normal plants (Dewald and Dayton 1985) is instrumental in the breeding program. A recessive major gene at a single locus changes most of the male flowers to female flowers. Little pollen is produced, seeds are more numerous but smaller, and total allocation to reproduction is greater. This condition, referred to here as "prolific," allows plant breeders efficiently to cross normal males onto prolific females and evaluate many progeny per cross. Although not directly related to forage quality, the trait is used as a breeding tool, and is thus common in breeding nursery populations, although found in only one wild population.

How will selection for domesticated traits affect a species' ability to survive and reproduce in the wild? Life history theory predicts that higher allocation to reproduction should be accompanied by a decrease in longevity or ability to withstand stress. Decreases in seed size should reduce seedling establishment. This paper compares the vegetative vigor and reproductive success of normal and prolific forms of eastern gamagrass.

METHODS

Vegetative Vigor

In spring of 1986, normal and prolific plants were established by transplant at the USDA-ARS Southern Plains Range Research Station, Woodward, Oklahoma in a randomized complete block design. On 23 April 1988, plants were clipped back to a height of 7 cm and reclipped every two weeks thereafter. Clippings were dried at 55 C to constant mass. Seed stalks, which began to elongate in early May, were left intact on the otherwise clipped plants.

For each plant, total regrowth over the summer was calculated by adding the weights of all clippings after the first. In order to account for initial plant size, the log of total regrowth was plotted against the log of the dry weight of the first clipping. Normal and prolific plants were plotted separately, and the slopes compared using analysis of variance (Snedecor and Cochran 1980).

Seed Rain and Seedling Establishment

Seedling establishment of normal and prolific plants was assessed by comparing the population of seedlings next to a breeding nursery with the seed source population of adult plants in the nursery. Seeds were assumed to have dispersed from plants on the edge of the nursery. Seed rain, or the proportion of normal and prolific seeds falling in the area, was estimated by counting the number of normal and prolific inflorescences falling into the nursery edge, and multiplying by the average number of seeds per inflorescence. Seeds on the soil surface were swept up with a broom and identified as described below as either normal or prolific. The proportion of normal and prolific seeds in the soil was determined by removing the top 5 cm of soil in 28 plots (112 x 15 cm) placed 0 and 50 cm from the nursery edge, and washing the soil through a 2 mm screen. Propagules remaining in the screen were opened and seeds were counted.

Seedling establishment of the two types was compared by determining the parentage of 1,043 seedlings growing within 2 m of the nursery. The spikelet and rachis segment ("propagule") of seeds from both normal and prolific plants can remain attached to the spent seed for one to three years after germination. Seedlings were carefully dug up and the attached propagule categorized as either normal, prolific-paired, or prolific-solitary. Ninety-two percent of the seedlings unearthed retained the propagule and were identified as either of normal or prolific maternal parentage.

Propagule Identification

Propagules from normal and prolific plants were distinguished by a combination of spikelet morphology and seed shape. A normal propagule consisted of a single spikelet set into a cupule formed by the rachis. Usually one round seed occurred within it. Two types of prolific propagules have been noted. The solitary type is a single cylindrical spikelet with two flattened seeds. It can be distinguished from a normal propagule by the number and shape of the seeds. Infrequently, normal propagules will hold two seeds instead of one, and prolific solitary propagules will mature only one seed instead of two. In these cases, misidentification will occur. The proportions of one-seeded prolific and two-seeded normal propagules were not quantified in this experiment. The paired propagule type consisted of two spikelets that did not sit within a cupule formed by the rachis, but are relatively free of it. This propagule type is immediately and definitely distinguished from the normal propagule by shape alone.

RESULTS

Vegetative Vigor

Repeated defoliation over the summer caused plants of both types to turn yellow and die back. Individual tillers stopped growing, produced few or no daughter tillers, and some eventually died. The relationship between initial size, measured as the grams dry weight of the first clipping, and total summer regrowth, the total grams dry weight clipped subsequently, was linear when log-transformed. The slopes of total regrowth as a function of initial plant size did not differ significantly for normal and prolific plants (Figure 1), indicating that for plants of a given size, normal and prolific grew back equally well.

Seedling Establishment

Estimates of seed rain agreed with numbers of seeds found in the surface and top 5 cm of the soil (Table 1). Although prolific plants contributed 90% of the seeds falling in the area, only 29% of the seedlings unearthed in the area were from a prolific maternal parent.

Table 1. Percent of normal and prolific genotypes represented in the seed rain, the soil seed bank, and seedling populations of eastern gamagrass.

	Normal	*Pistil*	*Unidentified*
		%	
Source population (nursery plants)	64	36	0
Seed rain	10	90	0
Soil surface	11	89	0
Soil seed bank	19	81	0
Seedlings	63	29	8

DISCUSSION

After being defoliated by an herbivore or mower, grasses must regrow in order to survive. Regrowth requires carbohydrates, nutrients, and water which initially must come from underground reserves (Langer 1979). If seed production draws from these reserves, prolific plants should show a diminished ability to respond to defoliation. This experiment showed no difference between normal and prolific plants' abilities to regrow after defoliation, as measured by grams dry weight regrowth. More detailed analyses of changes in plant size and direct measures of below ground reserves are needed to confirm this result. In natural populations, other factors, such as disease and interspecific competition, could differentially affect normal and prolific plants' survival. Furthermore, clipping by pruning shears does not adequately mimic the uneven tearing and trampling of grazing animals. However, bi-weekly defoliations nearly killed plants of both types, so the extremes of stress encountered in the wild were matched in this experiment.

Seedling establishment agreed with the general prediction that the smaller seeds of the prolific type should be less successful than seeds of the normal type. However, prolific plants made up 36% of the border plants and 29% of the seedlings, so high seed number was nearly making up for poor seed germination and establishment. In natural populations, where seedling establishment is deterred by competition by other plants, the difference between normal and prolific seeds should be much greater.

Other factors, besides vegetative vigor and seedling establishment, could affect the success of the prolific type in the wild. The heavier inflorescences are more susceptible to damage by wind, rain, hail, or simply their own weight. The more open structure of the glumes appeared to encourage insects, which were found in higher numbers on the prolific type. Pollen production was extremely low, so fitness as a male parent, although difficult to quantify, must have been negligible. Finally, according to population genetics, even if the prolific type were advantageous, it would spread slowly because its inheritance is recessive.

Seeds with the prolific gene are currently being released to farmers for evaluation, and pollen from the breeding nurseries in Woodward no doubt travels far enough to fertilize natural populations of eastern gamagrass in the area. Thus, it is inevitable that the prolific type will appear in natural populations in greater frequencies than it does today. Not because of its low adult survivorship, but because of limited ability to reproduce from seed and pollen, it is predicted that the prolific type will not increase substantially in wild populations.

LITERATURE CITED

Dewald, C.L., and R.S. Dayton. 1985. A prolific sex form variant of eastern gamagrass. Phytologia 57:156.

Harlan, J.R. 1975. Crops and man. American Society of Agronomy and Crop Science Society of America, Madison, Wisconsin.

Langer, R.H.M. 1979. How grasses grow. Edward Arnold, London.

Snedecor, G.W., and W.G. Cochran. 1980. Statistical methods. Iowa State University Press, Ames.

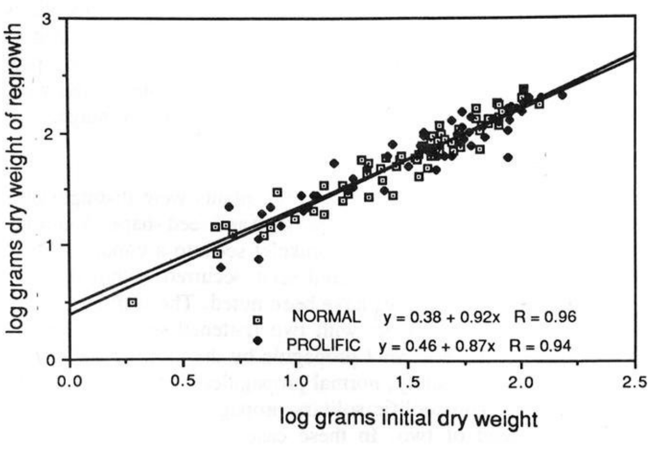


FIG 1. Regrowth after defoliation of eastern gamagrass as a function of initial size.

SILICA, NITROGEN, AND PHOSPHORUS DYNAMICS OF TALLGRASS PRAIRIE

T. R. Seastedt, R. A. Ramundo, and D. C. Hayes
Division of Biology, Kansas State University, Manhattan, Kansas 66506

Abstract. Experiments were conducted on big bluestem (*Andropogon gerardii* Vitman) in the greenhouse and on a tallgrass site on Konza Prairie to evaluate the effects of simulated grazing on the cycling of silica (SiO_2), nitrogen, and phosphorus. Concentrations of all elements increased in vegetation that had been clipped or pruned. The absolute amount of nitrogen obtained by plants in the greenhouse experiment was increased by clipping foliage. Phosphorus exhibited only neutral or negative responses, while the absolute amount of silica declined in all but one experiment involving root pruning. In that experiment, the absolute amount of silica in roots was increased 25% by cutting a portion of the root system. These results suggest that the direct effects of clipping or pruning on the absolute amounts of elements cycled through vegetation are usually neutral or negative. Increased silicification or grazed foliage is suggested to be a consequence of delayed senescence and reduced leaf area. This interpretation provides a proximate reason why silicification is an "inducible defense" against herbivores.

Key Words. big bluestem, *Andropogon gerardii,* simulated grazing, nutrients, productivity, roots, Kansas

INTRODUCTION

McNaughton and Tarrants (1983) and McNaughton *et al.* (1985) presented findings indicating that silica concentrations in African grasslands increase in response to herbivory. Subsequent work by Brizuela *et al.* (1986) indicated that the North American grasses western wheatgrass (*Agropyron smithii* Rydb.) and little bluestem (*Andropogon scoparius* Michx.) also had higher silica concentrations in more heavily grazed areas. These studies have also explored the possibility that silica deposition in leaf tissues was an inducible response to foliage removal. Certain grasses appeared to increase in silica content following foliage removal, but this response did not appear to be a characteristic of all grasses.

The present study used field and laboratory manipulations to test whether the dominant tallgrass species, big bluestem (*Andropogon gerardii* Vitman), and other grasses exhibited enhanced concentrations of silica in response to simulated grazing of foliage and/or roots. Increased concentrations of silica following grazing may not, however, represent an "inducible response" to herbivory. If plants maintained a constant rate of silica uptake with reduced leaf area (i.e., if root uptake of dissolved silica is not affected by foliage removal), then silica concentrations in foliage would increase as a consequence of reduced leaf area. In other words, the same amount of silica is deposited in a reduced area of foliage, thereby increasing the concentrations of this material. A better test of the hypothesis that plants use silica as an inducible defense would be to measure total silica uptake of grazed and ungrazed plants. If the absolute amount of silica found in plants increased in response to herbivory, then this finding would provide strong support for the hypothesis. Therefore, quantitative estimates of silica uptake were obtained by harvesting foliage, roots, and rhizomes on an area basis in the field, and similar measurements were obtained on greenhouse plants. In addition to silica measurements, nitrogen and phosphorus measurements were concurrently made to evaluate the overall nutrient status of clipped or pruned plants and control plants.

STUDY SITE AND METHODS

Research was conducted on Konza Prairie Research Natural Area in the Flint Hills of northeastern Kansas, a site owned by the Nature Conservancy and managed by Kansas State University. The area is on the western edge of the tallgrass prairie biome, and has a typical big bluestem, little bluestem, and indiangrass [*Sorghastrum nutans* (L.) Nash] dominated vegetation characteristic of this region (Hulbert 1973).

The prairie site was on a relatively deep soil, annually burned upland area. A randomized design was used to divide the area into eight mowed and eight unmowed plots (10 x 5 m). The mowed plots were clipped to a height of 5 cm five times during the growing season (twice in May and once per month thereafter to August). A final aboveground clipping to ground level in all plots was conducted in October. Samples of foliage were obtained by clipping a quadrat (0.1 m^2) from each plot at the time of mowing. Roots were obtained with soil cores (5 cm diameter x 30 cm deep), washed with a root elutriator (Smucker *et al.* 1982), then sorted into live and dead categories, dried and weighed using procedures discussed in Hayes and Seastedt (1987). Rhizomes were obtained by hand sorting soil monoliths (0.1 m^2), washed and sorted into live and dead categories as described in Seastedt (1988). All samples were dried at 70 C, weighed, and stored for subsequent nutrient analysis.

In early June, a subset of the unmowed plots were subjected to a treatment that cut approximately one-half of the roots at a depth of about 10 cm. In the autumn root cores were taken from these root-pruned plots, and results compared to root biomass from unmowed controls.

The effects of clipping and root pruning were also investigated using these variables in a two-factor factorial design in an indoor study. This greenhouse experiment was initiated by harvesting 48 individual rhizomes of big bluestem and planting in plastic pots (1.5 l). These pots were placed on a single table, numbered sequentially from 1 to 48, and a specific treatment was assigned to each pot using a random number generator. Treatments consisted of 1) foliage clipping, defoliating the plants to a height of 5 cm twice during the growing season; 2) root pruning, cutting roots by sawing half-way through the pots at 5 cm depth twice during the growing season; 3) by imposing both treatments; or 4) by allowing plants to grow undisturbed. Foliage, roots and rhizomes were harvested at the end of the growing season and processed as described above.

Silica (SiO_2), as reported here, is equivalent to acid insoluble residue (Kucera and Ehrenreich 1962). Values represent the filterable solids left after dry ashing samples at 500 C and treating the ash with 20% sulfuric acid. The filtrate from this procedure was collected in ash-free filter paper, re-ashed, and weighed. A second, largely equivalent method involved collecting filterable solids following sample digestion in hot concentrated sulfuric acid (i.e., following a micro Kjeldahl digestion). These solids were subsequently ashed and weighed. Comparisons of values obtained here with those obtained with more sophisticated procedures (Lanning and Eleuterius 1987) indicated comparable results for foliage, and values for roots fall within those reported by McNaughton *et al.* (1985). However data from this procedure likely includes some non-silica residue and some insoluble aluminum and iron compounds. Nonetheless, treatment comparisons should not be affected by this potential contamination, because there is no reason to believe that potential contaminants would differ in their relationship with silica across treatments. Nitrogen and phosphorus concentrations were measured using a micro Kjeldahl digestion followed by colorimetric determination using a Technicon Autoanalyzer.

RESULTS

Greenhouse Experiment

Both clipping and root pruning had a negative effect on the productivity of plants grown in the greenhouse. Total plant biomass (roots, rhizomes, and foliage) of clipped, root pruned, or plants subjected to both treatments averaged 53%, 88%, and 49%, respectively, of the biomass of controls. The relatively larger effect of clipping may reflect the fact that the plants were given adequate water and were grown on relatively nutrient rich soil. Hence, productivity was apparently limited more by the availability of leaf area than by water and nutrients. Clipping of foliage resulted in significantly higher nitrogen and phosphorus concentrations in plant foliage and rhizomes compared to unclipped controls (Table 1). Silica concentrations were also higher in foliage of clipped plants than in controls. Root pruning had less visible influence on elemental concentrations. An increase in the silica concentrations of rhizomes in response to root pruning was the only significant effect measured (Table 1). When the average concentrations of elements for the total plant biomass are analyzed relative to the treatments, only clipping was important, and then only for nitrogen and phosphorus concentrations (Figure 1). The absolute amounts of the various elements obtained by the plants, however, exhibited a variable response to the treatments. Based on the results of a two-factor factorial ANOVA, the absolute amount of silica was unaffected by root pruning, but significantly declined in response to foliage removal (Figure 2). Phosphorus amounts were unaffected by either treatment, while the absolute amount of nitrogen increased in response to foliage removal (Figure 2). The amount of nitrogen accumulated by foliage clipped plants was, on average, 14% higher than for unclipped plants ($p < 0.05$).

Table 1. Silica, nitrogen, and phosphorus concentrations (% of mass) of big bluestem (*Andropogon gerardii* Vitman) subjected to foliage and/or root cutting (n = 12/treatment).

		Concentration (standard error)			
Plant part	*Element*	*Foliage clipped*	*Root pruned*	*Both treatments*	*Controls*
Autumn foliage	Si	8.59a[1] (0.27)	6.15b (0.39)	9.04a (0.44)	7.87b (1.53)
	N	0.49a (0.05)	0.25b (0.01)	0.54a (0.04)	0.23b (0.02)
	P	0.35a (0.02)	0.14b (0.01)	0.36a (0.01)	0.12b (0.01)
Autumn rhizomes	Si	4.93b (0.38)	5.70a (0.67)	5.59a (0.45)	4.41b (0.35)
	N	0.91a (0.07)	0.70b (0.04)	0.83a (0.04)	0.77b (0.05)
	P	0.11a (0.01)	0.07b (0.01)	0.10a (0.01)	0.09b (0.01)
Autumn live roots	Si	14.44 (3.94)	9.12 (0.75)	12.56 (1.47)	10.06 (0.90)
	N	0.72a (0.05)	0.52b (0.02)	0.85a (0.05)	0.47b (0.02)
	P	0.20 (0.09)	0.08 (0.01)	0.13 (0.01)	0.08 (0.01)
Clipped foliage	Si	4.52 (0.28)	—	4.64 (0.17)	—
	N	1.44 (0.07)	—	1.44 (0.06)	—
	P	0.22 (0.01)	—	0.21 (0.01)	—
Clipped roots	Si	— (2.09)	13.05 (1.27)	14.94	—
	N	—	0.52b (0.02)	0.78a (0.08)	—
	P	—	0.17 (0.09)	0.08 (0.01)	—

[1]Means within rows followed by different letters are significantly different (Duncans New Multiple Range test following two-way ANOVA, $p < 0.05$).

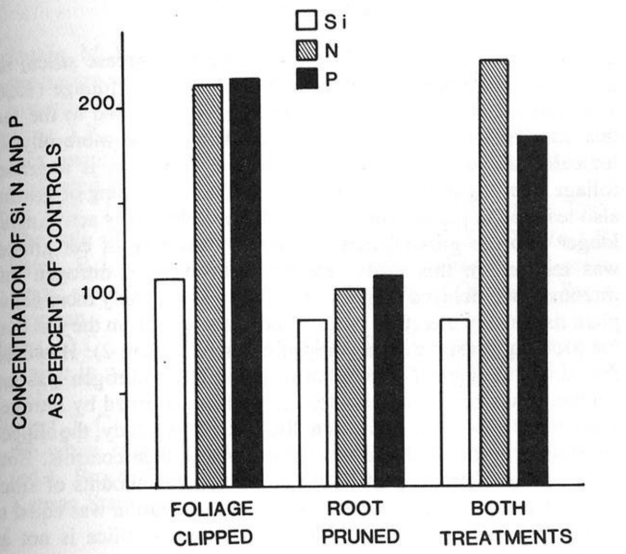


FIG. 1. Silica, nitrogen, and phosphorus concentrations for total plant biomass of foliage clipped and/or root pruned big bluestem as percentages of non-manipulated plants (Note: values for silica shown here and in subsequent figures are for SiO_2, not just Si).

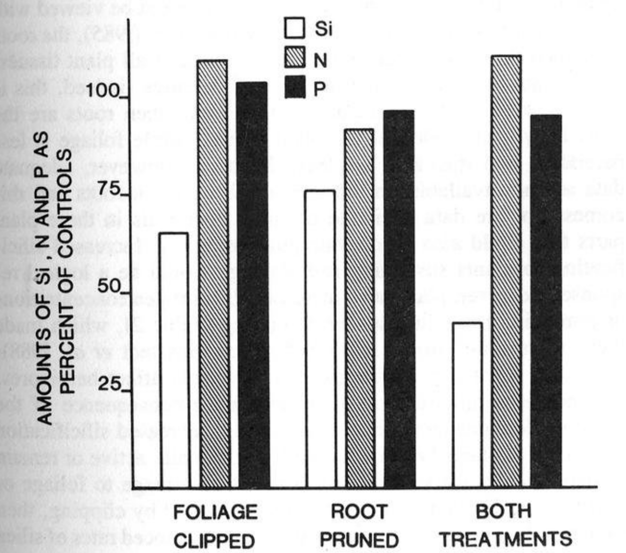


FIG. 2. Total amounts of silica, nitrogen, and phosphorus accumulated by plants subjected to foliage clipping and/or root pruning as percentages of non-manipulated plants.

Field Experiments

Plots mowed (to 5 cm) five times over the growing season averaged about 79% of the production of unmowed plots. Concentrations of silica in foliage increased through time (Figure 3). By autumn, silica content of the mowed plots was significantly greater than that of the controls. However, the differential abundance of flowering stems likely affected these results. Flowering stems of big bluestem were much lower in silica content than foliage (Lanning and Eleuterius 1987), and therefore ''diluted'' the total aboveground estimate. Flowering was not common on the mowed areas. Nitrogen and phosphorus concentrations tended to be higher in the clipped vegetation throughout the growing season. As in the greenhouse experiment, silica concentrations and amounts were highest in the roots (Figures 4 and 5). Less silica was found in foliage, and the least amount of silica was found in rhizomes. Dead roots and dead rhizomes had higher silica concentrations as a consequence of the loss of carbon compounds to microbial respiration. The absolute amounts of silica, nitrogen, and phosphorus in the plant tissues of mowed plants was 261, 16.9, and 1.3 g/m², respectively, as compared to 322, 22.3, and 1.8 g/m² of Si, N, and P, respectively, in unmowed plants (t-test, $p < 0.05$ for all tests). Thus, clipping the vegetation in this experiment resulted in a decline in the amount of all elements or compounds cycled by the plants.

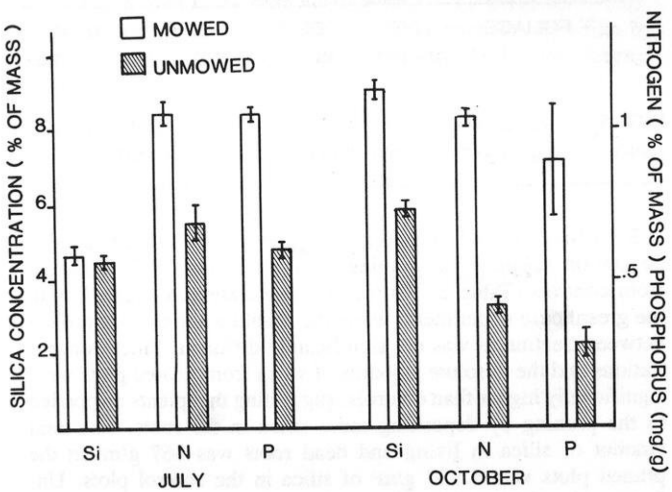


FIG. 3. Silica, nitrogen, and phosphorus concentrations of mowed and unmowed prairie foliage measured in July and October. The error bar represents one standard error of 8 replicates.

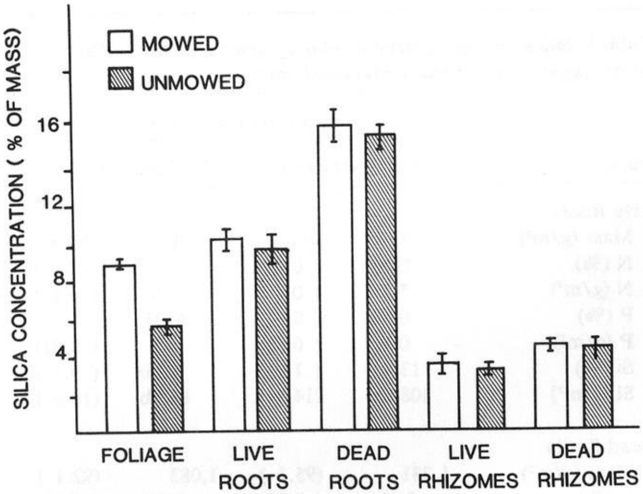


FIG. 4. Silica concentrations of plant parts harvested in October from mowed and unmowed plots.

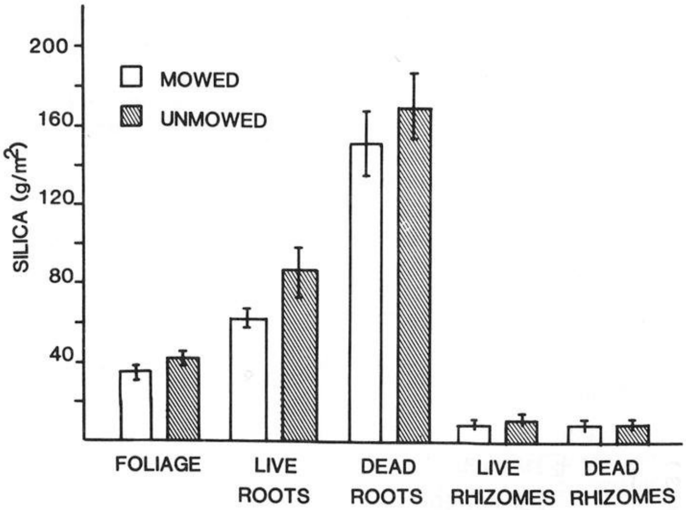


FIG. 5. Silica amounts in vegetation from mowed and unmowed prairie. Foliage amounts from mowed plots includes offtake.

Root biomass and phosphorus concentrations and amounts in vegetation subjected to pruning were not significantly different from controls (Table 2). Nitrogen concentrations increased as in the greenhouse experiment, while the absolute amount of nitrogen between treatments was not significantly different. Silica concentrations and the absolute amounts of silica from treated plots were significantly higher than controls, suggesting that plants responded to the pruning by depositing more silica in the roots. The total amount of silica in living and dead roots was 367 g/m² in the pruned plots versus 257 g/m² of silica in the control plots. Unfortunately, foliage from these plots was not concurrently harvested. Therefore, it is not know if the absolute amount of silica uptake increased in response to root pruning. The results do suggest, however, that silicification of roots occurs in response to damage occurring early in the growing season.

Table 2. Silica, nitrogen, and phosphorus concentrations and amounts of damaged (pruned) and undamaged roots.

	Mean (standard error)			
Variable	*Damaged roots*		*Undamaged roots*	
Live Roots				
Mass (g/m²)	794	(48.5)	878	(98.6)
N (%)	0.65a[1]	(0.02)	0.56b	(0.02)
N (g/m²)	5.2	(0.4)	4.9	(0.5)
P (%)	0.05	(0.01)	0.05	(0.01)
P (g/m²)	0.4	(0.03)	0.5	(0.07)
Si (%)	13.4a	(1.3)	9.0b	(0.7)
Si (g/m²)	108.8a	(14.0)	86.9b	(13.0)
Dead Roots				
Mass (g/m²)	1,231	(95.1)	1,083	(92.1)
N (%)	0.98a	(0.02)	0.89b	(0.02)
N (g/m²)	12.0a	(0.8)	9.5b	(0.9)
P (%)	0.06	(0.01)	0.06	(0.01)
P (g/m²)	0.7	(0.06)	0.6	(0.06)
Si (%)	20.6a	(0.72)	15.6b	(0.60)
Si (g/m²)	258.3a	(26.3)	170.3b	(18.5)

[1]Means within rows followed by different letters are significantly different ($P > 0.05$).

DISCUSSION

Clipping of foliage appears to consistently increase silica, nitrogen and phosphorus concentrations of regrowth foliage (Table 1, Figures 3 and 4). This response may be attributed to the fact that surviving and/or regrowth foliage tends to be more physiologically active per unit of mass or leaf area than is ungrazed foliage (Detling *et al.* 1979, Dyer *et al.* 1982). Clipping or grazing also resulted in plants remaining more physiologically active much longer into the growing season. While flowering of cut grasses was reduced in this study, the retranslocation of nitrogen into rhizomes was delayed (Figure 3). This physiologically more active plant tissue may therefore remove more nitrogen from the soil over the growing season than unclipped controls (Figure 2). However, this ability of grazed vegetation to pump more nitrogen was undoubtedly under climatic control as well as governed by nitrogen availability in soils. In contrast to the greenhouse study, the clipped vegetation in the field extracted less nitrogen than controls. Both field and greenhouse studies indicated that the amounts of silica and phosphorus cycled by foliage-clipped vegetation was equal to or less than controls. Such results suggest that silica is not an inducible defense to herbivory in the tallgrass prairie.

In contrast to other experiments, the root-pruning experiment conducted in June resulted in absolute increases in the amounts of silica in roots harvested in autumn. Unlike the other work, these results suggest that enhanced uptake of silica resulted from the manipulation and provides support that silicification can be induced by certain types of herbivory. These results should be viewed with some caution. Consistent with McNaughton *et al.* (1985), the roots contained the highest concentrations of silica of all plant tissues. If concentrations reflect the intensity of defenses (indeed, this is a basic premise for silicification of grasses), then roots are the most heavily defended of the plant tissues, while foliage is less defended, and rhizomes are least defended. However, adequate data are not available on the seasonal changes in roots and rhizomes, nor are data available on other chemicals in these plant parts that could also be discouraging herbivory. Increased silicification to plants sustaining root damage would be a logical response. However, plants also increased the nitrogen concentrations of remaining roots in response to cutting (Table 2), which made these roots more attractive to herbivores (Seastedt *et al.* 1988). Increased silica concentrations may adversely affect herbivores, but increased silicification could also be a consequence of the physiological changes induced by cutting. Increased silicification will occur if plants become more physiologically active or remain physiologically active longer as a result of damage to foliage or root tissues. If plant senescence can be delayed by clipping, then even absolute increases in silica uptake and enhanced rates of silica cycling by grazed plants could be a consequence of this response. The seasonality of dissolved silica in soil water might also explain these results. If silica concentrations of soil water increase during the growing season, then plants more physiologically active later in the growing season could passively accumulate more silica. Thus, while there exists little controversy that silicification has negative impacts on herbivores, and that the coevolution of grasses and grazers has likely resulted in the high levels of silica found in grasses (McNaughton and Tarrants 1983), the question as to whether silification is an inducible defense remains unresolved, at least for tallgrass species. Until the "cost" of silica uptake to the plants is established, alternative hypotheses cannot be rejected.

ACKNOWLEDGEMENTS

This research was part of a broader study designed to understand the effects of consumers on the prairie ecosystem. The study was supported by National Science Foundation grants BSR-8305436, BSR-8505861, and BSR-8514327 to Kansas State University. Present address of D. C. Hayes is Rocky Mountain Forest and Range Experiment Station, 2205 Columbia, SE, Albuquerque, New Mexico 87106.

LITERATURE CITED

Brizuela, M.A., J.K. Detling, and M.S. Cid. 1986. Silicon concentration of grasses growing in sites with different grazing histories. Ecology 67:1098-1101.

Detling, J.K., M.I. Dyer, and D. Winn. 1979. Net photosynthesis, root respiration and regrowth of *Bouteloua gracilis* following simulated grazing. Oecologia 41:127-134.

Dyer, M.I., J.K. Detling, D.C. Coleman, and D.W. Hilbert. 1982. The role of herbivores in grasslands. Pages 255-295. *In* J.R. Estes, R.J. Tyrl, and J.N. Bunken (eds.). Grasses and grasslands: systematics and ecology. University of Oklahoma Press, Norman.

Hayes, D.C., and T.R. Seastedt. 1987. Root dynamics of tallgrass prairie in wet and dry years. Canadian Journal Botany 65:787-791.

Hulbert, L.C. 1973. Management of Konza Prairie to approximate pre-white man fire influences. Pages 14-17. *In* L.C. Hulbert (ed.). Proceedings of the Third Midwest Prairie Conference. Kansas State University, Manhattan.

Kucera, C.L., and J.H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. Ecology 43:334-336.

Lanning, F.C., and L.N. Eleuterius. 1987. Silica and ash in native plants of the central and southeastern regions of the United States. Annals of Botany 60:361-375.

McNaughton, S.J., and J.L. Tarrants. 1983. Grass leaf silification: natural selection for inducible defense against herbivores. Proceedings of the National Academy of Science 80:790-791.

McNaughton, S.J., J.L. Tarrants, M.M. McNaughton, and R.H. Davis. 1985. Silica as a defense against herbivory and a growth promotor in African grasses. Ecology 66:582-535.

Seastedt, T.R. 1988. Mass, nitrogen and phosphorus dynamics in foliage and root detritus of tallgrass prairie. Ecology 69:59-65.

Seastedt, T.R., R.A. Ramundo, and D.C. Hayes. 1988. Maximization of soil animals by foliage herbivory: Empirical evidence, graphical and conceptual models. Oikos 51:243-248.

Smucker, A.J.M., S.L. McBurney, and A.K. Srivastava. 1982. Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. Agronomy Journal 74:500-503.

RHIZOME AND TILLER DEVELOPMENT OF THREE NEBRASKA SANDHILLS WARM-SEASON GRASSES

John J. Brejda
Mennonite Central Committee, GPO Box 785, Dhaka-2, Bangladesh

and

Lowell E. Moser and Steven S. Waller
Department of Agronomy, University of Nebraska, Lincoln, Nebraska 68583

Abstract. Rhizome and tiller development of ungrazed switchgrass (*Panicum virgatum* L.), prairie sandreed [*Calamolvilfa longifolia* (Hook) Scribn.], and sand bluestem [*Andropogon gerardii* var. *paucipilus* (Nash) Fern.] were studied for two years in the Nebraska Sandhills. Rhizome growth of switchgrass began at the 4- to 5-leaf stage. Following tiller elongation, no new rhizomes developed but rhizome elongation continued. Many of the prairie sandreed tillers were biennial similar to those of indiangrass [*Sorghastrum nutans* (L.) Nash]. Spring tiller development on prairie sandreed came from both vertical and horizontal rhizomes and continuing growth of late emerging tillers from the previous year. New rhizomes began growth at the 4- to 5-leaf stage. Prairie sandreed was the only grass to have rhizomes deeper than 10 cm. In sand bluestem, buds on rhizomes that were underneath the previous year's tiller lived over winter. In the spring after a tiller emerged through the soil and reached the 4- to 5-leaf stage meristematic tissue below the shoot apex elongated forming a rhizome which pushed the shoot apex to the soil surface. The newly formed rhizome initiated buds which served as the site of the following year's tiller development. Normal tiller elongation and inflorescence formation occurred later in the season. Prairie sandreed and sand bluestem are adapted to sand burial while switchgrass requires a more stable soil.

Key Words. sand bluestem, *Andropogon gerardii* var. *paucipilus*, prairie sandreed, *Calamovilfa longifolia*, switchgrass, *Panicum virgatum*, rhizomes

INTRODUCTION

The Nebraska Sandhills cover approximately 52,000 km^2 in north-central Nebraska (Seevers *et al*. 1975). Soils are composed primarily of fine sand, and are very susceptible to wind erosion (Frolik and Shepherd 1940). Despite the highly erosive nature of the soil, vegetated dunes are stable. Soil stability is due largely to the rhizomatous grasses common to the Sandhills.

Rhizomes and tillers function in propagation and competition in many Sandhills grasses. Tolstead (1942) reported that seeds seldom formed in well developed communities of sand bluestem [*Andropogon gerardii* var *paucipilus* (Nash) Fern.] and that prairie sandreed [*Calamolvilfa longifolia* (Hook.) Scribn.] reproduced almost entirely by rhizomes. Axillary buds located on the rhizomes, crowns, and stems of grasses are meristematic areas for vegetative reproduction (Heidemann and Van Riper 1967). Rhizomes enabled grasses to spread into open spaces, and invade underground to initiate new tillers between or beneath other plants (Weaver 1963).

A direct relationship existed between rhizome length and the area occupied by plants within a given time (Evans and Ely 1935). Mueller (1941) reported that grasses which quickly produced numerous, long, well-branched rhizomes were most effective in exploiting new areas. Efficiency in exploiting new areas was influenced by time of initiation, duration of the period of elongation, amount of elongation, branching, number of buds developed annually, and rhizome life (Mueller 1941). If energy was expended for numerous short rhizomes rather than for elongation, a smaller area was more completely occupied (Mueller 1941). Frequent appearance of new rhizomes compensated for shorter rhizomes (Evans and Ely 1935).

Rhizomes were important for the endurance of and recovery from drought and overgrazing (Weaver 1930 and 1963, Booysen *et al*. 1963). Rhizomes help grass withstand heavy grazing and trampling by providing protected underground growing points (Rechenthin 1956). Rhizomes may remain viable in the soil for several years and may resume growth when decreased grazing or favorable weather conditions permit (Weaver 1930).

The importance of sand bluestem and prairie sandreed to the Sandhills vegetation was recognized during initial botanical surveys (Smith and Pound 1892, Rydberg 1895, Pound and Clements 1900, Pool 1914). More recently Burzlaff (1962) considered sand bluestem and prairie sandreed as co-dominants with prairie sandreed being the most uniformly distributed and abundant grass on all upland range sites. Because of its vigorous rhizomatous habit prairie sandreed spread rapidly in the dune sand and played a major role in stabilizing exposed dunes and blowouts and contributed over 40% of the upland dune production (Frolik and Shepherd 1940). Tolstead (1942) reported that prairie sandreed was the most characteristic grass of the Sandhills, growing in a wide range of habitats from coarse sand to very fine sandy loam. Switchgrass is distributed widely both within and outside the Sandhills.

A thorough understanding of rhizome and subsequent tiller formation is essential for understanding the ecological role in the Sandhills and evaluating the response of these grasses to grazing and environmental conditions. The objective of this study was to describe the time of bud development, period of rhizome and tiller development, and growth of sand bluestem, prairie sandreed, and switchgrass.

METHODS

This descriptive study of rhizome and tiller development was conducted during the summers of 1984 and 1985 at the University of Nebraska Gudmundsen Sandhills Laboratory (GSL) located in Grant County, 12 km northeast of Whitman, Nebraska. The GSL lies in an annual precipitation zone of 500-560 mm of which about 75% falls during the growing season (April-September). Precipitation in 1984 was 362 mm during April through August. June precipitation was much above normal, July precipitation was normal, and August precipitation was below normal. In 1985, 183 mm fell in the same time period, and precipitation for all months was below normal. May, June, and July were especially dry. The soil was a Valentine fine sand (fine, sandy, mixed, mesic Typic Ustipsamment).

A fall-grazed pasture was the study site (sands range site). Sampling was at weekly intervals from 4 July through 2 September 1984 and from 16 May through 22 August 1985. Phenological stage at each sampling date was recorded. Leaf stage was determined by counting the true leaves produced during the year of sampling. On each date, three sections of sod, 30 cm deep, containing only sand bluestem, prairie sandreed, or switchgrass were excavated. A section contained a minimum of 20 tillers with attached roots and rhizomes. The sod was washed free of soil under a gentle stream of water, air dried, and taken to the laboratory for characterization. Specimens were arranged in chronological order to identify patterns of rhizome and tiller development. Notes were taken and photographs of representative samples were made to illustrate the developmental process. Cross sections of rhizomes were made and the anatomy of vertical rhizomes were compared to horizontal rhizomes.

DESCRIPTION AND DISCUSSION

Switchgrass

Switchgrass produced new tillers in the spring from buds located on the below-ground stem bases of the previous year's tillers and on rhizomes. A study of 'Caddo' switchgrass on a sands range site in eastern Colorado showed that new tillers in the spring developed from axial buds on the proaxis (stem base), from rhizomes, and from continuation of growth of vegetative tillers that survived the winter (Sims *et al.* 1971). Regrowth of vegetative tillers that had grown the previous season was not observed in our study of switchgrass in the Sandhills.

Both extravaginal (exits through subtending leaf sheath) and intravaginal (exits within subtending leaf sheath) tillers developed. Intravaginal buds developed vertical (apogeotrophic) rhizomes (Figure 1) that remained closely associated with the parent axis. Vertical rhizomes were unbranched, determinate, and produced tillers which were located close to the previous year's tiller. Development of vertical rhizomes in switchgrass studied in the Sandhills was similar to descriptions of rhizomatous varieties common to the southeastern United States (Beaty *et al.* 1978).

Tillers developed from both vertically and horizontally oriented rhizomes (Figure 1) which is similar to that reported by Beaty *et al.* (1978). Rhizome cross sections indicated that the anatomy of horizontal and vertical rhizomes was identical. Horizontal rhizomes occasionally branched. The tiller that originated from the terminal bud was larger than tillers that originated from buds located along the length of the rhizome. However, if the terminal bud was damaged, multiple tillers of near equal size developed from buds located along the rhizome. If a shoot apex was removed new shoots originated from axial buds on the proaxis of the damaged tiller. Switchgrass rhizomes were not located as deep as those of prairie sandreed or sand bluestem nor were they as long as those of prairie sandreed.

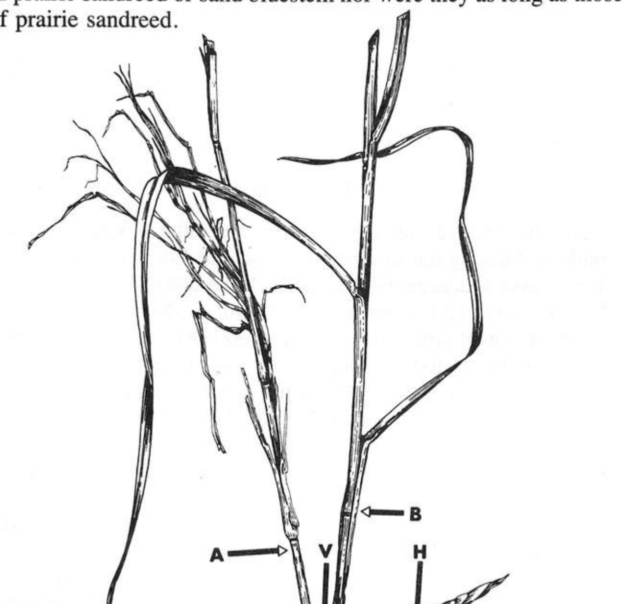


FIG. 1 Switchgrass plant showing previous year's tiller (A), current year's tiller (B), horizontally oriented rhizome (H), and a vertically oriented rhizome (V).

Switchgrass rhizomes initiated growth before early July in 1984 and in early to mid-June in 1985. During both years the rhizomes initiated growth when tillers were at the 4- and 5-leaf stage. Horizontal rhizomes initiated growth before vertical ones did. For six weeks, rhizomes elongated rapidly and new rhizomes were produced until the parent tillers began elongation. No new rhizomes were initiated thereafter but existing rhizomes continued to elongate.

Prairie Sandreed

New prairie sandreed tillers developed from rhizomes formed the previous year and from continuation of arrested vegetative growth of late emerging tillers from the previous year. Tillers originating from axial buds on the proaxis of last year's tiller were uncommon. Tillers that originated from axial buds emerged late, were smaller, and did not head (Figure 2). Many prairie sandreed tillers were biennial. Horizontal but more commonly, vertical rhizomes emerged late in the growing season in one year, overwintered, and then resumed growth from the same shoot apex (Figures 2 and 3). Growth of these tillers commenced early the second growing season and some developed culms and inflorescences. Biennial tiller development in prairie sandreed was similar to biennial tiller development for indiangrass [*Sorghastrum nutans* (L.) Nash] (McKendrick *et al.* 1975). However, prairie sandreed tillers in Montana did not live over winter but completed growth the same year they emerged (White 1977).

FIG. 2 Prairie sandreed plant showing previous year's tiller (A), current year's spring tillers (B), a late emerging current year's tiller from a vertically oriented rhizome (L), a horizontally oriented rhizome showing upward curvature in late summer (H), and the rhizosheath on the roots (RS).

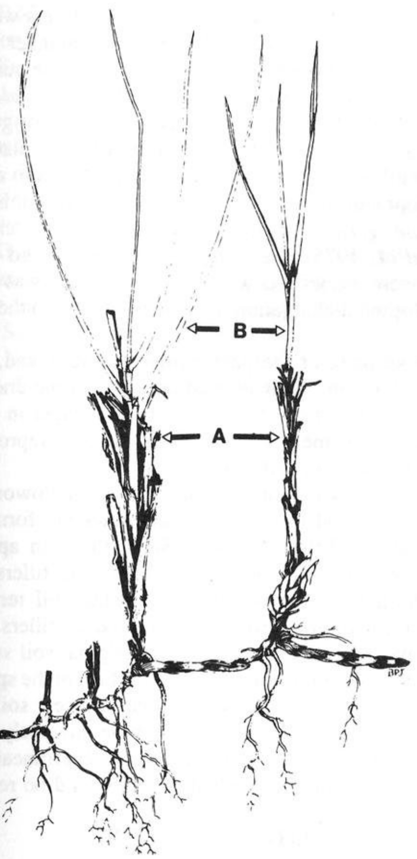


FIG. 3 Biennial tillers of prairie sandreed. Remains of previous year's tiller growth (A) and new spring growth from the same shoot apex (B).

In prairie sandreed extravaginal branching produced both horizontal and vertical rhizomes (Figure 2), which were identical anatomically. Rhizomes were strongly determinate with tillers produced only from rhizome tips. Tillers originating along the rhizome were not observed at any time. Rhizomes were unbranched even when the terminal bud was damaged. New rhizomes had begun growth by the time observations started in 1984. In 1985 rhizomes were just starting growth at the mid-May 1985 sampling date. Parent tillers were at the 4- to 5-leaf stage when rhizomes began growth so both tillers and rhizomes developed early in the growing season. During May and early June horizontal rhizomes elongated and a little later when parent tillers were generally at the 6-leaf stage vertical rhizomes began growth. Rhizomes continued elongation into August and many reached lengths of over 15 cm. Mueller (1941) reported a maximum length of 33 cm for prairie sandreed tillers and an average length of 15 cm.

In addition to producing the longest rhizomes of the three grasses studied prairie sandreed's rhizomes grew deep in the soil (below 10 cm). Mueller (1941) reported a depth range of 3.8-20.3 cm for prairie sandreed rhizomes. The production of long rhizomes with the ability to emerge from considerable depths allow prairie sandreed to be a early perennial colonizer in bare areas such as blowouts. Also prairie sandreed rhizomes can emerge through 15 cm of deposited sand (Mueller 1941). Weaver (1958) indicated that where prairie sandreed was subjected to blowing sand and shifting soil levels roots and rhizomes were intermixed in a dense mat to a depth of 0.6-1.0 m. Very few prairie sandreed tillers completed seed production and most tillers remained vegetative. Tillers that became reproductive often had their shoot apices removed by grasshoppers during stem elongation. Since prairie sandreed is less palatable than many other sandhills grasses it is not often grazed as closely as others. This gives it a competitive advantage in producing rhizomes. Selective grazing together with late emerging tillers can make it quite competitive in pasture situations.

Roots often had a surrounding sand sheath (Figure 2). Sheathed roots were young and actively growing and the sand sheath covered the upper 75% of the sampled roots. Rhizosheaths have been observed on both temperate and tropical grasses (Wullstein and Pratt 1981, Vermeer and McCully 1982, Duell and Peacock 1985). The significance of the rhizosheaths on prairie sandreed roots is not evident. Rhizosheaths were not present in switchgrass and poorly developed in sand bluestem.

Sand Bluestem

Buds on rhizomes beneath the previous year's tillers were the site of new growth in the spring (Figure 4). Buds near the soil surface generally did not develop into tillers. Early tillers originated from buds deeper in the soil, emerging through as much as 15 cm of sand before reaching the soil surface. When spring tiller growth initiated beneath the soil surface, the shoot apex was at the point of attachment to the rhizome of the previous year's tiller (Figure 5). When tillers emerged and reached the 4- to 5-leaf stage, elongation below the shoot apex occurred forming a rhizome that pushed the shoot apex to the soil surface (Figure 6). Examinations of cross-sections of above and below ground portions of stem and rhizome indicated that they were anatomically identical except the underground portion had larger vacuoles in the cells. Despite being anatomically similar, the aboveground portion died at the end of the season while the below ground portion remained alive giving rise to new tillers the following spring from buds along the rhizome (Figure 4). Tillers originating from buds near the soil surface often did not have rhizomes formed beneath them.

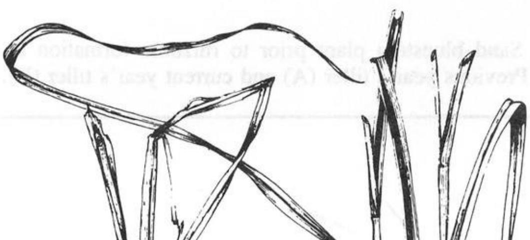


FIG. 4 Sand bluestem plant in midsummer showing bud formation on rhizomes. Previous year's tiller (A), current year's tillers (B), and buds (BU), formed on spring rhizomes.

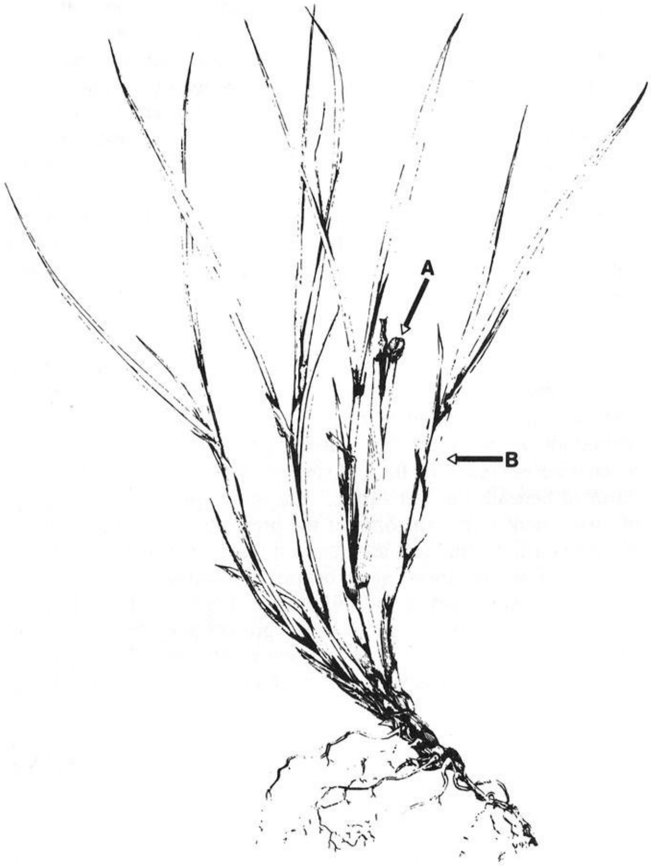


FIG. 5 Sand bluestem plant prior to rhizome formation in the spring. Previous year's tiller (A) and current year's tiller (B).

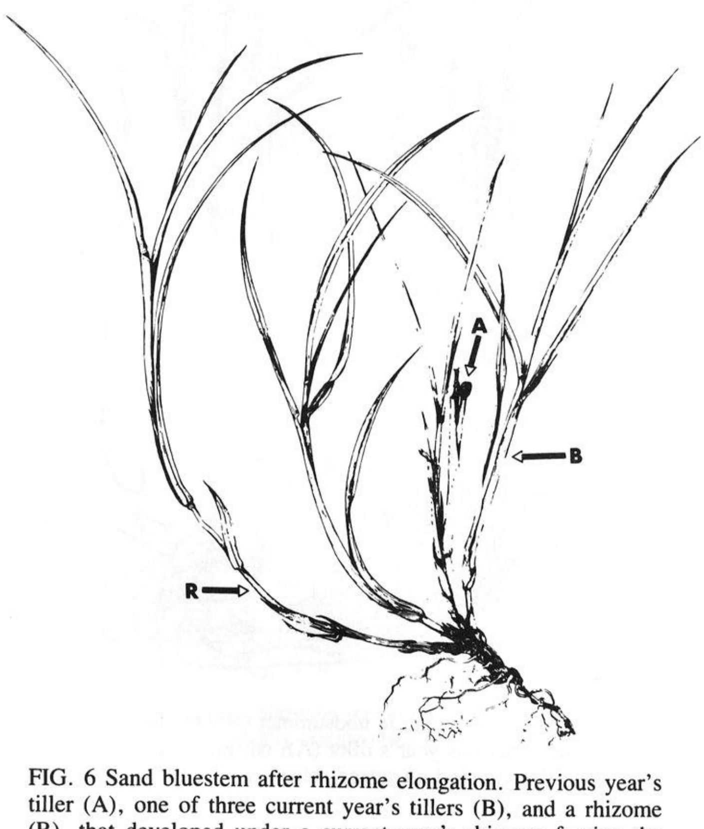


FIG. 6 Sand bluestem after rhizome elongation. Previous year's tiller (A), one of three current year's tillers (B), and a rhizome (R), that developed under a current year's rhizome forcing the shoot apex to the soil surface.

Bud formation occurred in late June when tillers were at about the 6-leaf stage. Buds increased in size and number in July and occasionally some elongated up to 1 cm during the current season but did not develop into tillers. However, Sims *et al.* (1973) reported that new tillers of 'Elida' sand bluestem originated from axial buds and apical meristems of short terminal rhizomes which turned upward in late summer or fall. Sand bluestem rhizome and tiller development in this study fit the description for big bluestem (*Andropogon gerardii* Vitman) in Kansas more closely (McKendrick *et al.* 1975). Generally, rhizomes of sand bluestem in this study were associated with tillers and there was limited rhizome development elongation from buds located on these rhizomes (Figure 6).

If the shoot apex of the parent tiller was removed, new tillers did not develop from buds located on the rhizome underneath the damaged tiller, but arose from axial buds located in leaf axes at the soil surface. Some vegetative tillers became reproductive and elongated, forming an inflorescence.

Sand bluestem is a common pioneer plant in blowouts. It maintained an open stand in mature communities but formed a dense sod in blowouts (Tolstead 1942). Sand bluestem appears to be adapted to shifting soil levels of blowouts and tillers commonly emerged through 10 cm of sand. Following soil removal, tiller buds further down on a rhizome would produce tillers and following sand deposition tillers closer to the original soil surface could develop. The elongation below the soil surface in the spring formed a rhizome and a source of new buds near the new soil surface for the following year. Sand bluestem may be adversely affected by heavy early spring grazing at a time when subterranean elongation occurs since the supply of carbohydrates would be reduced.

LITERATURE CITED

Beaty, E.R., J.L. Engel, and J.D. Powell. 1978. Tiller development and growth in switchgrass. Journal of Range Management 31:361-365.

Booÿsen, P. DeV., N.M. Tainton, and J.D. Scott. 1963. Shoot-apex development in grasses and its importance in grassland management. Herbage Abstracts 33:209-213.

Burzlaff, D.F. 1962. A soil and vegetation inventory and analysis of three Nebraska Sandhills range sites. University of Nebraska Agricultural Experiment Station Bulletin 206.

Duell, R.W., and G.R. Peacock. 1985. Rhizosheaths on mesophytic grasses. Crop Science 25:880-883.

Evans, M.W., and J.E. Ely. 1935. The rhizomes of certain species of grasses. Journal of American Society of Agronomy 27:791-797.

Frolik, A.L., and W.O. Shepherd. 1940. Vegetative composition and grazing capacity of a typical area of Nebraska Sandhill range land. University of Nebraska Agricultural Experiment Station Research Bulletin 117.

Heidemann, G.S., and G.E. Van Riper. 1967. Bud activity in the stem, crown, and rhizome tissue of switchgrass. Journal of Range Management 20:236-241.

McKendrick, J.D., C.E. Owensby, and R.M. Hyde. 1975. Big bluestem and indiangrass vegetative reproduction and annual reserve carbohydrate and nitrogen cycles. Agro-Ecosystems 2:75-93.

Mueller, I.M. 1941. An experimental study of rhizomes of certain prairie plants. Ecological Monographs 11:164-188.

Pool, R.J. 1914. A study of the vegetation of the Sandhills of Nebraska. Minnesota Botanical Studies 4:189-312.

Pound, R., and F.E. Clements. 1900. The phytogeography of Nebraska. Jacob North and Company, Lincoln, Nebraska.

Rechenthin, C.A. 1956. Elementary morphology of grass growth and how it affects utilization. Journal of Range Management 9:167-170.

Resource Conservation Glossary. 1970. Journal of Soil Water Conservation 25:1-52.

Rydberg, P.A. 1895. Flora of the Sandhills of Nebraska. Contributions from the U.S. National Herbarium 3:133-203.

Seevers, P.M., D.T. Lewis, and J.V. Drew. 1975. Use of ERTS-1 imagery to interpret the wind erosion hazard in Nebraska's Sandhills. Journal of Soil and Water Conservation 30:181-183.

Sims, P.L., L.J. Ayuko, and D.N. Hyder. 1971. Developmental morphology of switchgrass and sideoats grama. Journal of Range Management 24:357-360.

Sims, P.C., R.K. Lang 'At, and D.N. Hyder. 1973. Developmental morphology of blue grama and sand bluestem. Journal of Range Management 26:340-344.

Smith, J.G., and R. Pound. 1892. Flora of the sand hill region of Sheridan and Cherry counties and list of plants collected on a journey through the sand hills in July and August, 1892. Botanical Survey Nebraska 2:1-46.

Tolstead, W.L. 1942. Vegetation of the northern part of Cherry County, Nebraska. Ecological Monographs 12:255-292.

Vermeer, J., and M.E. McCully. 1982. The rhizosphere in Zea: New insight into its structure and development. Planta 156:45-61.

Weaver, J.E. 1930. Underground plant development and its relation to grazing. Ecology 11:543-557.

Weaver, J.E. 1958. Summary and interpretation of underground development in natural grassland communities. Ecological Monographs 28:55-78.

Weaver, J.E. 1963. The wonderful prairie sod. Journal of Range Management 16:165-171.

White, L.M. 1977. Perenniality and development of shoots of 12 forage species in Montana. Journal of Range Management 30:107-110.

Wullstein, L.H., and S.A. Pratt. 1981. Scanning electron microscopy of rhizosheaths of *Oryzopsis hymenoides*. American Journal of Botany 68:408-419.

PHENOLOGY OF NATIVE ANGIOSPERMS OF SOUTH PADRE ISLAND, TEXAS

Robert I. Lonard
Department of Biology, University of Texas-Pan American, Edinburg, Texas 78539

and

Frank W. Judd
Coastal Studies Laboratory, University of Texas-Pan American, P.O. Box 2591, South Padre Island, Texas 78597

Abstract. Flowering and fruiting patterns for 74 species of native angiosperms were studied on South Padre Island, Texas, from May 1984 to May 1986. Four patterns were recognized: 1) a continuous cycle of flowering and fruiting; 2) a cycle limited to spring through autumn; 3) a two season regime, either spring-summer or summer-fall; and 4) a cycle completed in one season or less (spring or fall). Marked year-to-year variation occurred in flowering and fruiting responses within individual species. Only one-fifth of the species exhibited the same monthly patterns in successive years. Number of species in flower or fruit was significantly correlated with mean monthly temperature and photoperiod, but showed no correlation with total monthly precipitation or precipitation with a one month time lag. Insect pollinated species had longer flowering/fruiting periods than wind pollinated species. Flowering and fruiting responses were compared among species common to other Gulf of Mexico islands and with species in common with temperate grasslands.

Key Words. flowering phenology, South Padre Island, Texas

INTRODUCTION

Phenological studies are important in interpreting the floristic relationships of a region. A clearer understanding of the structure and functioning of the ecosystem is effected when phenological information is combined with other biotic and abiotic data. Moreover, knowledge of flowering and fruiting phenophases is fundamental to investigations of angiosperm breeding systems.

Most of the phenological data available for Gulf of Mexico coastal areas are anecdotal information in checklists (Gillespie 1976, Anderson and Alexander 1985) or floristic treatments (Correll and Johnston 1970, Jones 1982, Clewell 1985), or it is applicable to marsh habitats on the coastal mainland (Eleuterius and Caldwell 1984). The only investigation focused specifically on the flowering and fruiting phenology of Gulf of Mexico barrier island plants was conducted in a tropical climate at Veracruz, Mexico, by Castillo and Carabias (1982). Thus, a study was initiated on the flowering and fruiting phenology of native angiosperm species on South Padre Island (a subtropical barrier island), Texas to: 1) provide descriptive information on the flowering and fruiting progression for the bulk of the native angiosperm species occurring on the island; 2) investigate the relationships between climatic factors and flowering and fruiting patterns; and 3) compare the patterns of flowering and fruiting phenologies among species in common between South Padre Island, other Gulf of Mexico barrier islands, Atlantic barrier islands, and various mainland habitats, especially temperate grasslands.

METHODS

Descriptions of the area, vegetation patterns, and edaphic factors were given in Dahl *et al.* (1974), Judd *et al.* (1977), and Judd and Lonard (1985). Temperature, precipitation, and photoperiod data were obtained for Port Isabel, Texas, which is on the mainland adjacent to the southern end of South Padre Island (Orton *et al.* 1967, National Oceanic and Atmospheric Administration 1984, 1985, and 1986). A list of the native species of flowering plants was compiled from information provided by Lonard and Judd (1981).

Flowering and fruiting data for species common to South Padre Island and other insular or coastal mainland areas of the Gulf of Mexico were obtained from Correll and Johnston (1970), Gillespie (1976), Castillo and Carabias (1982), Jones (1982), Eleuterius and Caldwell (1984), Clewell (1985), and Anderson and Alexander (1985). In several cases, authors listed the flowering/fruiting phenophases on a seasonal basis (e.g. spring-summer) rather than giving inclusive months. To quantitatively compare data a maximum of three months was assumed for a season. Flora of the Great Plains (Great Plains Flora Association 1986) was used extensively for phenological comparisons with widely distributed inland species. In addition, Turner (1959), Ashapanek (1962), Wagner (1964), and Lee and Bazzaz (1982) were examined for phenological data concerning specific species.

Phenological data on flowering and fruiting were obtained from three belt transects (5 m wide) extending across the width of the island (Figure 1). The southernmost transect (Number 3) was located in Isla Blanca Park near Brazos-Santiago Pass. Transect Number 2 was oriented parallel to the margin of a hurricane washover 18 km north of Brazos-Santiago Pass. Transect Number 1 crossed all the topographic zones identified by Judd *et al.* (1977), i.e. backshore, primary dunes, secondary dunes and vegetated flats, and tidal flats. It was located 19 km north of Brazos-Santiago Pass.

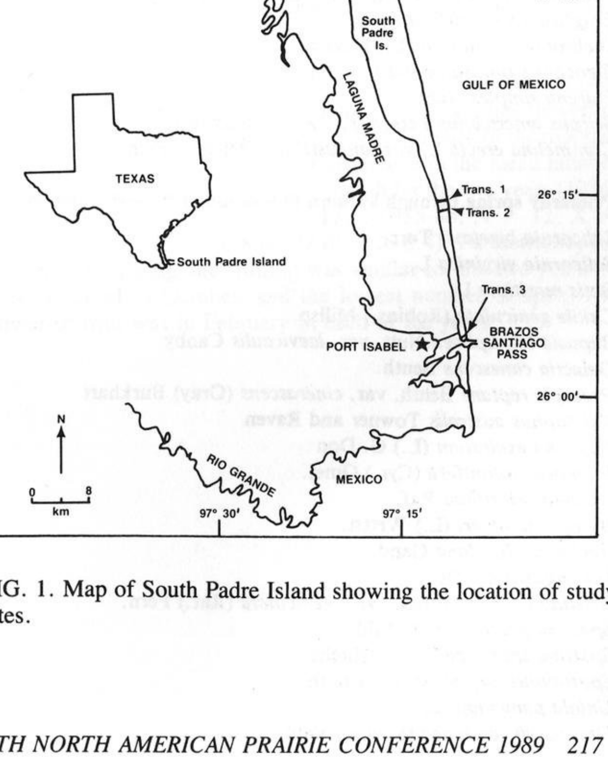


FIG. 1. Map of South Padre Island showing the location of study sites.

The study was initiated 27 May 1984 and terminated 10 May 1986. The transects were censused at 15-day intervals from March through November and at 30-day intervals from December through February. Data recorded were initiation of vegetative growth, time of budding, occurrence of flowering and fruiting, seed dissemination, and senescence. Flowering and fruiting data of native species were selected for presentation in this paper. Flowering and fruiting stages were combined for analysis, because these events were difficult or impossible to separate in many species (Eleuterius and Caldwell 1984). Data were analyzed on a monthly basis. Statistical procedures were those of Sokal and Rohlf (1981). A probability value less than 0.05 was considered significant.

RESULTS

This study was based on observation of the flowering/fruiting phenology of 74 native angiosperm species. The species represented 70 genera and 28 families. Forty-seven species were dicotyledons, and 27 were monocotyledons (Table 1).

Four flowering/fruiting patterns were evident (Table 1): 1) a

Table 1. Flowering and fruiting duration and relationships for 74 species of native angiosperms of South Padre Island, Texas. Entomophilous species = e, anemophilous species = a.

Species	*Duration of flowering/ fruiting (no. months)*		*Mode of pollination*
Continuous (10-12 month) flowering and fruiting:			
Philoxerus vermicularis (L.) R. Br.	Jan-Jun; Aug-Dec	(11)	e
Sesuvium portulacastrum L.	Mar-Jun	(11)	e
Cassia fasciculata Michx. var. *ferrisiae* (Britt.) Turner	Jan-May; Jul-Dec	(11)	e
Rhynchosia americana (Mill.) Metz.	Jan-Dec	(12)	e
Sophora tomentosa L.	Jan-Dec	(12)	e
Linum alatum (Small) Winkler	Jan-Dec	(12)	e
Polygala alba Nutt.	Jan-Dec	(12)	e
Croton punctatus Jacq.	Jan-Dec	(12)	e
Euphorbia cordifolia Ell.	Jan-Dec	(12)	e
Opuntia compressa (Salisbury) MacBride var. *fusco-atra* (Eng.) Winiger	Jan-Dec	(12)	e
Oenothera drummondii Hook.	Jan-Dec	(12)	e
Samolus ebracteatus H.B.K.	Jan-Dec	(12)	e
Polypremum procumbens L.	Apr-Jan	(10)	e
Ipomoea pes-caprae (L.) Sweet var. *emarginata* Hallier f.	Apr-Jan	(10)	e
Physalis viscosa L. var. *spathulifolia* (Torr.) Gray	Jan-Dec	(12)	e
Oldenlandia boscii (DC.) Chapm.	Jan-Dec	(12)	e
Borrichia frutescens (L.) DC.	Jan-Dec	(12)	e
Erigeron myrionactis Small	Jan-Dec	(12)	e
Eupatorium betonicifolium Mill.	Jan-Dec	(12)	e
Gaillardia pulchella Fouq. var. *picta* (Sweet) Gray	Jan-Dec	(12)	e
Heterotheca subaxillaris (Lam.) Britt. and Rusby	Jan-Dec	(12)	e
Machaeranthera phyllocephala (DC.) Shinners	Jan-Dec	(12)	e
Ratibida penduncularis (T. and G.) Barnh.	Jan-Dec	(12)	e
Solidago sempervirens L. var. *mexicana* (L.) Fern.	Jan-Dec	(12)	e
Dichanthelium nodatum (Hitchc. and Chase) Gould	Jan-Dec	(12)	a
Eragrostis secundiflora Presl.	Apr-Jan	(10)	a
Dichromena colorata (L.) Hitchc.	Mar-Jan	(11)	e
Eleocharis obtusa (Willd.) Schult.	Jan-Dec	(12)	a
Fuirena simplex Vahl	Jan-Dec	(12)	e
Scirpus americanus Pers. var. *longispicatus* Britt.	Feb-Dec	(11)	a
Commelina erecta L. var. *angustifolia* (Michx.) Fern.	Feb-Dec	(11)	e
Primarily spring through autumn (7-9 months) flowering and fruiting:			
Salicornia bigelovii Torr.	May-Oct	(6)	?
Salicornia virginica L.	May-Nov	(7)	?
Batis maritima L.	Apr-Nov	(8)	?
Cakile geniculata (Robins.) Millsp.	Feb-Aug; Dec	(8)	e
Baptisia leucophaea Nutt. var. *laevicaulis* Canby	Mar-Sep	(7)	e
Galactia canescens Benth.	Apr-Nov	(8)	e
Prosopis reptans Benth. var. *cinerascens* (Gray) Burkhart	May-Jan	(9)	e
Calylophus australis Towner and Raven	Mar-Oct	(8)	e
Eustoma exaltatum (L.) G. Don	May-Nov	(7)	e
Ipomoea stolonifera (Cyr.) Gmel.	Apr-Dec	(9)	e
Agalinus maritima Raf.	Mar-Nov	(9)	e
Bacopa monnieri (L.) Wettst.	May-Dec	(8)	e
Buchnera floridana Gand.	May-Nov	(7)	a
Iva angustifolia DC.	Jun-Dec	(7)	a
Aristida longespica Poir. var. *geniculata* (Raf.) Fern.	May-Dec	(8)	a
Spartina patens (Ait.) Muhl.	May-Nov	(7)	a
Spartina spartinae (Trin.) Hitchc.	Jan; Apr-Oct	(8)	a
Sporobolus virginicus (L.) Kunth	Apr-Nov	(8)	a
Uniola paniculata L.	Apr-Nov	(8)	a
Fimbristylis castanea (Michx.) Vahl	Jun-Dec	(7)	a

Table 1. Continued

Species	*Duration of flowering/ fruiting (no. months)*		*Mode of pollination*
Two season flowering and fruiting; either spring-summer, or summer-fall (4-6 months):			
Suaeda linearis (Ell.) Moq.	Jun-Nov	(6)	?
Lythrum alatum Pursh var. *lanceolatum* (Ell.) T. and G. *ex* Rothrock	Apr-Sep	(6)	e
Limonium nashii Small	Jul-Nov	(5)	e
Sabatia arenicola Greenm.	Jan-Jun	(6)	e
Lycium carolinianum Walt. var. *quadrifidum* (Dun.) C. L. Hitchc.	Aug-Jan	(6)	e
Stemodia tomentosa (Mill.) Greenm. and Thomps.	Apr-Sep	(6)	e
Distichlis spicata (L.) Greene	Aug-Nov	(4)	a
Panicum amarum Ell.	Aug-Nov	(4)	a
Paspalum distichum L.	Aug-Nov	(4)	a
Paspalum monostachyum Vasey	Sep-Dec	(4)	a
Schizachyrium scoparium (Michx.) Nash var. *littoralis* (Nash) Gould	Jul-Dec	(6)	a
Sporobolus tharpii Hitchc.	Jun-Nov	(6)	a
Caldium jamaicense Crantz	Apr-Jul	(4)	a
Juncus megacephalus M.A. Curtis	May-Aug	(4)	a
Sisyrinchium biforme Bickn.	Mar-Jun; Dec-Jan	(6)	e
One season flowering and fruiting (1-3 months), spring or fall:			
Schrankia latidens (Small) K. Schum.	May-Jun	(2)	e
Hydrocotyle bonariensis Lam.	May-Jun	(2)	e
Flaveria brownii A.M. Powell	Nov-Dec	(2)	e
Andropogon glomeratus (Walt.) B.S.P.	Oct-Nov	(2)	a
Monanthochloe littoralis Engelm.	Mar-May	(3)	a
Muhlenbergia filipes M. A. Curtis	Oct-Nov	(2)	a
Triplasis purpurea (Walt.) Chapm.	Oct-Nov	(2)	a
Spiranthes vernalis Engelm. and Gray	May	(1)	e

continuous cycle of flowering and fruiting; 2) a cycle limited to spring through autumn; 3) a two season regime, either spring-summer or summer-fall; and 4) a cycle completed in one season or less (i.e. spring or fall). Thirty-one species (41.9%) flowered and fruited more or less continuously during the year (10-12 months). Twenty species (27%) flowered and fruited during the spring, summer, and fall (7-9 months). Fifteen species (20.3%) flowered and fruited for two seasons, either spring and summer or summer and fall (4-6 months). Eight species (10.8%) flowered and fruited during only one season, usually either in the spring or the fall, and always for a duration of three months or less. Twisted lady's tresses (*Spiranthes vernalis* Engelm. and Gray) and gulf muhly (*Muhlenbergia filipes* M.A. Curtis) had the shortest flowering and fruiting responses. These were 1.0 and 1.5 months, respectively.

Table 1 identifies the mode of pollination and lists the beginning and ending months of flowering and fruiting response. Twenty-three species (31.1%) were anemomophilous, 47 species (63.5%) were entomophilus, and the mode of pollination was unclear for four species (5.4%). Mean duration of flowering and fruiting for insect pollinated species was 9.3 (s.d. = 3.2) months, and the mean for wind pollinated species was 6.3 (s.d. = 3.2) months. Duration of flowering and fruiting was significantly longer for insect pollinated species ($t = 3.689$, 58 df, $p < 0.001$).

Table 2 provides a comparison of the mean duration of flowering and fruiting for six Gulf of Mexico coastal sites, mainland Texas, and the Great Plains states with South Padre Island, Texas. Only species in common between South Padre Island and each of the other sites were included in the analyses. The mean duration of flowering and fruiting for shared species was significantly greater for South Padre Island in all the comparisons, except for Vera Cruz, Mexico (Castillo and Carabias 1982). Thirteen species were common to the Vera Cruz location and South Padre Island, and the means for both were approximately 10 months. Only 20.3% of the South Padre Island species exhibited the same flowering and fruiting initiation and cessation dates (i.e. months) in two years.

A comparison among months of the number of species in flower and/or fruit is given in Table 3. The number of species flowering or fruiting was different in successive years for each of the months. However, there was no significant difference in the mean number of species in flower and/or fruit per month for the two years (1984-85, $N = 12$, $X = 42.7$, s.d. $= 13.1$; 1985-86, $N = 12$, $X = 47.1$, s.d. $= 12.2$; $t = 0.838$, 22 df, $p > 0.4$). Furthermore, the pattern of flowering and fruiting was similar for the two years. A peak occurred in October, and the lowest number of species in flower or fruit was in February in each of the years.

Table 2. Comparison of mean duration of flowering and fruiting between South Padre Island, Texas, angiosperms and species in common at other sites. N = number of species shared, s.d. = standard deviation, t = student's t value.

Location (Citation)	*N*	*X Duration (months)*	*s.d.*	*t*	*Probability*
Great Plains States (Great Plains Flora Association 1986)	13	4.2	1.21		
vs				3.285	<0.01
South Padre Island, Texas	13	7.8	3.87		
Texas (Correll and Johnston 1970)	66	6.5	2.59		
vs				3.025	<0.01
South Padre Island, Texas	66	8.1	3.33		
Mississippi Tidal Marshes (Eleuterius and Caldwell 1984)	22	4.0	1.50		
vs				5.461	<0.001
South Padre Island, Texas	22	7.9	3.05		
Florida Panhandle (Clewell 1985)	42	4.3	2.09		
vs				5.250	<0.001
South Padre Island, Texas	42	7.7	3.59		
Dog Island, Florida (Anderson and Alexander 1985)	26	3.5	1.90		
vs				4.104	<0.001
South Padre Island, Texas	26	6.8	3.64		
Mustand Island, Texas (Gillespie 1976)	45	6.4	3.20		
vs				3.665	<0.001
South Padre Island, Texas	45	8.9	3.09		
Texas Coastal Bend (Jones 1982 and Gould and Box 1965)	51	7.5	2.69		
vs				3.119	<0.01
South Padre Island, Texas	51	9.2	2.84		
Vera Cruz, Mexico (Castillo and Carabias 1982)	13	10.0	2.38		
vs				0.268	>0.5
South Padre Island, Texas	13	9.6	3.50		

Table 3. Comparison among months, for two years (May-April), of number of species in flower and/or fruit and mean monthly temperature, mean monthly photoperiod and total monthly precipitation.

	Number of species in flower/fruit		*Temperature (C)*		*Precipitation (mm)*		*Photoperiod (hrs light)*
Month	*84-85*	*85-86*	*84-85*	*85-86*	*84-85*	*85-86*	*84-85 & 85-86*
May	38	54	25.8	26.3	98.3	111.0	13.42
Jun	53	58	27.6	28.3	3.3	21.3	13.75
Jul	53	58	28.4	27.6	36.6	45.7	13.59
Aug	52	57	28.7	28.3	23.1	15.5	13.04
Sep	52	50	26.5	28.4	666.0	188.7	12.30
Oct	56	59	26.0	24.8	44.5	100.1	11.54
Nov	55	54	21.1	22.8	1.8	39.9	10.88
Dec	42	35	20.7	15.7	40.1	33.0	10.54
Jan	32	30	12.3	15.8	72.4	20.1	10.72
Feb	16	25	13.9	17.6	32.5	37.3	11.29
Mar	25	36	20.9	20.2	22.4	1.8	12.01
Apr	39	49	23.4	24.5	40.6	42.4	12.78

Table 3 provides data for the correlation of flowering and fruiting with temperature, precipitation, and photoperiod. There was a strong positive correlation ($r = 0.809$, $t = 6.455$, 22 df, $p < 0.001$) between mean monthly temperature and number of species in flower and/or fruit. Conversely, the correlation between total monthly precipitation and number of species flowering or fruiting was not significant ($r = 0.154$, $t = 0.713$, 22 df, $p > 0.4$). Lack of correlation also held when a time lag of 30 days was introduced, i.e. when the number of species flowering or fruiting was compared with the previous month's precipitation total ($r = 0.258$, $t = 1.224$, 21 df, $p > 0.4$). Although photoperiod does not change annually, flowering and fruiting responses of the two years were compared separately. In 1984-85, there was no correlation between photoperiod and number of species flowering or fruiting ($r = 0.303$, $t = 1.006$, 10 df, $p > 0.4$), but in 1985-86 there was a positive correlation ($r = 0.647$, $t = 2.682$, 10 df, $p < 0.05$).

DISCUSSION

Flowering and fruiting phenophases were influenced by a variety of abiotic (i.e. photoperiod, temperature, precipitation, etc.) and biotic factors. In temperate grasslands various authors (Ashapanek 1962, Dickinson and Dodd 1976, Kebart and Anderson 1987) have shown that either precipitation or a combination of long-term mean monthly temperatures were important factors in determining flowering responses. These factors were important for individual species as well as for all species within a given community.

Clearly, temperature was a major factor affecting the flowering and fruiting phenology of the native angiosperms of South Padre Island, Texas. This study was initiated five months after a severe freeze occurred in the lower Rio Grande Valley of Texas. Fifty-three to 55 consecutive hours of freezing or below freezing temperatures were recorded with a minimum of -8.8 C. Extensive damage occurred to stands of blackmangrove [*Avicennia germinans* (L.) Stearn] on South Padre Island and elsewhere along the coast (Lonard and Judd 1985). Furthermore, the effects of the freeze on the flowering and fruiting responses of herbaceous species on South Padre Island were evident into the spring and summer of 1984. For example, yellow sophora (*Sophora tomentosa* L.) did not flower until November 1984, but this species flowered and fruited continuously in 1985. It was not until September 1984 that flowering and fruiting responses were similar in the same months in 1985. Additionally, when mean monthly temperatures dropped to 20 C or below from December to March the flowering and fruiting responses declined dramatically. Finally, the duration of flowering for species shared between South Padre Island and more northern locales was significantly longer at South Padre Island. The long flowering/fruiting periods reflect the subtropical environment of South Padre Island and a frost-free period of approximately 330 days.

Precipitation did not appear to be a significant factor influencing flowering and fruiting responses of the South Padre Island flora. Although, other investigators in the tropics (Opler *et al.* 1976, Castillo and Carabias 1982) found that precipitation was important in initiating sexual reproduction. For example, Castillo and Carabias (1982) reported that maximum flower production occurred during the months of highest precipitation on the barrier island at Vera Cruz, Mexico. Furthermore, they noted that the months of major flower production differed in successive years, and that flower production was correlated with differences in annual precipitation.

Precipitation may not be a limiting factor for flower and fruit production on South Padre Island as long as successive years of drought do not lower the water table. Judd *et al.* (1977) reported that depth to the water table in the secondary dunes and vegetated flats zone of South Padre Island was less than 1.0 m (except on tall dunes). It is likely that capillary action is sufficient to move water from the water table to roots, and that moisture is not a limiting factor on South Padre Island unless there is an extended drought.

Effect of photoperiod on flowering and fruiting responses was unclear. In 1984-85, no correlation was found between mean photoperiod for a given month and the number of species flowering or fruiting, but in 1985-86 a significant positive correlation occurred. The marked difference may have been due to differences in other light parameters, such as intensity, or to a factor (such as temperature) or factors that were correlated with photoperiod. Apparently, many tropical species are "short day" or "day-neutral" with respect to the photoperiod stimulus for anthesis (Opler *et al.* 1976). Studies are needed to separate the effects of temperature and photoperiod on flowering and fruiting of South Padre Island species.

Mean duration of flowering and fruiting was longer for insect pollinated species than for wind pollinated species. Rabinowitz *et al.* (1981) reported similar results in Missouri. The long duration for insect pollinated species was probably due to the virtual absence of freezing temperatures on South Padre Island. Thus, insects can be active year-round.

The flowering/fruiting response on South Padre Island exhibited marked year-to-year variation. Only 20% of the species were found in flower or fruit in the same months in successive years. Castillo and Carabias (1982) reported similar results for the flora of a barrier island at Vera Cruz, Mexico. They attributed the difference between years to differences in precipitation. Apparently, the differences were largely due to the freeze in December 1983 and its rather long-lasting effects into 1984.

Three dominant species on South Padre Island had longer flowering/fruiting durations than conspecific populations in temperate zones of the Gulf Coast or at mainland locations. Sea oats (*Uniola paniculata* L.), the dominant species of the backshore and primary dunes, initiated flowering as early as April and fruited until November. However, on a South Carolina barrier island, sea oats initiated anthesis in early July and concluded fruiting by late August (Wagner 1964). Seacoast bluestem [*Schizachyrium scoparium* var. *littoralis* (Nash) Gould], the dominant species of the secondary dunes and vegetated flats topographic zone, initiated flowering in July and fruited until early December. In central Oklahoma, a conspecific population flowered and fruited from August to early November (Ashapanek 1962). The robust annual prairie senna [*Cassia fasciculata* var. *ferrisiae* (Britt.) Turner] has high importance in the primary dune zone and was in flower or fruit every month except June. Lee and Bazzaz (1982) found that Illinois populations began flowering in late July and fruited until early October when frosts killed the plants. Apparently, little or no seed dormancy requirements were necessary for prairie senna. Seeds germinated shortly after dispersal; thus, the species acted essentially as a perennial on South Padre Island. A similar situation existed in bigelow glasswort (*Salicornia bigelovii* Torr.), a common annual species on the margins of the tidal flats.

Two observations made during this study merit comment. Bitter panicum (*Panicum amarum* Hitchc. & Chase), which occurred in exposed sites in the backshore zone and along the windward base of the primary dunes, typically flowered and fruited from mid-September to late November. However, plants in a partially shaded site, protected from prevailing winds, and receiving precipitation from a roof drip-line flowered and fruited from August to March. Although it is not native to the flora of South Padre Island, cherry tomato (*Lycopersicon esculentum* var. *cerasiforme* Mill.) is of interest to horticulturists. Plants of this species flowered and fruited from April to June in the crevices between the granite boulders that form the jetty at Brazos-Santiago Pass. The plants were only a few meters above mean high tide and eventually were killed by an unusually high tide.

ACKNOWLEDGMENTS

We are grateful for financial support (for the first year of study) provided by a University of Texas-Pan American Faculty Research Grant. Thanks go to Tesa Chavez for typing the manuscript. This is contribution Number 6 of the University of Texas-Pan American, Coastal Studies Laboratory

LITERATURE CITED

Ashapanek, D. 1962. Phenology of a native tall grass prairie in Central Oklahoma. Ecology 43:135-138.

Anderson, L.C., and L.L. Alexander. 1985. The vegetation of Dog Island, Florida. Florida Scientist 48:232-251.

Castillo, S., and J. Carabias. 1982. Ecologia de las vegetacion de dunas costernas fonologia. Biotica 7:551-568.

Clewell, A.F. 1985. Guide to the vascular plants of the Florida Panhandle. University Presses of Florida, Tallahassee.

Correll, D.S., and M.C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner.

Dahl, B.E., B.A. Fall, A. Lohse, and S.G. Appan. 1974. Stabilization and reconstruction of Texas foredunes with vegetation. Gulf University Research Consortium Number 139.

Dickinson, C.E., and J.L. Dodd. 1976. Phenological pattern in the shortgrass prairie. American Midland Naturalist 96:367-378.

Eleuterius, L.N., and J.D. Caldwell. 1984. Flowering phenology of tidal marsh plants in Mississippi. Castanea 49:172-179.

Gillespie, T.S. 1976. The flowering plants of Mustang Island, Texas: An annotated checklist. Texas Journal of Science 27:131-148.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Jones, F.B. 1982. Flora of the Texas Coastal Bend. Rob and Bessie Welder Wildlife Foundation. Sinton, Texas.

Judd, F.W., R.I. Lonard, and S.L. Sides. 1977. The vegetation of South Padre Island, Texas, in relation to topography. Southwestern Naturalist 22:31-48.

Judd, F.W., and R.I. Lonard. 1985. Effects of perturbations on South Padre Island. Pages 1855-1869. *In* Proceedings of the Fourth Symposium on Coastal Ocean Management "Coastal Zone '85". American Society of Civil Engineers. Baltimore, Maryland.

Kebart, K.K., and R.C. Anderson. 1987. Phenological and climatic patterns in three tallgrass prairies. Southwestern Naturalist 32:29-39.

Lee, T.D., and F.A. Bazzaz. 1982. Regulation of fruit maturation pattern in an annual legume, *Cassia fasciculata*. Ecology 63:1374-1388.

Lonard, R.I., and F.W. Judd. 1985. Effects of a severe freeze on native woody plants in the lower Rio Grande Valley, Texas. Southwestern Naturalist 30:397-403.

National Oceanic and Atmospheric Administration. 1984. Climatological data, annual summary, Texas. National Climatic Data Center, Asheville, North Carolina.

National Oceanic and Atmospheric Administration. 1985. Climatological data, annual summary, Texas. National Climatic Data Center, Asheville, North Carolina.

National Oceanic and Atmospheric Administration. 1986. Climatological data, annual summary, Texas. National Climatic Data Center, Asheville, North Carolina.

Opler, P.A., G.W. Frankie, and H.G. Baker. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. Journal of Biogeography 3:231-236.

Orton, R., D.J. Haddock, E.G. Bice, and A.C. Webb. 1967. Climatic guide: The lower Rio Grande Valley, Texas. Agricultural Experiment Station Miscellaneous Publication 841.

Rabinowitz, D., J.K. Rapp, V.L. Sork, B.J. Rathcke, G.A. Reese, and J.C. Weaver. 1981. Phenological properties of wind and insect pollinated prairie plants. Ecology 62:49-56.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry. The principles and practice of statistics in biological research. W.H. Freeman and Company, New York.

Turner, B.L. 1959. The legumes of Texas. University of Texas Press, Austin.

Wagner, R.H. 1964. The ecology of *Uniola paniculata* L. in the dune-strand habitat of North Carolina. Ecological Monographs 34:79-96.

BLOWOUTS IN THE NEBRASKA SANDHILLS: THE HABITAT OF *PENSTEMON HAYDENII*

James Stubbendieck, Theresa R. Flessner
Department of Agronomy, University of Nebraska, Lincoln, Nebraska 68583

and

Ronald R. Weedon
Department of Biology, Chadron State College, Chadron, Nebraska 69337

Abstract. The Nebraska Sandhills is the largest area of sand dunes in the Western Hemisphere, occupying over 5 million ha in northcentral Nebraska. The rolling to steep dunes range in height from a few meters to over 60 m. Soils are poorly developed in wind deposited sand. The continental climate is characterized by 425 to 625 mm of annual precipitation, an average annual temperature of 10 C, and a frost-free period of 130-155 days. Upland vegetation is primarily tall grasses and midgrasses such as sand bluestem [*Andropogon gerardii* var. *paucipilus* (Nash) Fern.], prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], and switchgrass (*Panicum virgatum* L.). Forbs are common. Wind erosion occurs when the protective cover of vegetation is destroyed. Blowouts are active sites of erosion. Blowouts are irregular or conical craters formed when the deep, loose sands are removed by swirling action of the prevailing northwesterly winds. Blowout penstemon (*Penstemon haydenii* S. Wats.) is only found on these sites of active wind erosion and is an early successional species. Important associated species in blowouts include blowoutgrass [*Redfieldia flexuosa* (Thurb.) Vasey] and lemon scurfpea (*Psoralea lanceolata* Pursh). The number of blowouts has decreased with the control of fire and improved range management techniques. Loss of suitable habitat is one of the reasons for the decline of blowout penstemon. At the same time, there are many blowouts in the Sandhills that seem to offer suitable habitat where blowout penstemon is not found.

Key Words. blowout penstemon, *Penstemon haydenii,* blowouts, erosion, Sandhills, Nebraska

INTRODUCTION

Blowout penstemon (*Penstemon haydenii* S. Wats.) was placed on the Federal Endangered Species List in October, 1987. It is endemic to the Nebraska Sandhills and is the only plant species in the state to be classified as endangered. It is the rarest plant species in the Great Plains.

The Nebraska Sandhills is an extensive area with unique vegetation. Blowouts, the habitat of blowout penstemon, are depressions in the topography caused by wind erosion. Vegetation associated with blowouts is distinctly different than vegetation associated with adjacent, noneroding areas. The purpose of this paper is to describe briefly the climate, soils, erosion processes, blowouts, and vegetation of the Nebraska Sandhills as an introduction to the Symposium on Blowout Penstemon held at the Eleventh North American Prairie Conference and to the papers on blowout penstemon which follow in these proceedings.

REVIEW OF THE LITERATURE

Soils and Climate

The Nebraska Sandhills occupies over 5 million hectares of northcentral Nebraska (Keech and Bentall 1971, Bleed and Flowerday 1989). It is the largest sand dune area in the Western Hemisphere, with nearly level areas and rolling hills with slopes exceeding 30% (Keech and Bentall 1971, Bleed and Flowerday 1989). The area is primarily used for cattle grazing on relatively large ranches (Burzlaff 1962, Gosey 1986, Stubbendieck 1989). The sandy soils (mixed, mesic Typic Ustipsamment) are characterized by low organic matter, low water-holding capacity, low natural fertility, and a high risk of wind erosion if the soil is exposed (Elder 1969, Keech and Bentall 1971). The soil is usually stabilized by a grass cover. Beneath the soil is a thick sequence of permeable rocks filled to overflowing with water. This water-filled rock layer, known as the Ogallala aquifer, feeds the many existing streams and lakes of the area (Bose 1977, Bleed 1989).

The climate of the area may be classified as continental, with 70% of the total precipitation (425-625 mm) falling during the growing season (Burzlaff 1962, U.S. Department of Commerce 1973, Wilhite and Hubbard 1989). The frost-free period is 130-155 days (Neild 1977). Cold winters and warm summers are characteristic. Average maximum and minimum temperatures for January are about 1 C and -12 C (Neild *et al.* 1967). Extreme lows of less than -40 C have been recorded. July is the hottest month with maximum and minimum temperatures of about 32 C and 15 C (Neild *et al.* 1967). Extreme highs of more than 45 C have been recorded.

Wind is an ever-present part of the climate of the Nebraska Sandhills. The state has little surface relief, and with the lack of surface roughness winds can attain high velocities. Winds are generally strongest in winter and early spring and blow from a northwesterly direction (Dewey 1977, Wilhite and Hubbard 1989). During these periods, sustained winds of about 50 m/sec with gusts to nearly double that velocity are not uncommon.

Wind Erosion

Wind erosion and blowout formation do not occur as long as vegetative cover is not disturbed. Once wind erosion starts, it is difficult to stop. Causes of wind erosion in the Sandhills are best explained by the physics of wind action on the soil particles. The mechanism of wind erosion involves three factors: 1) wind velocity, 2) nature of the surface, and 3) soil (Baver *et al.* 1972). Bagnold (1941) reported that almost 75% of the soil particles were transported from the soil surface by saltation. Several factors are involved in saltation. Wind may roll sand grains along the surface until they hit objects such as other sand grains, and then they bounce back into the air or knock the obstructing sand grains into the air. These grains fall back to the surface at a rather flat angle varying from 10 to 16 degrees, depending on the size of grain, height of rise, wind velocity, and other factors (Ordway 1972). These falling grains put themselves or other grains in motion by their impact.

Blowouts

Blowouts are one of the most striking features of the Sandhills. These blowouts are different in form and ecological relationships from those in historical reports from other parts of the world (Cowles 1899, Gleason 1910, Cockayne 1911). Blowouts originate on the exposed upper slopes when the vegetative cover is disturbed or removed. Historically, repeated fires and concentrations of grazing animals caused the disturbance (Pool 1914). Over the period of a few years to a few decades, an embryonic blowout develops into a full scale, active blowout. Sand is blown from the exposed windward side of the slope and deposited onto the leeward size. As the erosion becomes more active and the blowout deepens, roots of the prairie vegetation are exposed, and soon whole plants blow away. As the crater deepens, the sand on the sides slides into the depression. The sharp, steep edges caused by the sliding sand help to catch the wind and cause increased turbulence breaking more sand particles free. The loose sand is quickly blown out and deposited on the leeward side of the crater (Pool 1914).

The northwest inner slope of an active blowout generally has a gradient of about 30 degrees and has the longest slope. This side is never directly exposed to the wind. The opposite side is usually much steeper, sometimes nearly perpendicular, because sand continually rolls down from this side and is blown out over the side. The leeward side of the hill, the area of sand deposition, usually has a gradient of about 60 degrees. This slope is usually vegetated by perennial grass species that can yearly grow up through 0.2-0.7 meters of deposited sand (Pool 1914).

Nebraska Sandhills blowouts are irregularly conical or rounded depressions of varying depth and diameter (Figure 1). They usually occur on the northwest sides of upper slopes and hills. The northwest side of the rim is usually much lower than the southeast rim. Sand is continually deposited in a southeasterly direction building that rim. Initially, blowouts may cover a few square meters and be a few centimeters deep. Extreme cases may reach an area of more than 3 hectares and a depth of over 30 meters. An average size is about 0.1 to 0.3 hectares in area and 4 to 10 meters in depth.

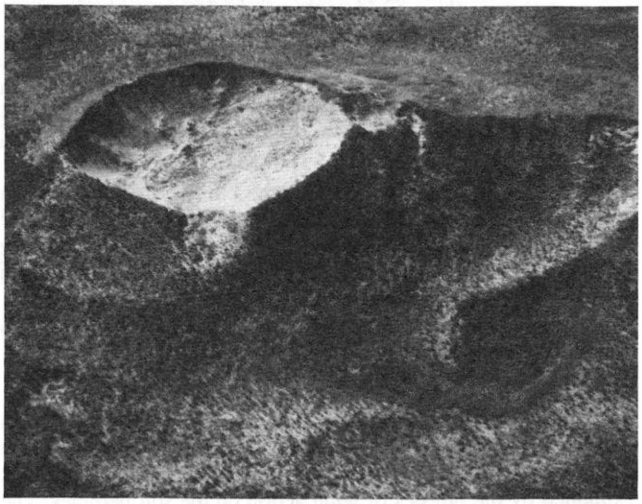


FIG. 1. A Nebraska Sandhills blowout, the habitat of blowout penstemon (*Penstemon haydenii*).

These natural blowouts should not be confused with wind eroded fields or plane sand sweeps. Nor should they be confused with eroded areas around wind-mills or in other areas where livestock congregate and disturb the vegetation. The term "blowout" should be restricted to the naturally occurring, crater-shaped depressions.

A blowout is not static. The area of active wind erosion continually moves across the landscape at the speed of a few meters a year. Succession constantly occurs on the windward side. A blowout may exist for decades before it reaches maturity. Maturity is reached when the blowing sand is deposited in a deep valley or lake, and no longer accumulates on the leeward side (Pool 1914). The leeward side then is lowered as the wind blows through the hilltop. The steep front slope is eliminated, which eliminates the wind turbulence and the erosion force of the wind.

Vegetation

The first careful botanical work in the Sandhills was done by H. J. Webber in 1889 (Pool 1914). Webber made a list of the plant species and carefully recorded notes for each of his collections. Smith (1892) described the distribution of plants in the Sandhills as well as the topography. A taxonomic study by Rydberg (1895) produced the most extensive collection of plants and notes on the Sandhills up to that time.

Raymond Pool (1914) conducted an extensive study of the vegetation of the Sandhills. His doctoral thesis included an inventory and ecological interpretation of the flora based on plant community associations. Pool (1914) named and described the Bunchgrass, Muhlenbergia, Speargrass, Wiregrass Transition, and Blowout Associations as occurring on Nebraska Sandhills upland. The "Bunchgrass Association" was identified as the most extensive and important climax community present in the Sandhills prairie in the early 1900's (Pool 1914). This association was dominated by little bluestem [*Schizachyrium scoparium* (Michx.) Nash] and sand bluestem [*Andropogon gerardii* var. *paucipilus* (Nash) Fern.]. Other important species of this association were prairie sandreed [*Calamovilfa longifolia* (Hook.) Scribn.], needleandthread (*Stipa comata* Trin. & Rupr.), prairie junegrass [*Koeleria pyramidata* (Lam.) Beauv.], sand lovegrass [*Eragrostis trichodes* (Nutt.) Wood], and indian ricegrass [*Oryzopsis hymenoides* (R. & S.) Ricker]. Switchgrass (*Panicum virgatum* L.) was present in this association but was not common.

Dominants of the Blowout Association were prairie sandreed, lemon scurfpea (*Psoralea lanceolata* Pursh), and blowoutgrass [*Redfieldia flexuosa* (Thurb.) Vasey]. Other important species were cristatella (*Cristatella jamesii* T. & G.), sand lovegrass, plains muhly [*Muhlenbergia cuspidata* (Torr.) Rydb.], sandhill muhly (*Muhlenbergia pungens* Thurb.), birdegg milkvetch [*Astragalus ceramicus* Sheld. var. *filifolius* (Gray) Germ.], clammyweed [*Polanisia dodecandra* (L.) DC. subsp. *trachysperma* (T.& G.) Iltis], and blowout penstemon.

Burzlaff (1962) subdivided the grasslands of the Nebraska Sandhills into three range sites: the dry valley, the rolling sands, and choppy sandhill range site. Each site possessed different soil and vegetation characteristics.

On the dry valley site, prairie sandreed, blue grama [*Bouteloua gracilis* (H.B.K.) Lag. *ex* Steud.], sixweeks fescue [*Vulpia octoflora* (Walt.) Rydb.], sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray], and needleandthread dominated species composition, in order of decreasing abundance. Soils were considered to be loamy fine sands.

On the rolling sands site, the most important dominant was prairie sandreed, followed by sand bluestem, sand dropseed, hairy grama (*Bouteloua hirsuta* Lag.), and sixweeks fescue. Soils of this site were classified as Valentine fine sands.

Tall grasses, prairie sandreed and sand bluestem, dominated the choppy sandhill range site. Subdominants, little bluestem and sand lovegrass, were restricted to the north and east-facing slopes of the choppy hills. Sandhill muhly and hairy grama were more common on ridge tops and south and west exposures. Soils were classified as stabilized dune sand. Although blowoutgrass was of minor importance on stabilized soils of the choppy sandhill site, it is the first to establish in blowouts, or other areas of wind erosion, followed by lemon scurfpea, sandhill muhly, and other grasses and forbs (Weaver 1965). Currently, dominant species are sand bluestem, little bluestem, prairie sandreed, and needleandthread (Weaver 1965, U.S. Department of Agriculture 1981).

Blowout Penstemon

Another of the initial species to establish in a blowout was blowout penstemon. This perennial, multistemmed forb is generally found growing in areas of bare sand or in association with blowoutgrass within the blowout and near its leeward side, in the area of sand deposition (Weedon *et al.* 1982). Blowout penstemon is especially well adapted to blowouts, for its stems root adventitiously, maintaining the plant in the shifting sands of these sites (Stubbendieck *et al.* 1983, Stubbendieck and Weedon 1984). Also, its nearly horizontal buried stems produce fibrous roots, providing anchorage in this unstable environment (Weedon *et al.* 1982). However, blowout penstemon is successional in nature, colonizing the blowout once the sand has been physically stabilized and declining when other vegetation becomes well established (Weedon *et al.* 1982).

Blowout penstemon was once a common plant in blowouts (Pool 1914). However, it was thought to be extinct from 1940 until it was rediscovered in 1968 (Stubbendieck *et al.* 1983). Since that time, extensive searching has led to the rediscovery of nearly 4,250 plants. The reason(s) for its decline from being a common plant in the early 1900's to its current population are unknown. With wildfire control and improved range management practices, the amount of Sandhills blowout habitat has greatly decreased (Stubbendieck *et al.* 1982). Also, the drought of the 1930's severely impacted numerous prairie plant species, and it may also have had a negative influence on blowout penstemon (Weaver 1954, Stubbendieck 1986).

Even though blowout penstemon is taxonomically in a genus of plants widely appreciated for its appearance, it is distinguished by a striking beauty of its own. Its large, milky blue to lavender flowers also possess a distinct fragrance. Aside from its beauty and ability to invade and stabilize blowouts, other intrinsic values of this species are yet unknown. Thus, the preservation of blowout penstemon and its habitat, the blowout, is essential to realize fully the values of this unique plant.

ACKNOWLEDGEMENTS

Appreciation is expressed to the Nebraska Game and Parks Commission for financial support of the research on blowout penstemon. Journal Series Number 8410, Agricultural Research Division, University of Nebraska.

LITERATURE CITED

Bagnold, R.A. 1941. The physics of blown sand and desert dunes. Methuen, London.

Baver, L.D., W.H. Gardner, and W.R. Gardner. 1972. Soil physics. John Wiley and Sons, New York.

Bleed, A. 1989. Groundwater. Pages 67-92. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division, Resource Atlas No. 5.

Bleed, A., and C. Flowerday. 1989. Introduction. Pages 1-15. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division, Resource Atlas No. 5.

Bose, D.R. 1977. Rangeland resources of Nebraska. Society for Range Management Old West Regional Range program, Denver.

Burzlaff, D.F. 1962. A soil and vegetation inventory and analysis of three Nebraska Sandhills range sites. University of Nebraska Agricultural Experiment Station Research Bulletin 206.

Cockayne, L. 1911. Report on the dune-areas of New Zealand, their geology, botany, and reclamation. Department of Lands, Government of New Zealand.

Cowles, H.C. 1899. The ecological relations of the vegetation of the sand dunes of Lake Michigan. The Botanical Gazette 27:95-391.

Dewey, K.F. 1977. Wind. Pages 72-74. *In* M. P. Lawson, K. F. Dewey, and R. E. Meyers (eds.). Climatic atlas of Nebraska. University of Nebraska Press, Lincoln.

Elder, J.A. 1969. Soils of Nebraska. University of Nebraska, Conservation and Survey Division, Resource Report Number 2.

Gleason, H.A. 1910. The vegetation of the island sand deposits of Illinois. Illinois State Laboratory, Natural History Survey Bulletin 9:23-174.

Gosey, J. 1986. Beef improvement impact seen in Sandhills today. University of Nebraska, Institute of Agriculture and Natural Resources Quarterly 32:12-13.

Keech, C.F., and R. Bentall. 1971. Dunes on the plains: The Sandhills region of Nebraska. University of Nebraska, Conservation and Survey Division, Resource Report Number 4.

Neild, R.E. 1977. The freeze-free season. Pages 29-31. *In* M.P. Lawson, K. F. Dewey, and R.E. Neild (eds.). Climatic atlas of Nebraska. University of Nebraska Press, Lincoln.

Neild, R.E., N.J. Rosenberg, and R.E. Meyers. 1967. Temperature patterns and some relations to agriculture in Nebraska. University of Nebraska Agricultural Experiment Station Miscellaneous Publication 16.

Ordway, R.J. 1972. Earth science. Second edition. Van Nostrand Reinhold, New York.

Pool, R.J. 1914. A study of the vegetation of the Sandhills of Nebraska. Minnesota Botanical Studies IV:188-312.

Rydberg, P.A. 1895. Flora of the Sandhills of Nebraska. Contributions from the United States National Herbarium 3:133-203.

Smith, J.G. 1892. Grasses of the Sandhills of Nebraska. Nebraska State Board of Agriculture Annual Report.

Stubbendieck, J. 1986. Blowout penstemon: The Sandhills rare jewel. Nebraska Quarterly 32:17

Stubbendieck, J. 1989. Range management. Pages 227-233. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division, Resource Atlas No. 5.

Stubbendieck, J., and R.R. Weedon. 1984. Germination and establishment of blowout penstemon (*Penstemon haydenii* S. Wats.) Abstracts of papers, Society for Range Management 37:199.

Stubbendieck, J., J. Traeger, and R.R. Weedon. 1983. Propagation of blowout penstemon (*Penstemon haydenii* S. Wats.). Proceedings of the Nebraska Academy of Sciences 93:16.

Stubbendieck, J., R.K. Engel, W. Schacht, J. Traeger, and R.R. Weedon. 1982. Germination characteristics of *Penstemon haydenii* Wats. Proceedings of the Nebraska Academy of Sciences 92:18.

United States Department of Agriculture. 1981. Nebraska range site descriptions and guide for determining range condition and suggested initial stocking rates. United States Department of Agriculture, Soil Conservation Service, Washington, DC.

United States Department of Commerce. 1973. Monthly normals of temperature, precipitation, and heating and cooling degree days, 1941-70. Climatography of the United States Number 81.

Weaver, J.E. 1954. North American prairie. Johnsen Publishing Company, Lincoln, Nebraska.

Weaver, J.E. 1965. Native vegetation of Nebraska. University of Nebraska Press, Lincoln.

Weedon, R.R., J. Stubbendieck, and M. Beel. 1982. Blowout penstemon. NEBRASKAland 60:49-51.

Wilhite, D.A., and K.G. Hubbard. 1989. Climate. Pages 17-28. *In* A. Bleed and C. Flowerday (eds.). An atlas of the Sand Hills. University of Nebraska Conservation and Survey Division, Resource Atlas No. 5.

BLOWOUT PENSTEMON: DESCRIPTION AND PRESENT SITUATION

Joyce Phillips Hardy, Ronald R. Weedon, and William R. Bowlin
Department of Biology, Chadron State College, Chadron, Nebraska 69337

Abstract: Blowout penstemon (*Penstemon haydenii* S. Wats.) appears to be the rarest flowering plant species endemic to Nebraska. It has received a great deal of attention, for endemism is rare in Great Plains states. This attractive species is confined to a small number of active blowout areas in the Nebraska Sandhills, often in relatively small colonies that are many kilometers apart in a relatively vast grassland. Blowout penstemon, thus, is confined to particular habitats which have distinct boundaries in space. It is also successional in nature, which places individual colonies in distinct and, perhaps, limited boundaries in time. It is apparent after eleven years of study that numbers of individuals in a particular colony may vary widely, with the tendency for catastrophic decline. The authors review the morphology of the species, its potential taxonomic relationships, and the fluctuations in known numbers of this species in the recent past.

Key Words. blowout penstemon, *Penstemon haydenii,* penstemon, blowouts, endangered species, Sandhills, Nebraska

INTRODUCTION

Blowout penstemon (*Penstemon haydenii* S. Wats.) has received a great deal of attention in the last eleven years. Endemism is rare in the Great Plains, and this species is limited to the Sandhills region of Nebraska. The plants are confined to a few relatively small active blowout areas, which are often quite distant from one another within these generally well vegetated sand dunes. The optimum habitat for blowout penstemon appears to be in the areas of sand deposition near the blowouts. The blowout penstemon populations decline in number and vigor as these blowouts become revegetated. The demographic problems of these colonies are comparable to those problems of oceanic island colonizing species, with the favorable blowout habitats isolated from one another by a vast sea of grassland prairie.

The authors have been involved in monitoring known blowout penstemon colonies through time. The fluctuations of nine representative colonies are presented. The morphology of blowout penstemon and its potential taxonomic relationships to other penstemon species in the area are discussed.

METHODS

During their early search for this plant, the authors relied heavily on a verbal description of blowout penstemon given by Claude A. Barr. His written description is quite accurate: "*Penstemon haydeni* (sic) has very long and narrow, channeled, waxy, glaucous green leaves, not basal but low on a heavy stalk that rises stiffly to 10 to 24 inches. Subtending the closely set and ample clusters of large, milky blue flowers are bracts of astonishing width, broadly spoon-shaped and sharp-tipped. They give the plant a distinctive effect. Enticing to bees and pleasing to the human sense, the flower has a strong and carrying fragrance. Branches put out from the lower leaf axils dip to the ground and turn up at the tip; these, when partly covered by drifting sand, strike root" (Barr 1983). Freeman (1981) stated that "morphologically, *Penstemon haydenii* is one of the most striking members of the *Coerulei* (section of *Penstemon*), due to its compact cylindrical inflorescence with prominent long-acuminate bracts and its habit of forming large multi-stemmed clumps . . . The species is apparently unique in the *Coerulei* in that its flowers possess a distinctive fragrance."

Extensive searches for new blowout penstemon populations have been conducted by the authors since 1977. Colonies of blowout penstemon have been observed through time, with population counts for these known colonies being recorded. The populations were counted in the late flowering-early fruiting stage when individual plants are most easily seen. Rooting stems from a single crown were determined to be a single organism. Separate plant crowns interconnected by rooting stems from a single crown were determined to be individual plants. Tabulations of the population size were recorded. Relative reproductive/vegetative ratios were recorded for many sites.

RESULTS

The figures present the tabulation results for nine representative populations of blowout penstemon. Figure 1 shows the relative

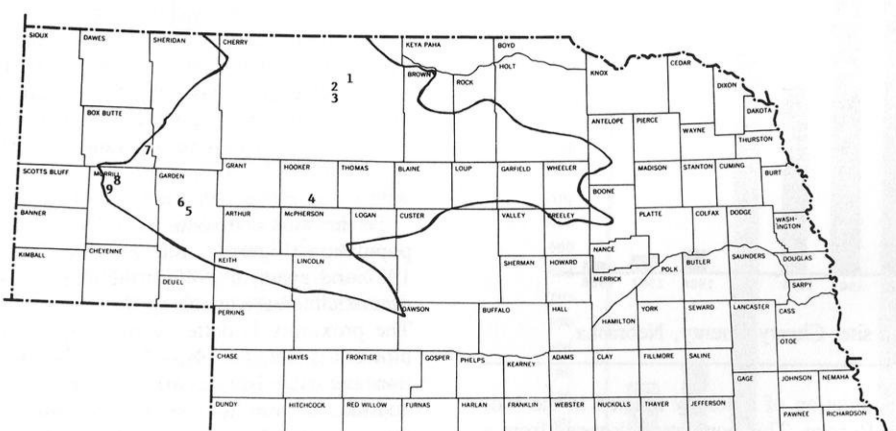


FIG. 1. General location of representative populations of *Penstemon haydenii* S. Wats. within the Nebraska Sandhills.

COUNTY OUTLINE
NEBRASKA
Scale of Miles
0 10 20 30 40 50

relationships of the different monitored sites of blowout penstemon. Figures 2 through 10 chart the population sizes at these sites. The solid lines represent total population counts for those years when the relative number of reproductive plants to vegetative plants was not available. The dark areas with white diagonal lines represent reproductive plants while the white areas with black hash lines represent vegetative plants.

In north-central Cherry County, north of the Valentine National Wildlife Refuge, a site has been monitored for ten years (Figure 1, Site 1). The colony has ranged in size from over 230 in 1982 to a low of 11 in 1987. This colony appears to be in poor condition, with few vegetative plants surviving among scattered, old plants (Figure 2).

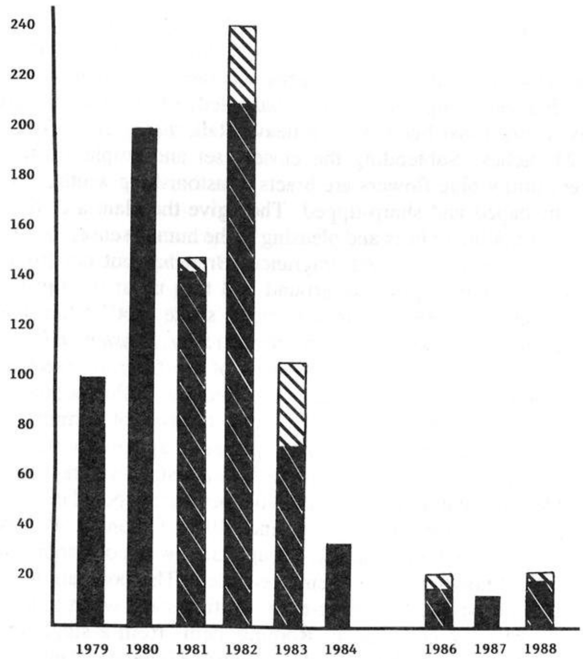


FIG. 2. Site north of wildlife refuge; Cherry County, Nebraska.

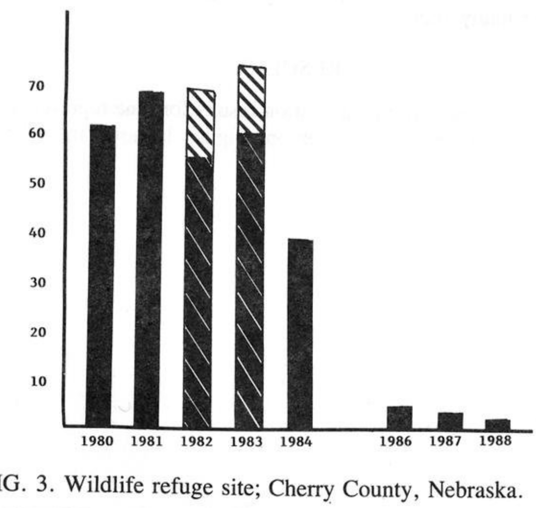


FIG. 3. Wildlife refuge site; Cherry County, Nebraska.

Figure 3 charts the population of a colony located in the Valentine National Wildlife Refuge. This population dropped from a high of 73 in 1983 to just 2 widely spaced plants in 1988. The future of this colony seems to be bleak (Figure 1, Site 2).

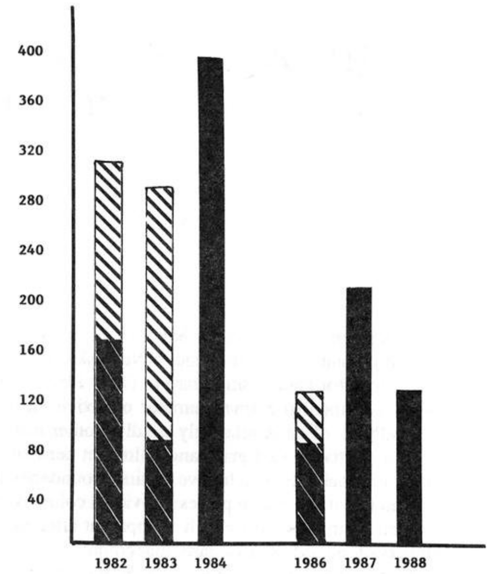


FIG. 4. Site near wildlife refuge; Cherry County, Nebraska.

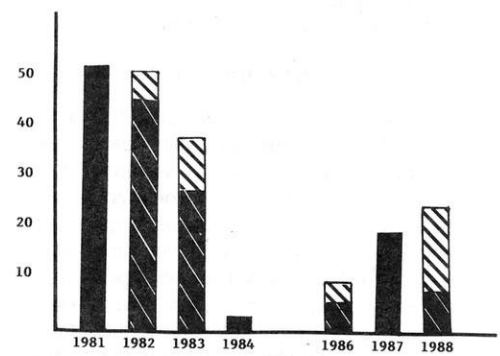


FIG. 5. Hooker County site.

Near the Valentine Wildlife Refuge exists a complex of blowouts which harbor blowout penstemon (Figure 1, Site 3). In 1984, 391 plants survived in the main blowout. In 1988, only 140 plants survived. This site has a history of high vegetative counts relative to reproductive counts (Figure 4).

The south-central Hooker County site is located approximately 100 km south and west of the previous sites (Figure 1, Site 4). In spite of extensive searching, this remains the nearest known population to the preceding three sites. This colony has remained small during the monitoring period, ranging from a high of 51 individuals in 1981 to a low of three in 1984. A slight resurgence in numbers within this colony occurred in 1987 and 1988 (Figure 5).

To the west and south in Garden County is the Crescent Lake population (Figure 1, Site 5). Over 900 plants were counted in 1982 and again in 1986 in the main blowout area (Figure 6). A dramatic increase in colony size occurred between 1981 and 1982. The proximity is dotted with many potential locations, and this blowout is situated relatively near the following colony. Immigration and establishment of new seedlings in this area is possible and may account for the dramatic resurgence in numbers seen in the last several years (Figure 6). The rejuvenating of blowouts through wind erosion during these years may also be involved.

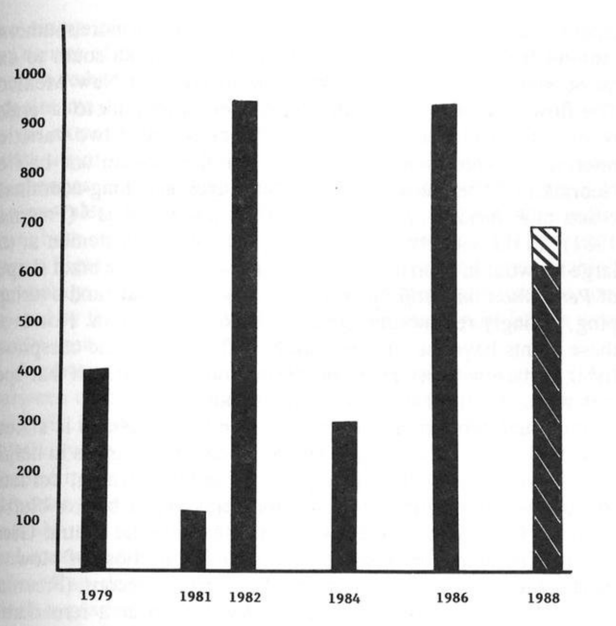


FIG. 6. Crescent Lake site; Garden County, Nebraska.

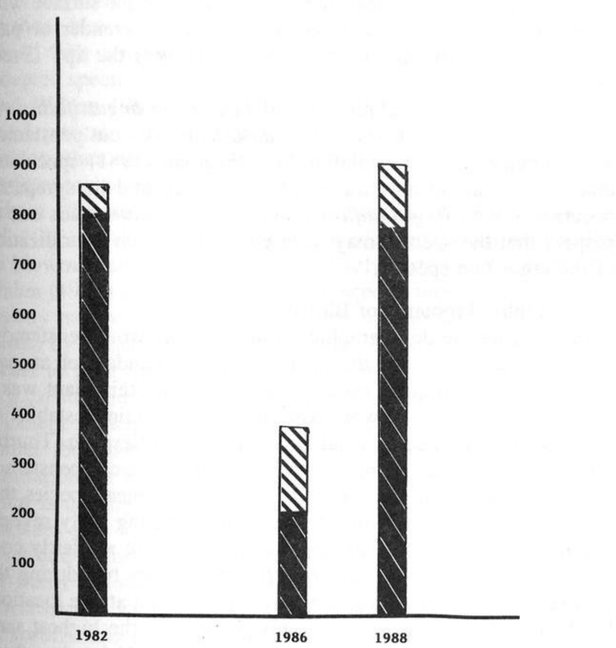


FIG. 7. Graves Ranch Preserve, Nature Conservancy; Garden County, Nebraska.

The Graves Ranch Preserve is located to the northwest of the Crescent Lake site and the Crescent Lake National Wildlife Refuge (Figure 1, Site 6). This area is owned by the Nature Conservancy, and land management is for the protection and preservation of blowout penstemon. Nine hundred plants were counted at the monitored blowout in 1988 (Figure 7).

To the west and north of this location is the Box Butte County site (Figure 1, Site 7). With the exception of 1984, this site has had a low colony count. The summer count in 1984 revealed mostly vegetative seedlings in the large area of newly deposited sand on the leeward side of the blowout (Figure 8).

A small complex of blowouts in northwestern Morrill County reveals a population which has fluctuated between 40 and 120 (Figure 1, Site 8). The choppy hills surrounding this area reveal

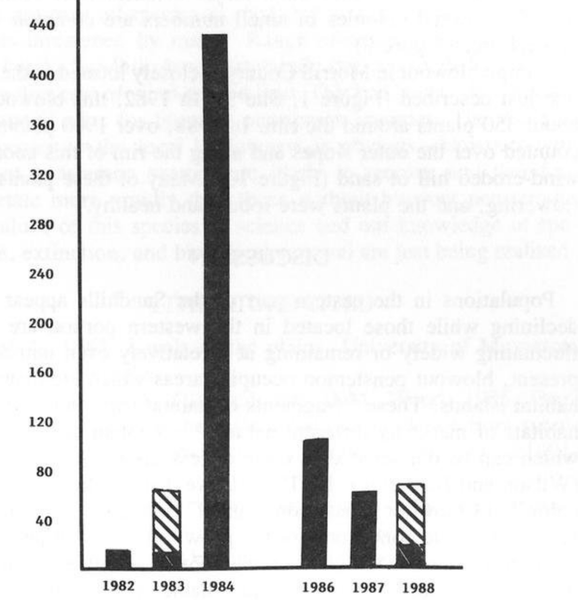


FIG. 8. Box Butte County site.

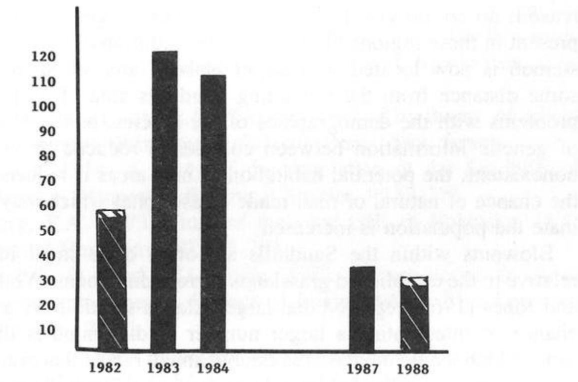


FIG. 9. Small blowout complex; Morrill County, Nebraska.

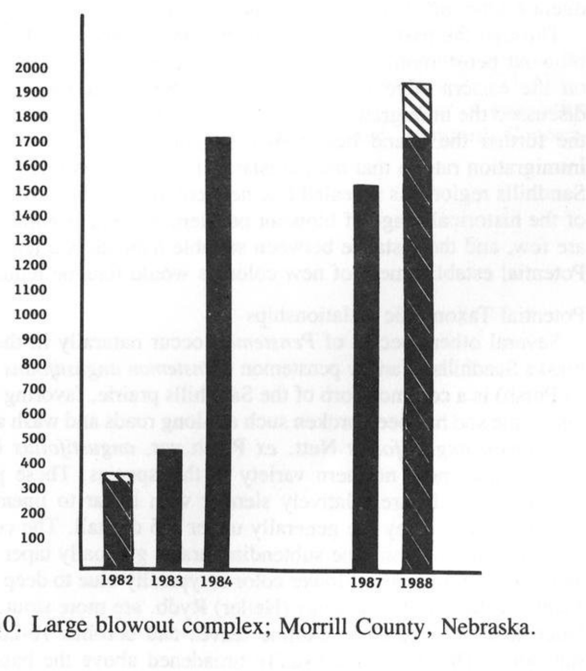


FIG. 10. Large blowout complex; Morrill County, Nebraska.

many potential sites. Few other major colonies were found, although scattered colonies of small numbers are common in the general area (Figure 9).

A large blowout in Morrill County is closely located to the small one just described (Figure 1, Site 9). In 1982, this blowout had about 350 plants around the rim. In 1988, over 1900 plants were counted over the outer slopes and along the rim of this enormous wind-eroded hill of sand (Figure 10). Many of these plants were flowering, and the plants were robust and healthy.

DISCUSSION

Populations in the eastern part of the Sandhills appear to be declining while those located in the western portion are either fluctuating widely or remaining at a relatively even number. At present, blowout penstemon occupies areas which are essentially habitat islands. These "fragments of habitat surrounded by other habitats of markedly different nature . . . contain sets of species which can be demarcated as more or less discrete communities" (Wilson and Bossert 1971). The relative distance between known colonies of blowout penstemon is great. Habitats which appear to provide suitable conditions for the growth of blowout penstemon often do not harbor the plant species. Possible causes of this may be the lack of seed in the area, unavailable moisture at the proper time for germination, deficiency of proper nutrients, or difference in size of the sand separates of that particular soil type. There appears to be great expanses of Sandhills area which, for some reason, do not provide habitable areas, even though blowouts are present in these regions. The major concentration of blowout penstemon is now located in a rather isolated area of Sandhills at some distance from the remaining Sandhills area. This presents problems with the demographics of the species, as the exchange of genetic information between colonies is reduced or virtually nonexistent, the potential habitation of new areas is reduced, and the chance of natural or man-made catastrophes which may eliminate the population is increased.

Blowouts within the Sandhills are often quite small in size, relative to the established grasslands surrounding them. Whitehead and Jones (1969) reported that larger islands should have a better chance of intercepting a larger number of disseminules through time, which would increase the establishment rate of that organism. Conversely, a smaller habitat island, such as a Sandhills blowout, has a reduced chance of propagule immigration. In addition, smaller islands hold smaller populations, which are subject to more frequent extinction (Wilson and Bossert 1971).

Through the past 11 years of the exploration and monitoring of blowout penstemon, a general decrease in numbers has occurred on the eastern edge of its range. Whitehead and Jones (1969) discussed the immigration rate to new habitats, and concluded that the further the island lies from a source region, the lower the immigration rate to that habitat island. Extensive searching of the Sandhills region has revealed few new colonies in the eastern part of the historical range of blowout penstemon. Source populations are few, and the distance between suitable habitats is often great. Potential establishment of new colonies would thus be reduced.

Potential Taxonomic Relationships

Several other species of *Penstemon* occur naturally in the Nebraska Sandhills. Narrow penstemon (*Penstemon angustifolius* Nutt. *ex* Pursh) is a common forb of the Sandhills prairie, favoring areas where the sod has been broken such as along roads and wash areas. *Penstemon angustifolius* Nutt. *ex* Pursh var. *angustifolius* is the western and more northern variety of this species. These plants characteristically are relatively slender with linear to linear-lanceolate leaves. They are generally under 4.5 dm tall. The corolla is 14-18 mm long and the subtending bracts gradually taper to an acute or acuminate tip. Flower color is typically blue to deep blue. Plants of the variety *caudatus* (Heller) Rydb. are more stout, with lanceolate to lance-ovate cauline leaves and corollas 16-20 (23) mm long. The bracts are usually broadened above the base and taper to short or long-acuminate tips. This variety is more southern, ranging from northwest and north-central Nebraska south to extreme western Kansas and Oklahoma to northern New Mexico. The flower color is often variable, ranging from pink to lavender or blue to deep blue. The characteristics of these two varieties intergrade where their ranges overlap in the western one-half of Nebraska. "The linear shape of the leaves and long-acuminate bracts of *P. haydenii* are suggestive of *P. angustifolius*" (Freeman 1981). In the vicinity of the colony of blowout penstemon at the large blowout in Morrill County (Figure 1, Site 9), the bract shapes of *Penstemon angustifolius* var. *caudatus* are cordate and overlapping, strongly resembling those of blowout penstemon. However, these plants have the smaller dark blue flowers and the caespitose habit of narrow penstemon, and taxonomically approach that species more closely than blowout penstemon.

Shell-leaf penstemon (*Penstemon grandiflorus* Nutt.) is a stout perennial which arises from a taprooted crown. It ranges in height from 5 to 9.5 dm. The interrupted thyrse has clasping, cordate-based bracts subtending 35-48 mm long pink to pale blue or bluish-lavender flowers. This species occurs mostly in the central Great Plains. The bracts on this species are similar to those of blowout penstemon. The leaves are thick, firm, and glaucous (Freeman 1986). "The flowers of *Penstemon haydenii* bear a remarkable resemblance to those of *P. grandiflorus*. Both species have corollas that are distinctly bilabiate, inflated and ventricose posteriorly, moderately ampliate, lined internally on the anterior surface with magenta guidelines and colored milky blue to lavender or pale lavender externally, and staminodes bearded near the tip" (Freeman 1981).

The morphological similarities of *Penstemon angustifolius* variety *caudatus* and *Penstemon grandiflorus* to blowout penstemon may indicate a genetic relationship. Freeman (1981) speculates that "the chimeric appearance of *P. haydenii* and its sympatric occurrence with *P. grandiflorus* and *P. angustifolius* leads one to suspect that the species may have evolved through hybridization of the latter two species."

Demographic Problems of Blowout Penstemon

In studying the demographic problems of blowout penstemon, it is often assumed that the plant was once abundant or at least common in this region. Pool (1914) stated that this plant was a principal species in blowout associations, becoming established after the first species, blowout grass [*Redfieldia flexuosa* (Thurb.) Vasey], became established in the blowout. Blowout penstemon was listed as one of the "more common and typical species that become a part of the blowout association" during early revegetation. "These later arrivals are not numerous but are fairly constant" (Pool 1914). In Rydberg's floristic survey trip during the summer of 1893, he collected blowout penstemon at one location. He found the species "in fruit only, on one of the highest sand hills, Plummer Ford", which is south of Seneca, Nebraska, about 24 km and then approximately 5 km east, on the Dismal River (Rydberg 1893). If this plant were abundant throughout the Sandhills, surely the striking beauty and fragrance would have enticed more collections than what are now known. Soulé (1983) pointed out that "some species might be rare from the time they become genetically independent of their forebearers and never become common relative to other species of a similar body size, taxonomic group, or tropic level . . . If such a rare species also is confined to a small geographic area, it will not persist long because it will be expunged by a local catastrophe, or be driven to extinction by stochastic events such as genetic drift or demographic stochasticity." This may be an alternate explanation for the demographic problems of this species.

One of the results of a small population size may be the lack of genetic variability that will allow for evolutionary adaptation to changing environments. The decreased vigor, viability, and fecundity that is associated with inbreeding depression can be the result of genetic deterioration which often occurs in small out-crossing populations. Futuyma (1983) cited the following two major causes of populations extinctions: "In an unchanging environment a reduction in the sizes of the populations of an outbreeding species may result in inbreeding depression and a loss of fitness to the extent that the populations may dwindle to extinction. The other major cause of extinction is the failure of species to adapt to changes in the ecological environment that lower the fitness of the prevalent genotypes." While blowout penstemon may suffer from both of these causes, the situation is paradoxical. The species seems highly fecund and seed viability may be at a "reasonable" percentage, in nature. However, during the population studies conducted by the authors, natural seedlings in native populations were rarely seen.

A certain amount of genetic variability within a colony and between colonies seems to be present. Future detailed population analysis is necessary. While this analysis is forthcoming, it is relatively easy to conclude that the species is in danger, due to the decline in the number of suitable available habitat islands, and the increasing isolation of colonies from each other. The most healthy colonies are relatively narrowly confined to the extreme western and southwestern areas of the Nebraska Sandhills. Even if neither inbreeding depression nor a loss of fitness are involved in the bleak-appearing destiny of blowout penstemon, the decreasing range of viable colonies and the resulting increased restriction of suitable habitats is likely to be a factor.

A large amount of species interference is apparently occurring in these blowouts. "Species already present on habitat islands are faced with constant pressure of high immigration from less well-adapted species drawn from the surrounding habitats" (MacArthur and Wilson 1967). In addition, "if interference causes narrower fundamental niches and competitive exclusion of similar species occurs, then species growing at equilibrium in habitats where interference has been important should be more specialized than where other factors dominate evolutionary forces" (Del Moral *et al.* 1985). This interference between adjacent species has resulted in blowout penstemon having a relatively narrow niche width. Van Valen (1965) stated that, in general, species niches are "relatively tightly packed together by the action of stabilizing selection imposed by ecologically adjacent species." Blowout penstemon appears to be a successional species confined in or near blowouts, e.g., disturbed Sandhills prairie. It requires slightly stabilized soil. Nutrient presence and availability is usually sparse, and may be either the main limiting constituent or a contributing factor of limitation for the plants growing in this habitat. Blowout penstemon is usually found in blowouts with blowout grass or on the leeward side of blowouts in the loose sand which was deposited over native sod. It stabilizes the soil by means of its large clumps of stems and also its rooted decumbent stalks, thereby setting the successional stage for the next species, usually lemon scurfpea (*Psoralea lanceolata* Pursh).

Simberloff and Abele (1982) state that "conservation strategy should not treat all species as equal but must focus on species and habitats threatened by man." Range management techniques in the Nebraska Sandhills have historically stressed sodded grasslands and the decrease of wind-eroded land. This had lead to the decrease of potential sites for blowout penstemon colonies. The value of this species to the local landowners is obvious—blowouts with blowout penstemon seem more likely to recover and therefore revegetate more rapidly than those without blowout penstemon. The values of this species to science and our knowledge of speciation, extinction, and biological survival are just being realized.

LITERATURE CITED

Barr, C.A. 1983. Jewels of the plains. University of Minnesota Press, Minneapolis.

Del Moral, R., C.A. Clampitt, and D.M. Wood. 1985. Does interference cause niche differentiation? Evidence from subalpine plant communities. American Journal of Botany 72:1891-1901.

Freeman, C.C. 1981. A biosystematic study of the genus *Penstemon* (*Scrophulariaceae*) in the Great Plains. Master of Science Thesis, Kansas State University, Manhattan.

Freeman, C.C. 1986. *Penstemon*. Pages 774-789. *In* Great Plains Flora Association. Flora of the Great Plains. University Press of Kansas, Lawrence.

Futuyma, D.J. 1983. Interspecific interactions and the maintenance of genetic diversity. Pages 364-373. *In* C. M. Schonewald-Cox, *et al.* (eds.). Genetics and conservation. The Benjamin/Cumings Publishing Company, Incorporated, Menlo Park, California.

MacArthur, R.H, and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, New Jersey.

Pool, R.J. 1914. A study of the vegetation of the Sandhills of Nebraska. Minnesota Botanical Studies 4:189-312.

Rydberg, P.A. 1893. Flora of the sand hills of Nebraska. U.S. National Herbarium III:133-203.

Simberloff, D., and L.G. Abele. 1982. Refuge design in island biogeographic theory: Effects of fragmentation. The American Naturalist 120:41-50.

Soulé, M.E. 1983. What do we really know about extinction? Pages 111-124. *In* C.M. Schonewald-Cox *et al.* (eds.). Genetics and conservation. The Benjamin/Cumings Publishing Company, Incorporated, Menlo Park, California.

Van Valen, L. 1965. Morphological variation and width of ecological niche. The American Naturalist 99:377-390.

Whitehead, D.R., and C.E. Jones. 1969. Small islands and the equilibrium theory of insular biology. Evolution 23:171-179.

Wilson, E.O., and W.H. Bossert. 1971. A primer of population biology. Sinauer Associates, Incorporated, Stamford, Connecticut.

POLLEN COLLECTORS AND OTHER INSECT VISITORS TO *PENSTEMON HAYDENII* S. WATS.

H. Randy Lawson
School of Science and Mathematics, Chadron State College, Chadron, Nebraska 69337

V. J. Tepedino and T. L. Griswold
USDA-ARS Bee Biology and Systematics Lab, Utah State University, Logan, Utah 84322-5310

Abstract. Records of insects visiting the flowers of *Penstemon haydenii* (S. Wats.) are supplied. The flower-visitor fauna was different at the two sites censused. Primary pollinators appeared to be four species of megachilid bees which consistently visited the flowers for pollen. While bees exhibited high fidelity to flowers of the genus *Penstemon,* analysis of the pollen carried by females suggests that crossing over between *Penstemon* species on a particular foraging trip may be common. Opportunities for interspecific hybridization almost certainly occur.

Key Words. blowout penstemon, *Penstemon haydenii,* endangered plant, pollination, pollen collection, flower visitors, Apoidea, Nebraska

INTRODUCTION

The preservation of endangered plant species such as blowout penstemon (*Penstemon haydenii* S. Wats.) in the wild ultimately rests on preservation of sufficient habitat to contain all the necessary requisites for that species' continued existence. While the identity of many of those requisites (and their complex interactions) remains hidden, one essential biotic requisite is pollinators. It has been estimated that about 67% of flowering-plant species depend to some extent upon insect intermediaries to transfer viable pollen from anthers to receptive stigmas (Axelrod 1960). Indeed, many species cannot reproduce sexually at all without the aid of certain insect "helpmates."

Despite the beauty of the flowers of many *Penstemon* species, the size of the genus and the opportunities it offers for the study of evolutionary biology, relatively little work has been conducted on pollination. However, pollination mechanisms and pollinators are known to be quite diverse: Birds (Lyon 1976), flies (Straw 1963, Schmidt 1976), and wasps and bees (Crosswhite and Crosswhite 1966) have been recorded as pollinators of different species. Many species of *Penstemon* in the western United States appear to be closely associated with bees of the family Megachilidae, particularly in the genera *Osmia* and *Anthocopa* (*Atoposmia*), and with wasps of the genus *Pseudomasaris* (Masaridae) (Crosswhite and Crosswhite 1966).

Blowout penstemon was shown to be primarily cross-pollinated, but the pollinator affinities of blowout penstemon are largely unknown (Flessner 1988). Aside from reports that several kinds of bees and other insects (all unnamed) visit the flowers for pollen and nectar, no other information appears to be available (Fish and Wildlife Service 1987, Flessner 1988). This is surprising not only because of the plants' endangered status, but also because of the suggestion by Freeman (1981) that blowout penstemon may be a hybrid of its sympatric congeners, narrow penstemon (*Penstemon angustifolius* Nutt. *ex* Pursh) and shell-leaf penstemon (*Penstemon grandiflorus* Nutt.). When Straw (1955, 1956) originally proposed a hybrid origin for another western species, *Penstemon spectabilis* Thurb. *ex* Gray, he suggested that its origin was mediated by the species-specific flower-visiting behavior of certain pollinators.

The objective of this research was to provide a preliminary survey of the insects visiting the flowers of blowout penstemon. Because this species usually exists in small, isolated populations, an additional objective was to determine whether the flower-visitor fauna from eastern and western parts of the species range was similar. Because many insects visit flowers without pollinating them, the actual pollinator fauna would be some subset of these flower-visiting species. Additional studies, currently underway, will separate the pollinators from the non-pollinating parasites.

METHODS

Insects were collected from blowout penstemon plants at one site in both Cherry and Morrill counties in 1987 during peak bloom. The Cherry County site, which contained about 100 plants, was in a typical blowout of about 40 m in diameter, situated near rather large sandhill lakes. The Morrill County site contained about 2,000 plants in an extremely large blowout with no lakes nearby (Weedon, Hardy, and Bowlin, personal communication).

Four two-hour collections were made at the Cherry County site between 30 May and 10 June 1987. Two collections of two-hour duration were made at the Morrill County site on 11 and 13 June 1987. All collecting was completed between 10:00 a.m. and 3:00 p.m. Only insects actually in the blowout penstemon corolla were captured. Most specimens were collected when they exited into an ethanol-filled vial that was being held at the flower entrance. Larger insects, such as butterflies, were captured by placing a sweep net over the flowers being visited.

Insects were sorted to order and sent to experts for specific identification. Aculeate Hymenoptera were determined by T. L. Griswold. Voucher specimens were placed at the USDA-ARS, Bee Biology and Systematics Lab, Logan, Utah.

Pollen was removed from the scopa of each pollen-collecting female bee, treated on a microscope slide with ethanol, and stained with fuchsin glycerin jelly (Beattie 1971). Random transects across each slide were taken under the light microscope at 400X until 500 grains had been examined and identified to genus by comparison with a reference collection. Further separation of these pollen grains was done by size into the three sympatric and synchronic species *Penstemon angustifolius, Penstemon haydenii,* and *Penstemon grandiflorus*. At 400X, 50 pollen grains were measured from each of three flowers, each from a different herbarium specimen, for the first two species, and 50 pollen grains from one flower of the latter species. A nested ANOVA was used to test for differences in grain size between *Penstemon angustifolius* and *Penstemon haydenii. Penstemon grandiflorus* could not be tested because only one flower was sampled. These measurements were used to assign the pollen carried by bees to one of the three species.

RESULTS AND DISCUSSION

The diversity and relative abundance of insects visiting blowout penstemon is shown in Table 1. At both sites, the predominant group of visitors were solitary bees of the family Megachilidae. Four species from this group deserve special attention because they are probably important pollinators of the plant.

Table 1. Diversity and relative abundance of insects visiting blowout penstemon.

Species	*Location and Numbers*		
	Cherry County		*Morrill County*
Hymenoptera:			
Halictidae-			
Dialictus pruinosiformis (Crawford)		7[1]	
D. pilosus (Smith)	4		—
D. sp. 1	—		15
D. sp. 2	2		—
Agapostemon splendens (Lep.)	—		1
Andrenidae			
Perdita sp.	1		—
Megachilidae			
Hoplitis pilosifrons (Cresson)	39		5
Osmia cyaneonitens Cockerell	1		70
O. distincta Cresson	63		—
O. integra Cresson	3		11
Anthophoridae			
Emphoropsis sp.	1		1
Apidae			
Bombus fervidus (Fabricius)	—		1
B. n. nevadensis Cresson	—		1
B. pennsylvanicus (Degeer	—		
B. vagans Smith	1		—
Braconidae	—		1
Scoliidae			
Campsomeris pilipes (Sauss.)	—		1
C. plumipes confluenta (Say)	3		—
Vespidae			
Polistes sp.	1		1
Pterocheilus quinquefasciatus Say	1		—
Pompilidae			
Anoplius sp. 1	—		1
A. sp. 2	—		2
Sphecidae			
Ammophila sp. 1	1		—
A. sp. 2	1		—
Podalonia sp. 1	1		—
P. sp. 2	1		—
Prionoyx atratus (Lep.)	1		—
Coleoptera:			
Cleridae			
Phyllobaenus pubescens LeConte	1		—
Phalacridae			
Phalacrus politus Melsh.	—		1
Mordellidae			
Mordellistena sp.	1		4
Meloidae			
Epicauta sericans LeConte	—		1
Lytta reticulata Say	1		—
Chrysomelidae			
Chelymorpha cassidea (F.)	1		—
Gastrophysa formosa (Say)	—		1
Curculionidae			
Odontocorynus sp.	1		2
Lepidoptera:			
Hesperiidae			
Atrytonopsis hianna (Scudder)	3		1
Noctuidae	3		2
Pyralidae	1		—
Diptera:			
Chironomidae			
Chironomus sp.		11	
Stratiomyidae			
Odontomyia sp.		2	
Asilidae		2	
Bombyliidae			
Bombylius sp.		2	
Poecilanthrax sp.		1	
Villa sp.		1	
Dolichopodidae		3	
Syrphidae		2	
Conopidae		2	
Muscidae		1	
Sarcophagidae		1	
Tachinidae		1	

[1]County location not available for data in center column.

Hoplitis pilosifrons (Cr.) is a mostly eastern species that ranges from the east coast, west to Alberta, Colorado and Texas. It is known to nest in stems and wood, usually excavating pith from weed stems (Michener 1955). A variety of plants are known to be visited for pollen, including *Penstemon* spp. (Hurd 1979).

Osmia distincta Cr. is another eastern species that ranges from the east coast, west to North Dakota and Colorado. The nesting biology is unknown. It is known to visit several genera of plants, including *Penstemon* but no pollen plant has previously been recorded (Hurd 1979).

Osmia cyaneonitens Ckll. is a rare western species recorded previously only from Colorado and South Dakota. Its nesting biology is also unknown. The type specimen was collected from *Penstemon* sp. at Florissant, Colorado, in 1906 (Hurd 1979).

Osmia integra Cr. is the largest of the four species. It ranges from the Pacific coast, east to Texas and Manitoba. It is known to build mud nests under rocks (Hicks 1926). It has not been previously recorded as a visitor of *Penstemon* (Hurd 1979).

It is of interest to note that no species of bees in the taxon *Anthocopa* (*Atoposmia*) nor the wasp genus *Pseudomasaris* were collected. Many species in these groups are known for their strong preference for *Penstemon* pollen (Parker 1977, Torchio 1974).

The insects visiting blowout penstemon at Morrill were quite different from those at Cherry County, approximately 225 km to the east (Table 1). The Morrill County site was frequented mostly by the western and prairie species *Osmia integra* and *Osmia cyaneonitens*. At Cherry County, the eastern species *Osmia distincta* and *Hoplitis pilosifrons* were most abundant. The two most abundant species, *Osmia distincta* and *Osmia cyaneonitens*, exhibited distributions that were almost mutually exclusive. Questions about interspecific competition between them for pollen and/or nectar need to be answered. More importantly, are there morphological differences in flowers between blowout penstemon populations that would favor different suites of pollinators at different sites?

Collection of *Penstemon* pollen by foragers was common. Of 198 females in the four species of megachilid bees, 88 were found to have been collecting pollen at the time of capture (Table 2). Of these, all but five *Osmia cyaneonitens* and three *Hoplitis pilosifron* carried pollen loads of pure *Penstemon* pollen. The three non-pure *Hoplitis pilosifrons* pollen loads had over 70% *Penstemon* pollen. Thus, these four species of megachilids were extremely constant to flowers within the genus *Penstemon*.

Table 2. *Penstemon haydenii* 1987 pollen carriers.

Bee Species	*Females with Penstemon Pollen*	*Females with ≥ 95% Penstemon pollen*	*Females with ≥ 70% Penstemon pollen*
Osmia integra	3	3	
Osmia distincta	30	30	
Osmia cyaneonitens	44	39	39
Hoplitis pilosifrons	11	8	11

To determine if females were flower-constant to *Penstemon haydenii*, it was first established that pollen grains of *Penstemon angustifolius* and *Penstemon haydenii* differed significantly in size (nested ANOVA, $F = 15.8$, $df = 1, 4$; $P < 0.05$). A normal distribution of pollen-grain sizes for each of the three *Penstemon* species is shown in Figure 1. These estimates were in close agreement with those of Freeman (1981). Grains were assigned to species by greatest probability for a given grain size: Thus, a 24-micron grain was assigned to *Penstemon haydenii* but a 23-micron grain to *Penstemon angustifolius* (Figure 1).

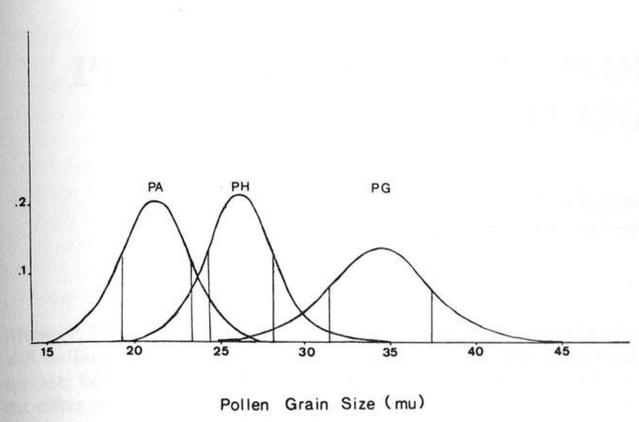


FIG. 1. Normal distributions of pollen-grain sizes for *Penstemon angustifolius* (PA), *Penstemon haydenii* (PH) and *Penstemon grandiflorus* (PG). Vertical lines mark ± 1 standard deviation.

Using this method, bees do not appear to have been so constant to flowers of blowout penstemon during a particular foraging trip. Although over 60% of the pollen in an average pollen load is that of blowout penstemon (Table 3), pollen of the other two species was commonly incorporated as well. This conclusion should be regarded as tentative for three reasons: 1) the number of flowers used to obtain the estimates was small; 2) the nested ANOVA yielded a significant within species term ($F = 46.3$, $df = 4,294$, $P < 0.001$), i.e., a substantial variation in pollen size occurred among flowers within species; and 3) a considerable overlap existed in grain size, particularly between *Penstemon angustifolius* and *Penstemon haydenii* in the 22- to 25-micron range, and between *Penstemon haydenii* and *Penstemon grandiflorus* in the 29- to 31-micron range.

Table 3. Percent of *Penstemon haydenii* pollen carried by pollen carriers.

Species	*Sample size*	*Pollinators carrying P. haydenii pollen*
		------------- % -------------
Osmia integra	3	74.0
Osmia distincta	30	62.6
Osmia cyaneonitins	44	63.3
Hoplitis pilosifrons	11	67.6

Nevertheless, bees seem to have commonly crossed over between species on individual foraging trips. Even allowing that these estimates are somewhat inflated, it is still highly likely that ample opportunities occur for hybridization among these species of Penstemon.

ACKNOWLEDGEMENTS

We thank R. R. Weedon for the herbarium specimens; W. R. Bowlin for help with collections; M. E. Klomps for measuring pollen grains; M. Cha for the figure; G. Eickwort for the identifications of *Dialictus* spp.; N. M. Downey for the identification of all Coleoptera; and D. Webb for the identification of the Diptera.

LITERATURE CITED

Axelrod, D.I. 1960. The evolution of flowering plants. Pages 227-305. *In* S. Tax (ed.). Evolution after Darwin, Vol. 1, The evolution of life. University of Chicago Press, Chicago.

Beattie, A.J. 1971. A technique for the study of insect-borne pollen. Pan Pacific Entomologist 47:82.

Crosswhite, F.S., and C.D. Crosswhite. 1966. Insect pollinators of *Penstemon series Graciles* (Scrophulariaceae) with note on *Osmia* and other Megachilidae. American Midland Naturalist 76:450-467.

Fish and Wildlife Service. 1987. Final rule to determine *Penstemon haydenii* (blowout penstemon) to be an endangered species. Federal Resister 52:32926-32929.

Flessner, T.R. 1988. Propagation, establishment, and ecological characteristics of *Penstemon haydenii* S. Watson. Master of Science Thesis. University of Nebraska, Lincoln.

Freeman, C.C. 1981. A biosystematic study of the genus *Penstemon* (Scrophulariaceae) in the Great Plains. Thesis, Kansas State University, Manhattan.

Hicks, C.H. 1926. Nesting habits and parasites of certain bees of Boulder County, Colorado. University of Colorado Studies 15:217-252.

Hurd, P.D., Jr. 1979. Superfamily Apoidea. Pages 1741-2209. *In* K.V. Krombein, P.D. Hurd, Jr., D.R. Smith and B.D. Burks (eds.). Catalog of Hymenoptera in America north of Mexico, Vol. 2. Smithsonian Institution Press, Washington, D.C.

Lyon, D.L. 1976. A montane hummingbird territorial system in Oaxaca, Mexico. Wilson Bulletin 88:280-299.

Michener, C.D. 1955. Some biological observations on *Hoplitis pilosifrons* and Stelis lateralis (Hymenoptera, Megachilidae). Journal of the Kansas Entomological Society 28:81-87.

Parker, F.D. 1977. Nests of *Anthocopa enceliae* (Cockerell) and *Anthocopa elongata* (Michener) (Hymenoptera: Megachilidae). Pan-Pacific Entomologist 53:45-52.

Schmidt, R. 1976. Fly pollination of *Penstemon davidsonii* and *P. procerus* (Scrophulariaceae). Madrono 23:400-401.

Straw, R.M. 1955. Hybridization, homogamy, and sympatric speciation. Evolution 9:441-444.

Straw, R.M. 1956. Floral isolation in *Penstemon*. American Naturalist 90: 47-53.

Straw, R.M. 1963. Beefly pollination of *Penstemon ambiguus*. Ecology. 44:818-819.

Torchio, P.F. 1974. Mechanisms involved in the pollination of *Penstemon* visited by the masarid wasp, *Pseudomasaris vespoides* (Cresson) (Hymenoptera: Vespoidea). Pan-Pacific Entomologist 50:226-234.

PROPAGATION OF BLOWOUT PENSTEMON (*PENSTEMON HAYDENII* S. WATS.)

Theresa R. Flessner and James Stubbendieck
Department of Agronomy, University of Nebraska, Lincoln, Nebraska 68583

Abstract. Propagating and developing plants for successful transplanting will be important for the recovery of Nebraska's only endangered plant species, blowout penstemon (*Penstemon haydenii* S. Wats.). Therefore, the effect of various cultural treatments on seedling growth was examined in a greenhouse study. Young blowout penstemon seedlings, fertilized with both nitrogen and phosphorus, exhibited significantly greater weekly growth rates than seedlings fertilized with one or no nutrient. After removal of the upper part of the shoot to the third pair of true leaves, only those seedlings fertilized with both nutrients exhibited a temporary increase in weekly growth rate and more axillary shoots.

Key Words. blowout penstemon, *Penstemon haydenii*, endangered, propagation, fertilization, growth rate, Sandhills, Nebraska

INTRODUCTION

Blowout penstemon (*Penstemon haydenii* S. Wats.) is Nebraska's only officially endangered plant species (Nebraska Game and Parks Commission 1986). This perennial, multistemmed forb occurs naturally in only a few blowouts in the Nebraska Sandhills (Weedon *et al*. 1982a). Blowout penstemon is successional in nature, colonizing the blowout just after the sand has physically stabilized and declining when vegetation has become well established (Weedon *et al*. 1982b).

Blowout penstemon was once a common plant in blowouts (Pool 1914). However it was thought to be extinct from 1940 until it was rediscovered in 1968 (Stubbendieck *et al*. 1983). Since that time, extensive searching has led to the rediscovery of fewer than 4250 plants. The reasons for its decline from being a common plant in the early 1900's to its current population are unknown. With wildfire control and improved range management practices, the amount of Sandhills blowout habitat has greatly decreased (Stubbendieck *et al*. 1982b). Also, the drought of the 1930's severely reduced or influenced numerous prairie plant species (Weaver 1954), and it may also have had a negative influence on blowout penstemon (Stubbendieck 1986).

Even though blowout penstemon is protected by law (Fish and Wildlife Service 1987), its continued existence is not assured. Large fluctuations in plant numbers have been noted from one year to the next (Stubbendieck and Weedon 1984).

Blowout penstemon primarily reproduces by rhizomes, and naturally occurring seedlings are relatively rare (Stubbendieck *et al*. 1983, Stubbendieck and Weedon 1984). The supply of blowout penstemon seed is limited, and germination rates are also low (Weedon *et al*. 1982a, Stubbendieck *et al*. 1982a, 1982b; Stubbendieck *et al*. 1983, Stubbendieck and Weedon 1984). Researchers have been able to increase germination to over 90% through a combination of scarification and removal of soluble inhibitors (Stubbendieck *et al*. 1982a, Stubbendieck *et al*. 1983, Stubbendieck and Weedon 1984). Once hand-scarification techniques were found to enhance germination, efforts were made to determine proper methods of producing healthy transplants (Stubbendieck *et al*. 1982a, Stubbendieck *et al*. 1983, Stubbendieck and Weedon 1984). These researchers have shown it was best to grow seedlings in seedling tubes in the greenhouse and to transplant them outside in mid-May. Seedlings also did not tolerate heavy watering and were initially subject to damping-off, a fungal disease. Therefore, the effect of various cultural treatments on the growth of blowout penstemon seedlings was examined in a greenhouse study.

METHODS

Blowout penstemon seeds were collected in August 1986 from plants growing in Garden County, Nebraska. Seeds were separated from fruiting stalks, separated in an air column into heavy and light fractions, and stored at 3-4 C in plastic vials. Only heavy seeds were used in this study, within six months after harvest.

In January 1987, blowout penstemon seeds were soaked in a nylon bag under running tap water for 24 hours to remove soluble germination inhibitors (Stubbendieck *et al*. 1982a). Seeds were then hand-scarified by removing the seed coat at the root end of the seed using a razor blade with the help of a dissecting microscope. Hand-scarified seeds were immediately planted at a depth of 1 cm in seedling tubes (four per tube) containing pure, steamed (120 C, 120 min) river sand. Seedlings which emerged within one to two weeks received 14 hours of continuous supplemental light daily. Greenhouse temperatures ranged between 20-30 C. Seedlings were watered as needed and sprayed with a combination fungicide/insecticide weekly.

Blowout penstemon seedlings having two pairs of true leaves were given 0, 75, or 150 ppm of nitrogen and/or phosphorus weekly (Table 1). Those plants fertilized with both nitrogen and phosphorus received 10 ml of 0.26 molar or 0.52 molar $Ca(NO_3)_2$ solution and 10 ml of 0.24 or 0.48 molar NaH_2PO_4 solution. Seedlings fertilized with only one nutrient received an additional 10 ml of distilled water. Those plants not fertilized received 20 ml of distilled water only. Thus, all seedlings received an equal amount of solution (fertilizer and/or distilled water) at each fertilization to eliminate the effect of additional moisture on growth. One-half of these seedlings were pinched back to the third pair of true leaves using a razor blade, after the ninth week of the study had passed. Pinching was done to stimulate growth and number of axillary breaks, or shoots, emerging from the axils of leaves.

Table 1. Amount of phosphorus and/or nitrogen (ppm) applied per treatment.

Treatment	*Phosphorus*	*Nitrogen*
	------ppm------	
1	0	0
2	75	0
3	150	0
4	0	75
5	0	150
6	75	75
7	150	75
8	75	150
9	150	150

Each of the 18 treatments was replicated five times in a randomized complete block design. The experimental unit consisted of a group of three blowout penstemon seedlings of similar height and two pairs of true leaves.

Plant height was measured weekly from the cotyledonary node to the tip of the longest leaf. After the pinching date, the height of pinched plants was measured from the "pinching point" to the tip of the longest leaf of a shoot emerging from an axil just below this point. Height data were used to calculate growth rate, in cm per week. The average weekly growth rate per treatment was computed as the mean of 15 (five replications with three plants per replication) weekly growth rates. The number of new axillary breaks per plant was recorded weekly after the pinching date. The study was terminated after its 14th week.

Repeated measures analysis of variance was used to detect overall differences among treatments, and over weeks, for weekly growth rate. Treatment differences over weeks were evaluated using Wilks' criterion test statistic. Preplanned contrasts were used to compare individual treatment means (Steel and Torrie 1980). Univariate analysis of variance (ANOVA) on final number of new axillary breaks was performed to partition the variance into main effects and interactions between the factors (Steel and Torrie 1980).

DISCUSSION

Before pinching, average weekly growth rates of nonpinched and "to-be-pinched" young blowout penstemon seedlings were not significantly different ($p = 0.45$). Thus, these "before pinching" growth rates were pooled for further statistical analysis.

Generally, before pinching, average weekly growth rates of blowout penstemon seedlings increased to a point and then declined (Figure 1). Also, the seedlings fell into two distinct groups. The group of seedlings exhibiting higher weekly growth rates were fertilized with both nitrogen and phosphorus. These seedlings exhibited the highest average weekly growth rates in weeks 4 and 5 (Figure 1). The second group of seedlings were fertilized with one nutrient only, or no nutrient. These seedlings exhibited low, stable weekly growth rates (Figure 1).

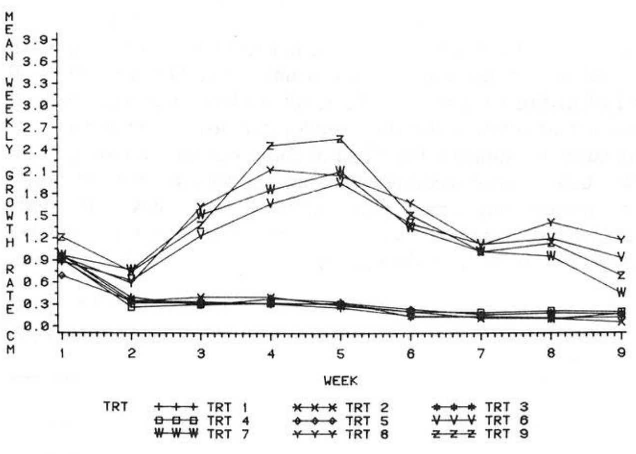


FIG. 1. Effect of treatment on average weekly growth rate of blowout penstemon seedlings before pinching. Treatments 6 through 9 involved the application of both nitrogen and phosphorus; treatments 1 through 5 involved the application of either nutrient, or no nutrient.

Thus, before pinching, nitrogen and phosphorus fertilization interacted to enhance the growth rate of blowout penstemon seedlings, although the nature of this interaction differed weekly ($p < 0.01$). Treatments involving the application of both nutrients enhanced the weekly growth rate to a greater degree than those treatments which involved the application of one or no nutrient ($p < 0.01$).

After the pinching date, average weekly growth rates of nonpinched plants were low and did not change over time (Figure 2). Also, the seedlings did not fall into two distinct groups. However, average weekly growth rates of pinched plants were similar to those exhibited before the pinching date (Figure 3). Weekly growth rates of pinched plants generally increased to a point and then declined, and the pinched seedlings fell into two distinct groups. Pinched seedlings fertilized with both nutrients exhibited the highest weekly growth rates in week 12 and the lowest in week 10, just after pinching (Figure 3). Pinched seedlings not fertilized or fertilized with one nutrient exhibited low, stable weekly growth rates (Figure 3).

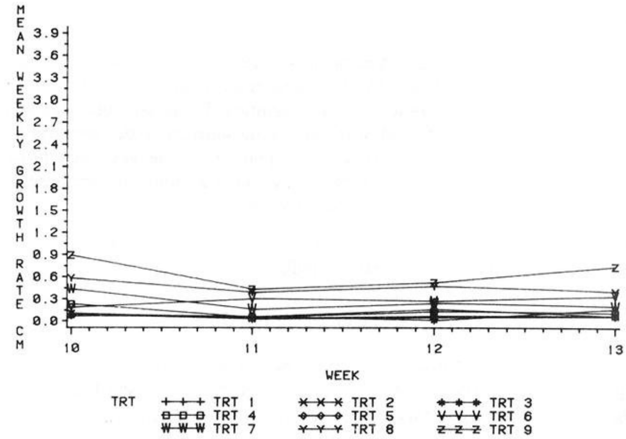


FIG. 2. Effect of treatment on average weekly growth rate of nonpinched blowout penstemon seedlings. Treatments 6 through 9 involved the application of both nitrogen and phosphorus; treatments 1 through 5 involved the application of either nutrient, or no nutrient.

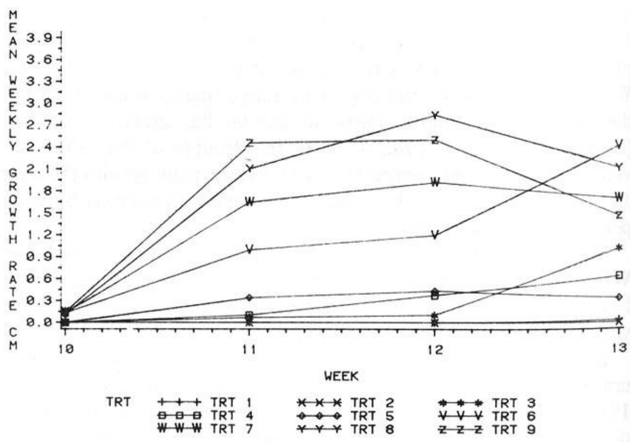


FIG. 3. Effect of treatment on average weekly growth rate of pinched blowout penstemon seedlings. Treatments 6 through 9 involved the application of both nitrogen and phosphorus; treatments 1 through 5 involved the application of either nutrient, or no nutrient.

Thus, after pinching, nitrogen and phosphorus fertilization increased weekly growth rates of pinched plants only ($p = 0.02$), although this increase was short-lived. Treatments involving the application of both nutrients enhanced weekly growth rates of pinched plants to a greater degree than those involving the application of one or no nutrient ($p < 0.01$).

Pinching had no effect on number of axillary breaks produced, over all levels of nitrogen and phosphorus fertilization ($p = 0.38$)

(Table 2). Those plants fertilized with both nutrients produced more breaks than those fertilized with one or no nutrient ($p = 0.11$). Perhaps the age of the seedling as well as its nutrient status primarily determined the total number of axillary breaks produced, rather than a pinching treatment.

Table 2. Effect of pinching and level of nitrogen and phosphorus fertilization on mean total number of axillary breaks per seedling formed after the pinching date.

Fertilization Level	*Nonpinched*	*Pinched*
	number of axillary breaks/seedling	
None	1.1	1.3
One nutrient, N or P	1.9	1.8
Both N and P	3.3	3.7
OVERALL	2.1	2.3

CONCLUSIONS

Nitrogen and phosphorus fertilization may be used to produce vigorous blowout penstemon seedlings in the greenhouse, when seedlings are grown on river sand. Pinching fertilized plants just prior to transplanting outside may be desirable to stimulate growth. These production methods could be used in the recovery and re-establishment of blowout penstemon, Nebraska's only endangered plant species.

ACKNOWLEDGEMENTS

Appreciation is expressed to the Nebraska Game and Parks Commission for financial support of the research on blowout penstemon. Journal Series Number 8412, Agricultural Research Division, University of Nebraska.

LITERATURE CITED

Fish and Wildlife Service. 1987. Final rule to determine *Penstemon haydenii* (blowout penstemon) to be an endangered species. Federal Register 52:32926-32929.

Nebraska Game and Parks Commission. 1986. Title 163, Chapter 6, Section 004: Regulations governing protection, conservation, and management of endangered and threatened wildlife species.

Pool, R. J. 1914. A study of the vegetation of the Sandhills of Nebraska. Minnesota Botanical Studies 4:188-312.

Steel, R.G.D., and J.H. Torrie. 1980. Principles and procedures of statistics. McGraw-Hill Book Company, New York.

Stubbendieck, J. 1986. Blowout penstemon: The Sandhill's rare jewel. Nebraska Quarterly 32:17.

Stubbendieck, J., and R.R. Weedon. 1984. Germination and establishment of blowout penstemon (*Penstemon haydenii*). Abstracts 37th Annual Meeting, Society for Range Management 37:199.

Stubbendieck, J., J. Traeger, and R.R. Weedon. 1983. Propagation of blowout penstemon (*Penstemon haydenii* S. Wats.). Proceedings 93rd Annual Meeting, Nebraska Academy of Sciences 93:16.

Stubbendieck, J., R.R. Weedon, J. Traeger, and D.T. Lindgren. 1982a. Blowout penstemon (*Penstemon haydenii* S. Wats.): Description, status, and culture of a rare species. American Penstemon Society Bulletin 41:4-6.

Stubbendieck, J., R.K. Engel, W. Schacht, J. Traeger, and R.R. Weedon. 1982b. Germination characteristics of *Penstemon haydenii* Wats. Proceedings 92nd Annual Meeting, Nebraska Academy of Sciences 92:18.

Weaver, J.E. 1954. North American prairie. Johnsen Publishing Company, Lincoln, Nebraska.

Weedon, R.R., D.J. Norton, and J. Stubbendieck. 1982a. Blowout penstemon (*P. haydenii* S. Wats.): A rare Sandhills endemic (Nebraska). Restoration and Management Notes 1:213.

Weedon, R.R., J. Stubbendieck, and D.J. Norton. 1982b. The botanical contributions of Claude Barr, II: *Penstemon haydenii* S. Wats. American Penstemon Society Bulletin 41:6-9.

DETERMINING FEDERALLY LISTED ENDANGERED AND THREATENED SPECIES, EMPHASIZING BLOWOUT PENSTEMON

Wallace G. Jobman
U.S. Fish and Wildlife Service, Federal Building, 203 West Second Street,
Grand Island, Nebraska 68801

Abstract. Blowout penstemon (*Penstemon haydenii* S. Wats.) was federally listed as an endangered species on 1 September 1987. This paper describes the process by which species, emphasizing blowout penstemon, are listed. The five listing factors described in Section 4 of the Endangered Species Act, candidate species, and the listing process are discussed. The blowout penstemon listing process progressed as follows: 1) petition to list; 2) designation as Category 2 Candidate Species; 3) status survey; 4) designation as Category 1 Candidate Species; 5) proposed rule to list; and 6) the final listing rule. The primary reasons for listing were the stabilization of blowout complexes and the low probabilities of seed fertilization, maturation, dispersal, and seedling establishment.

Key Words. blowout penstemon, *Penstemon haydenii*, endangered, blowouts, Sandhills, Nebraska

INTRODUCTION

The Endangered Species Act of 1973 (Act) (16 U.S.C. 1531 et seq.) is one of the most far-reaching wildlife conservation laws ever enacted by any nation. The U.S. Fish and Wildlife Service (USFWS) shares responsibility for administering the Act with the National Marine Fisheries Service. As a rough index, the National Marine Fisheries Service is responsible for all marine species, except birds, and the USFWS is responsible for all birds and terrestrial species. Approximately 500 native American species of wildlife and plants have been placed on the U.S. List of Endangered and Threatened Wildlife and Plants and now receive protection under the Act. An endangered species is one in danger of extinction throughout all or a significant portion of its range. A threatened species is one that is likely to become endangered in the foreseeable future.

To list a species the USFWS follows a legal process known as a "rulemaking procedure." This procedure is followed by federal agencies to propose and later adopt regulations that have the effect of law and apply to all persons and agencies under the jurisdiction of the United States. All notices throughout the rulemaking process are published in the Federal Register, a daily Federal Government publication (Department of the Interior 1981).

DISCUSSION

Listing Factors

A species may be determined to be an endangered or threatened species due to one or more of the five factors described in Section 4(a)(1) of the Act. The factors and their application to blowout penstemon, federally listed as an endangered species on 1 September 1987, are as follows (U.S. Fish and Wildlife Service 1987):

(1) The present or threatened destruction, modification, or curtailment of its habitat or range.

Blowout penstemon habitat has declined due to the control of unstable sand dunes through improved range management practices and wildfire control. The decrease in existing blowout complexes has made dispersal to remaining blowouts difficult.

(2) Over utilization for commercial, recreational, scientific, or educational purposes.

Blowout penstemon is sought after for scientific purposes and private gardens.

(3) Disease or predation.

Insects, small mammals, and man are predators on blowout penstemon. Kangaroo rats are known to dig out seedlings.

(4) The inadequacy of existing regulatory mechanisms.

The Nebraska Nongame and Endangered Species Conservation Act regulates possession, transportation, exportation from the State, processing, sale or offer for sale, or shipment of blowout penstemon within the State. The Act prohibits removal and reduction to possession of listed plants on Federal lands.

(5) Other natural or manmade facts affecting its continued existence.

Drought may have a detrimental affect on blowout penstemon. It is unknown why there is a large fluctuation in blowout penstemon numbers from year to year and a low rate of seed germination and seedling establishment.

Candidate Species

When biological evidence concerning a species' status is not conclusive enough to justify a listing proposal, the process may begin with publication of a "notice of review" in the Federal Register listing "candidate" species which appear to warrant consideration for addition to the List of Endangered and Threatened Wildlife and Plants (Department of the Interior 1981). Candidate species are assigned one of three categories (U.S. Fish and Wildlife Service 1985). Category 1 comprises taxa for which the USFWS currently has on file substantial information on biological vulnerability and threat(s) to support the appropriateness of proposing to list the species. Category 2 comprises taxa for which information now in possession of the USFWS indicates that proposing to list the species is possibly appropriate, but for which substantial data on biological vulnerability and threat(s) are not currently known. Category 3 comprises taxa that are no longer being considered for listing.

Listing Process

In most cases, the listing process begins with a petition, which may be submitted by anyone, to have a species placed on the list of endangered and threatened species. The Act requires that substantial information to warrant review must be included with such a petition. Within 90 days following receipt of a petition the USFWS must make a finding on whether the petition presents substantial information that the petitioned action may be warranted. In either case, the finding is published in the Federal Register. If listing may be warranted, a status review of the species is initiated. Within 12 months after a petition is received, depending on the findings of the status review, the USFWS must make a finding that listing is or is not warranted, and publish the results in the Federal Register. If it is found that listing is warranted, either a proposed rule is published or the action is determined to be precluded by other pending proposals. An action precluded by other pending proposals, means that other proposals to list or remove species from the list of endangered and threatened species are ahead of the subject proposal, and have listing priority. A warranted action, precluded by other listing actions, is treated as a resubmitted petition, and an additional year is allowed for the proposed rule to be published. Once a species is proposed in the Federal Register, the final listing rule should be published within 12 months.

Chronology of the Blowout Penstemon Listing

The chronology of events leading to the final rule to list blowout penstemon as an endangered species occurred as follows:

12/15/80 The USFWS published in the Federal Register a list of plant taxa being considered for listing as endangered or threatened. Blowout penstemon was listed as a Category 2 Candidate Species. The list was accepted as a petition from the Smithsonian Institute.

09/27/82 The status report was completed which recommended listing as endangered.

10/13/82 The 1982 amendments to the Act required all petitions pending on this date be treated as having been newly submitted on 10/13/82.

02/15/83 The USFWS published a notice in the Federal Register that the petitioned action on this species may be warranted.

10/13/83 Petition finding was made that listing was warranted but precluded by other petition listing actions.

11/28/83 The USFWS published a supplement to the 12/15/80 list of plant taxa. Blowout penstemon was listed as a Category 2 Candidate Species.

10/12/84 Petition finding was made that listing was warranted but precluded by other petition listing actions.

09/27/85 The USFWS published a list of plant taxa considered for listing. Blowout penstemon was listed as a Category 1 Candidate Species.

10/11/85 Petition finding was made that listing was warranted but precluded by other petition listing actions.

04/29/86 The proposed rule to determine blowout penstemon to be an endangered species was published in the Federal Register.

09/01/87 The final rule to determine blowout penstemon to be an endangered species was published in the Federal Register. The final rule was delayed beyond the one year deadline because the USFWS was reorganizing and overloaded with listing packages.

Recovery

The principal goal of the USFWS and National Marine Fisheries Service is to return listed species to a point at which protection under the Act is no longer required. Recovery plans provide a means to combine varied programs of federal, state, local, and private organizations into concentrated efforts, which should result in improvement in the status of the species and, hopefully, ultimately lead to delisting. A recovery plan will be developed for blowout penstemon, which will identify the actions necessary to reduce or resolve the problems or limiting factors which contribute to its endangered status.

LITERATURE CITED

Department of the Interior. 1981. Placing animals and plants on the list of endangered and threatened species. Government Printing Office.

U.S. Fish and Wildlife Service. 1985. Review of plant taxa for listing as n nendangered or threatened species. Federal Register 50(188):39526-39527.

U.S. Fish and Wildlife Service. 1987. Final rule to determine *Penstemon haydenii* (blowout penstemon) to be an endangered species. Federal Register 52(169):32926-32929.

SMALL BISON HERD UTILIZATION OF TALLGRASS PRAIRIE

Lorence Larson
Missouri Department of Natural Resources, Prairie State Park, Liberal, Missouri 64762

and

G.K. Murdock
Department of Psychology, Missouri Southern State College, Joplin, Missouri 64801

Abstract. The utilization of a tallgrass prairie remnant by a small bison (*Bison bison*) herd is described. Three bulls and six cows were introduced to a 257 ha section of Prairie State Park, Liberal, Missouri in 1985. Between 1985 and March 1988, ten calves were born; four cows and a bull were introduced to the herd in 1988. Since March 1986, the behavior of the herd has been observed three times per week, year-round. The portion of the herd using mowed fire breaks or burned or unburned portions was determined at ten-minute intervals; for 3,249 observations over 213 days. In addition, the daily location of the herd within the 257 ha was noted. The herd used fescue (*Festuca* spp.) areas during winter and native grass areas during summer. Individuals spent more time on mowed fire breaks than other areas, possibly because those areas have the most new shoots. Burned areas were also preferred, perhaps because fire reduced brambles (*Rubus* spp.) and ticks. The herd cut a few trails traversing ridges and created about 25 wallowing sites in areas adjacent to rubbing features. These had been sparsely vegetated before. At this time, there has been little noticeable effect of the herd on the prairie.

Key Words. bison, tallgrass prairie, burning, mowing, foraging, Missouri

INTRODUCTION

Since the Great Plains once supported millions of wild grazing animals, Larsen (1940) has suggested that the prairie ecosystem can only be understood by studying areas that are experiencing grazing pressure. Regrowth of burned prairie grasses is attractive to grazing livestock (Hobbs and Spowart 1984, Coppock and Detling 1986). However, few systematic studies have been conducted on how large native herbivores utilize prairie remnants (Glenn-Lewin and Landers 1978). In addition, McNaughton *et al*. (1982) cautioned against separating the plant-herbivore components and identified fire as an important interacting force. Edwards (1976) argued that knowledge of the effects of bison (*Bison bison*) on tallgrass prairie was limited by a lack of direct investigations. Data from domestic cattle, and from bison on shortgrass prairie, have led to conclusions that are misleading in a tallgrass context. Although bison are similar to cattle, cattle exhibit more selective foraging habits (Wentz 1978) and different social behavior (McHugh 1958, Shult 1972) which may affect area utilization. The data reported in this study were collected to describe the effect of burning and mowing treatments on the foraging patterns of bison on a prairie remnant at Prairie State Park and to help develop management strategies for this and other prairie remnants with bison herds.

METHODS

Study Site and Herd

Prairie State Park is a tallgrass prairie remnant near Liberal in the southwest corner of Missouri. The entire park is about 1,036 ha in size, divided by electric fences into three sections. The data reported here were collected while the bison were confined to one 257-ha section. The management plan of the park includes controlled burns at intervals of three years or less and mowing fence lines and fire breaks annually from July to November. A herd of six cows and three bulls was introduced to the park in 1985 from the U.S. Fish and Wildlife Service's Wichita Mountain herd. During 1985, 1986, and 1987, ten calves were born; during the winter of 1987-1988, four cows and one bull were brought from the Wichita Mountain herd. Ten calves were born in 1988, for a current total of 34 bison.

Data Collection

Since February 1986, the behavior of the herd has been observed three times per week, year-round. All of the data collection methods and some of the preliminary results were reported by Murdock and Larson (1986). The observations reported here were taken on 213 days between 1 April 1986 and 31 March 1988. Among the data recorded were the three management treatments (burned, mowed, or unburned and unmowed) on which individual herd members were located. These data were collected at 10-minute intervals and consisted of 3,249 samples whenever all herd members were visible. An area was classified as "burned" if it had been burned since the vernal equinox, in September.

RESULTS

Monthly Utilization

Table 1 shows a comparison of the management treatments and the difference between proportions of those utilized and available to the bison for each month of the two-year period. A highly significant difference occurred between the number of observations of the bison using the treatments compared to the number that would be expected given their availability $\chi^2 = 6154.4$, df = 46, $p < 0.005$, Chi Square Goodness of Fit Test). During July 1986 and June and July 1987, the bison used the burned treatment in greater proportion than it was available. The herd used the mowed treatment in greater proportion than its availability at all times, except during June and July 1987. The peak of mowed treatment use occurred during August in both 1986 and 1987. At that time of year, the mowed portions are usually freshly mowed. Both years, the herd used the unmowed and unburned treatment most between October and February.

Two-year Utilization

The data for the two-year period accounted for changes in the number of individuals in the herd and variation in numbers of observations taken each month. The proportion of burned, mowed, and unburned and unmowed area available at all times was also averaged over the entire two year period. The observed average proportion of each treatment used by the herd, and the estimated average proportion of each treatment that existed for its use are shown in Figure 1. If the herd did not have specific preferences for particular categories, it would be expected to use the category in proportion to its availability. Little difference occurs between the observed use of burned grass and its expected use. However, the herd used the unburned and unmowed grass much less than expected, and the mowed grass much more than expected (Figure 1).

The bison used unmowed and unburned areas most from October to February of both years of the study. During these periods, they preferred the one area with a mixture of fescue (*Festuca* spp.) and native grasses.

Table 1. Monthly differences between proportions of management treatments utilized and available to bison. Positive values indicate utilized proportion > available proportion. Negative values indicate utilized proportion < available proportion. Zero indicates that there was no proportion available.

Month and Year	*Treatment*		
	Burned	*Unburned-Unmowed*	*Mowed*
1986			
April	.144	-.342	.198
May	.129	-.176	.047
June	-.052	.012	.040
July	.344	-.393	.049
August	-.321	-.274	.595
September	.113	-.270	.157
October	0	.300	.252
November	0	-.265	.265
December	0	-.104	.134
1987			
January	0	-.020	.050
February	0	-.007	.023
March	-.320	-.060	.380
April	-.056	-.149	.205
May	.246	-.252	.006
June	.555	-.524	-.031
July	.536	-.503	-.033
August	-.235	-.320	.555
September	-.269	-.177	.446
October	-.435	.017	.418
November	0	-.221	.221
December	0	-.397	.397
1988			
January	-.143	.061	.082
February	-.218	.183	.035
March	-.062	-.065	.127

DISCUSSION

The bison definitely preferred to graze on new, fresh shoots, as also reported by Coppock and Detling (1986). This probably accounts for their preference for burned areas in early summer and mowed areas all year. After rain, fresh shoots appear in the mowed areas almost year-round. As a cool-season species, fescue is more likely than the native warm-season grasses to have fresh shoots at this time. Burned areas are relatively free of brambles (*Rubus* spp.) and dried grass from the previous year. This probably accounts for the herd's preference for these areas in early summer. But, after July of each year, the grass in the large burned areas probably grew too quickly and became too rank for the bison to select for grazing.

In May 1988, the herd was moved into another section of the park, all of which had been burned in the previous month. This allowed observation on the short-term use of the bison on a new section and to observe the old section's recovery from bison use. The impact of bison wallows has been investigated for example, by Polley and Collins (1984). They found that plants in old wallows were primarily mesic prairie species which are adapted to extremes of desiccation and moisture. In 1988, Prairie State Park was particularly dry during the month of June. The old wallows did have grass coming up consistently all over the wallow, although the grass was taller at the edges. The herd created several wallowing sites in the new section, the largest around the salt block.

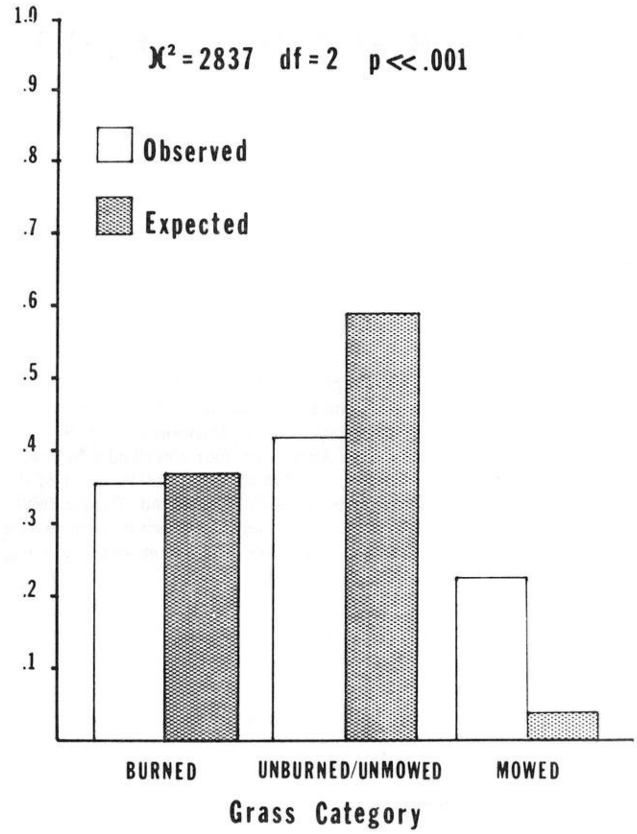


FIG. 1. Overall proportions of burned, mowed, and unburned and unmowed treatments utilized of that available to bison.

Bison did use trees and smaller saplings on which to rub but, contrary to Edwards (1976), individuals only occasionally browsed on woody vegetation. However, as noted by Edwards (1976) the bison at Prairie State Park selected certain vegetation types (i.e. grass species) over others and showed seasonal variation in their use of vegetation.

In the first two months, the herd cut several distinct trails, of which two led from a salt block or a pond. In the section to which the herd had previously been confined, trails tended to traverse the ridges.

It is clear that by controlling the location of mowed and burned areas and areas with stands of fescue mixed with native species, the location of bison herds could be controlled to meet additional management concerns. In parks where the public and bison share space, there could thus be greater control over their interactions.

ACKNOWLEDGEMENTS

The authors would like to thank John Couper for his help in collecting the data and preparing the photographs for the conference presentation. We also appreciate the Missouri Southern Foundation for financial support for part of this study. We thank two anonymous reviewers for their comments.

LITERATURE CITED

Coppock, D.L., and J.K. Detling. 1986. Alteration of bison and black-tailed prairie dog grazing interaction by prescribed burning. Journal of Wildlife Management 50:452-455.

Edwards, T. 1976. Buffalo and prairie ecology. Pages 110-112. *In* D.C. Glenn-Lewin and R.Q. Landers (eds.). Proceedings of the Fifth Midwest Prairie Conference. Iowa State University, Ames.

Glenn-Lewin, D.C. and R.Q. Landers (eds.) 1978. Editors' note. Page 112. *In* D.C. Glenn-Lewin and R.Q. Landers (eds.) Proceedings of the Fifth Midwest Prairie Conference. Iowa State University, Ames.

Hobbs, N.T., and R.A Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. Journal of Wildlife Management 48:551-560.

Larsen, F. 1940. The role of bison in maintaining the short grass plains. Ecology 21:113-121.

McHugh, T. 1958. Social behavior of the American buffalo (*Bison bison*). Zoologica 43:1-40.

McNaughton, S.J., M.B. Coughenour, and L.L. Wallace. 1982. Interactive processes in grassland ecosystems. Pages 167-193. *In* J.R. Estes, R.J. Pyrl, and J.N. Brunken (eds.). Grasses and grasslands — systematics and ecology. University of Oklahoma Press, Norman.

Murdock, G.K., and L. Larson. 1986. Behavioral study of a small bison herd at Prairie State Park, Number 07.03. *In* A. Davis and G. Standord (eds.). Proceedings of the Tenth North American Prairie Conference. Native Prairie Association of Texas, Dallas.

Polley, H.W., and S.L. Collins. 1984. Relationship of vegetation and environment in buffalo wallows. American Midland Naturalist 112:178-186.

Shult, M.J. 1972. American bison behavior patterns at Wind Cave National Park. Doctor of Philosophy Thesis, Iowa State University, Ames.

Wentz, W.A. 1978. Prevention and control of wildlife damage: Buffalo. Kansas State University Cooperative Extension Service.

SMALL MAMMALS OF A RELICT WET PRAIRIE IN OHIO

Eric D. Osborn and Carl W. Hoagstrom
Department of Biological Sciences, Ohio Northern University, Ada, Ohio 45810

Abstract. Killdeer Plains is a Wildlife Area in northwest Ohio managed primarily for waterfowl. At the turn of the century, the area was a wet prairie remnant of the prairie peninsula. Despite attempts at drainage and farming, parts of the area retain the characteristics of a wet prairie. Two spruce-pine (*Picea - Pinus*) clumps in the plains are used as winter roosts by long-eared owls (*Asio otus*). Pellets regurgitated by these owls were examined to determine the species and relative numbers of small mammals in the area. Nearly 90% of all individuals taken by the owls were meadow voles (*Microtus pennsylvanicus*). The rest were prairie deer mice (*Peromyscus maniculatus bairdi*), white-footed mice (*Peromyscus leucopus*), northern short-tailed shrews (*Blarina brevicauda*), masked shrews (*Sorex cinereus*), southern bog lemmings (*Synaptomys cooperi*), prairie voles (*Microtus ochrogaster*), and house mice (*Mus musculus*). This small mammal community may be quite similar to the one that occupied the area in its natural state.

Key Words. prairie peninsula, relict prairie, owl pellets, mammals, wildlife reserves, Ohio

INTRODUCTION

The prairie peninsula (Transeau 1935, Purdue and Stiles 1987) was an extension of tallgrass prairie that reached east into Michigan, western Pennsylvania, Kentucky, Indiana, and Ohio during the hypsithermal (xerothermal, altithermal) period following the retreat of the Wisconsin glacier. This relatively dry, warm period was followed by climatic change leading to the relatively mesic conditions which persist in the area today. With the increase in available moisture, forests replaced most of the prairie in the prairie peninsula (Semken 1984). Relicts of prairie remained in especially dry areas and under very moist conditions where the soil was waterlogged much of the year. Most of these relicts have been destroyed by human activity, but some occurred on such rugged terrain or were so difficult to drain that they were left in their natural state. Others were farmed for a time, but eventually abandoned. Killdeer Plains Wildlife Area in southern Wyandot County, Ohio, is one of the latter.

A wet prairie at the turn of the century, the area within which the Killdeer Plains Wildlife Area is presently located was drained and farmed in the first half of the twentieth century. Farming was never very successful, apparently because of wet, difficult to work soils. In 1952, the Ohio Department of Natural Resources purchased a portion of the area and began managing it as a wildlife area. Emphasis has been on management for waterfowl, but some restoration of prairie plants and plant communities has also been conducted (Cusick and Troutman 1978). The effect of such management on nontarget community components (species and groups of species which were not a part of the management plant) is of interest in light of the current concern for the maintenance of biological diversity (Miller and Ford 1988). The presence of long-eared owls (*Asio otus* L.), which use two pine-spruce (*Picea - Pinus*) groves in the wildlife area for a communal winter roost, provided a means to determine how effective the restoration of Killdeer has been in preserving, or restoring, the small mammal community of the original wet prairie.

METHODS

Killdeer Plains Wildlife Area

The wildlife area currently consists of about 3,500 ha (of an original 12,000 ha) containing a number of constructed ponds and marshes as well as several small woodlots all surrounded by fields. The woods contained cottonwood (*Populus deltoides* Bartr.), American elm (*Ulmus americana* L.), slippery elm (*Ulmus rubra* Muhl.), white ash (*Fraxinus americana* L.), silver maple (*Acer saccharinum* L.), sugar maple (*Acer saccharum* Marsh.), shagbark hickory (*Carya ovata* K. Koch), bur oak (*Quercus macrocarpa* Michx.), pin oak (*Quercus palustris Muench.), red oak (Quercus rubra* L.), white oak (*Quercus alba* L.), and other trees common in northwest Ohio woodlots. The ponds are bordered by cattails (*Typha latifolia* L.), bulrushes (*Scirpus* spp. L.), and other plants typical of northwest Ohio pond edges. Shrubs such as roses (*Rosa multiflora* Thunb. and *Rosa carolina* L.), willows (*Salix* spp. L.), red-osier dogwood (*Cornus stolonifera* Michx.), and red-panicle dogwood (*Cornus racemosa* Lam.) occur at woods and pond edges and in the fields. The fields are primarily covered with herbaceous plants. Some are planted to corn (*Zea mays* L.) as food for the waterfowl. Others are planted to bluegrass (*Poa* spp. L.) and other forage grasses, but many contain prairie species.

Some areas have extensive cover of prairie grasses such as big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Andropogon scoparius* Michx.), indiangrass [*Sorghastrum nutans* (L.) Nash], slough grass or prairie cord grass (*Spartina pectinata* Link), and forbs such as prairie dock (*Silphium terebinthinaceum* Jacq.), dense blazing-star (*Liatris spicata* Willd.), gray-headed coneflower (*Ratibida pinnata* Barnh.), Sullivant's milkweed (*Asclepias sullivantii* Engel.), stiff goldenrod (*Solidago rigida* L.), and others. A distinct prairie component occurs throughout the area (Cusick and Troutman 1978).

The entire prairie area is thought to be an ancient lake bed. It is level throughout which slows runoff. The clay soils retard drainage. As a result, in many years much of the original prairie remained under water or was water-logged throughout the spring and dried only in late summer. Prairie cord grass stands were extensive in the wetter areas. Big bluestem, indiangrass, and other prairie plants grew in the areas with better drainage. Trees occurred primarily as individuals rather than in woodlots as they do today, though the area was surrounded by forests (Dobbins 1937). Shrubs grew in other wet prairies in Ohio, and Killdeer may have had clusters of shrubs as well (Sears 1926, Gordon 1969).

Two planted groves of white pine (*Pinus strobus* L.) and Norway spruce (*Picea abies* Karst.) house the roosting owls in winter. Long-eared owls roosted in both groves in all three winters of the study. They were the most important pellet producers. Short-eared owls (*Asio flammeus* Pontoppidan), saw-whet owls (*Aegolius acadicus* Gmelin) and great-horned owls (*Bubo virginianus* Gmelin) were also seen in the area, but the birds flushed from and seen in the groves were invariably long-eared owls.

Procedures

The use of owl pellets (indigestible, regurgitated remains of owl prey) allowed the collection of information with minimal impact on the community. In many studies, owls have been shown to take the same species taken by traps (Getz 1961b, Kotler 1985, Longland and Jenkins 1987). However, the relative numbers of individuals taken by the owls reflects the habitats in which the owls hunt most intensively (Getz 1961b), the ease of capture of the prey (Kotler 1985), and other variables (Longland and Jenkins 1987). Therefore, interpretation of relative population sizes must be done with caution.

Collection and analysis of pellets.

Pellets were collected in early January and early March of 1986 through 1988. A collection was also made in May, 1988. The pellets were spread in cardboard boxes to dry and then stored in cabinets until they could be examined. Each pellet was dissected. The hair was discarded, and the bones were stored in plastic vials identified to site, date of collection, and pellet number. Skull and jaw bones were identified to species primarily on the basis of tooth characteristics (Gottschang 1981, Hall 1981, Zakrzewski 1985). Not all pellets of the 1988 collections could be dissected and analyzed in the time available. Sixty pellets from each site were dissected for the January collection, and ten from each site for the March and May collections. These samples indicated that the pattern of 1986 and 1987 was continued in 1988.

Most skulls and jaws were easily identified to species, but two problems occurred. The differences between the skulls of the prairie deer mouse (*Peromyscus maniculatus bairdi* Wagner) and the white-footed mouse (*Peromyscus leucopus* Rafinesque) are subtle. The shape of the anterior palatine foramina and the least interorbital distance (Gottschang 1981) were used to differentiate the two. If only lower jaws were present, or if the two criteria suggested different species, the specimen was assigned to *Peromyscus* without designating the species.

The other problem involved only one species and one specimen in the collection. Prairie voles (*Microtus ochrogaster* Wagner) and pine voles or woodland voles (*Microtus pinetorum* LeConte) are difficult to distinguish using only skull characteristics (Kurten and Anderson 1980, Zakrzewski 1985). Comparisons with known prairie and pine vole skulls, the habitat, and the Ohio distribution of the two species (Gottschang 1981) all indicated that the specimen was a prairie vole, and it was recorded as such.

For each species, site and date of collection, the number of skulls, the number of right jaws, and the number of left jaws were counted. The largest of these numbers was used as the minimum number of individuals of that species in the pellet collection. Absolute numbers were not comparable, so a percentage of individuals captured was calculated for each species at each site for the January and March 1986 and 1987 collections and the January 1988 collection. To test for differences between sites, season, and years, the confidence limits of the percentages were obtained from a table (Sokal and Rohlf 1987). These confidence limits were compared (site to site, season to season, and year to year). No differences approaching significance were found in any comparison. Therefore, all the data from all sites and collection times were combined for analysis.

Determination of community composition before drainage.

The characteristic habitats and recent distributions of the species of small mammals taken by the owls were used to determine whether each species was a probable member of the wet prairie community at the turn of the century. The characteristic habitats and recent distributions of small mammal species not taken by the owls were also studied to determine whether any other small mammals were probable members of that community. Brayton (1882), Baker (1968), Hooper (1968), Long (1974), Diersing (1980), Kurten and Anderson (1980), Gottschang (1981), Hall (1981), Jones *et al.* (1983), Zakrzewski (1985), Kirkland *et al.* (1987), and Jones and Birney (1988) were used to determine habitat and recent distribution for all species. Any species which is commonly found in grasslands and fields was considered to have the appropriate habitat affinity to be a potential nineteenth century community member. Evidence that the species occurred in or around northwest Ohio at or before the turn of the century was the biogeographic requirement for potential membership. Moles, strictly diurnal mammals, and those that hibernate or migrate would not normally be taken by the owls in winter and were eliminated from the comparison.

RESULTS

All species taken, except the house mouse (*Mus musculus* L.), have appropriate habitat requirements and biogeographic histories to be expected to have been present in the wet prairie at the end of the nineteenth century (Table 1). Using the same criteria for habitat affinities and recent distribution, only one small mammal species, the least shrew (*Cryptotis parva* Say), was not found in pellets, although it was determined to be a potential member of the native community at Killdeer. In addition, the proportions in which the seven new world species were found in the owl pellets was consistent with a probable organization of the community.

Table 1. Data collected from the owl pellets, 738 individuals were collected from 651 pellets.

Species[1]	*Number*[2]	Percent[3]	*Origin*[4]	*Habitat*[5]	*Length*[6]
					--------- mm ---------
Meadow vole	663	89.8	Boreal	Grass	111
Prairie vole	1	0.1	Prairie	Grass	110
Southern bog lemming	3	0.4	Eastern	Grass	99
White-footed mouse	6	0.8	Eastern	Brush	90
Prairie deer mouse	25	3.4	Prairie	Fields	83
Peromyscus spp.	22	3.0			
House mouse	2	0.3	Europe	Buildings	82
Short-tailed shrew	14	1.9	Eastern	Varied	90
Masked shrew	2	0.3	Boreal	Varied	55

[1]*Microtus pennsylvanicus, Microtus ochrogaster, Synaptomys cooperi, Peromyscus leucopus, Peromyscus maniculatus bairdi, Peromyscus* species not determined, *Mus musculus, Blarina brevicauda,* and *Sorex cinereus*, respectively.

[2]The total number of individuals of the species in the pellet collection.

[3]The percentage of the total number of individuals in the collection, which are members of the species.

[4]Geographic center of the species current distribution, from Jones and Birney (1988). These authors do not break deer mice down to subspecies. Hooper (1968) and Gottschang (1981) were used for this subspecies. Boreal = boreal forest, eastern = eastern deciduous forest.

[5]Literature sources used for habitat information are listed in the text.

[6]Head and body length is given instead of total length to eliminate the misleading effect of variable tail length. Measurements are averages of 25 to 50 Ohio adults (Gottschang 1981).

DISCUSSION

The results suggest that the modern small mammal community at Killdeer is quite similar to that expected in the wet prairie community of the late nineteenth and early twentieth century. Several aspects of this interpretation need to be explored further.

Owls as Sampling Devices

Optimal foraging theory (Colinvaux 1986) would suggest that the owls should maximize their nutritional intake per energetic cost. This may best be done if the owls take the largest and/or most easily captured prey. In addition, several studies have reported that long-eared and other owls are selective predators (Kotler 1985, Longland and Jenkins 1987). Therefore, both theoretical consideration and experimental evidence suggest that the owls do not collect random samples of their prey. The meadow vole (*Microtus pennsylvanicus* Ord) is often the most common small mammal in grassy areas in the eastern United States. It is also the largest of the animals taken by the owls (Table 1). In the situation at Killdeer then, use of the owls for sampling should overestimate the meadow vole population, and underestimate populations of other community members.

On the other hand, the owls must act as opportunists from time to time and, as such, may well take every species in the community. In most studies involving both trapping and owl pellet analysis, the owls take the same species as do the traps, though relative numbers usually differ between the two sampling techniques (Getz 1961b, Kotler 1985, Longland and Jenkins 1987). Therefore, an extensive collection of pellets should contain some members of all the small mammal species in the owls' foraging area.

The data suggest that the meadow vole was the most abundant small mammal in the area, though it is probably not as abundant with respect to the other species as suggested by that data. The data may be more accurate with respect to the relative abundance of the other species, assuming that they were taken more or less randomly as the owls searched for meadow voles. The species of rodents and shrews taken may represent all the species present that are active at night and in the winter, although the sample analyzed is not extensive enough to assure that no important component of the small mammal community has been missed.

Biogeography

With the exception of the house mouse, the Killdeer Plains small mammal community was derived from eastern deciduous forest, boreal forest, and prairie (Table 1). However, all species present in the owl pellets are, and have been for hundreds of years, established in appropriate habitats in the main body of the prairie (Hooper 1968, Kurten and Anderson 1980, Hall 1981, Zakrzewski 1985). Biogeographically, this is one type of community that should be in a remnant of the prairie peninsula. All biomes that have occupied the area contributed species to the community, but these species were well adapted for life in prairie habitats.

There are alternative theoretical possibilities for the membership of the community. One is that a larger number of species originated on the prairie. However, many of the small mammals which originated on the plains and prairies failed to move far into the prairie peninsula and were, thus, unavailable to occupy the wet prairie. Harvest mice (*Reithrodontomys* spp. Giglioli), pocket mice (*Perognathus* spp. Weid-Neuwied), and kangaroo rats (*Dipodomys* spp. Gray) are examples (Kurten and Anderson 1980, Semken 1984).

Another hypothetical community contains a larger number of northern species. Several of these passed through the area as the glacier retreated, and so had biogeographic access to the area. Most of them, however, required boreal habitats and continued north with these habitats. None of the northern species absent from Killdeer today has habitat requirements that suggest that it could have been part of the prairie peninsula or the nineteenth century wet prairie community.

Habitats and Community Organization

The habitats commonly occupied by the various species taken by the owls are also consistent with their ability to have lived in the original prairie. In addition, the relative numbers of individuals of each species is consistent with a probable community organization.

All three species of microtine rodent, the southern bog lemming (*Synaptomys cooperi* Baird) and the voles, in the pellet collection are found most commonly in grassy areas. Each can live in various types of grassland. But, where two occur together, each becomes associated with a particular aspect of the habitat. In association with the meadow vole, the bog lemming usually occupies the wetter habitat (Getz 1961a, Gottschang 1981). In contrast, when the meadow vole and prairie vole occur together, the prairie vole occupies the dryer and more sparsely vegetated grasslands (Getz 1985, Klatt and Getz 1987).

Currently at Killdeer, the meadow vole habitat is apparently abundant while that which the other two can occupy in the presence of the meadow vole is much more restricted. This may have been the case in the original prairie as well. The habitat requirements of the prairie vole suggest that it would be uncommon in a wet prairie, especially in the presence of the meadow vole. The bog lemming is seldom common and widespread in any community (Gottschang 1981). Especially in the presence of meadow voles, it would also be expected to be uncommon. The microtines in Killdeer today have a relationship similar to that expected in the natural community.

The overwhelming numerical dominance of the meadow vole may also have been a characteristic of the nineteenth century wet prairie. Microtines often dominate the grassland communities in which they occur, even to the extent shown in the owl pellets (Rose and Birney 1985). Meadow voles are commonly the dominant species in moist areas of heavy grass cover.

The house mouse was probably not a permanent member of the community at the turn of the century. the human habitation with which it is usually associated (Gottschang 1981) was not as abundant around the area as it is today. That is sufficient reason to assume the absence of the house mouse, except in years of spread from exceptionally dense commensal populations. The increase of the human population in the Killdeer area assures its presence today. However, it is probably restricted to the vicinity of buildings in most years and so may not be a central part of the modern community either.

The white-footed mouse lives in woods, at woods edges and in shrub covered areas (Baker 1968). It may have been a peripheral member of the community at the turn of the century, since the prairie was surrounded by forest but contained only scattered trees (Dobbins 1937). However, many Ohio wet prairies contained considerable shrub cover (Sears 1926, Gordon 1969) and the white-footed mouse is often found among scattered trees and shrubs. Therefore, it is also possible that this species was an integral part of the community.

The deer mouse lives in many habitats, but the prairie deer mouse (the subspecies at Killdeer) is a grassland and open field form (Baker 1968, Gottschang 1981). The various fields and grasslands in the original wet prairie almost certainly supported more deer mice than white-footed mice. The relative numbers of these mice taken by the owls suggests that this numerical relationship has also been preserved.

The northern short-tailed shrew (*Blarina brevicauda* Say) and the masked shrew (*Sorex cinereus* Kerr) have imprecise habitat requirements. They are found in woods, fields, and grasslands but are often associated with moist situations (Gottschang 1981, Jones and Birney 1988). In contrast, the least shrew apparently occurs more often in relatively dry fields (Gottschang 1981), Jones and Birney 1988). Jones and Birney (1988) also said that the least shrew is seldom taken with any species of *Sorex*. These observations suggest that habitat affinities or some form of interspecific interaction may be responsible for the absence of the least shrew from the modern community. In any case, the habitat tendencies of the three shrews is consistent with the conclusion that the wet prairie community contained the same two shrews that occur in the modern community at Killdeer.

The relative number of shrews taken by the owls may simply be another example of optimal foraging and not a reflection of relative numbers in the community. The larger, presumably containing more total nutrition, shrew was taken more often than the smaller.

Overall, these considerations suggest that the modern small mammal community at Killdeer is similar to the wet prairie community on the site at the turn of the century. Management for waterfowl has either restored or preserved a small mammal community similar to the one that occupied the site before disturbance. Thus, restoration of the area for one purpose was effective in conserving a nontarget component of the ecosystem.

The extent to which the above conclusion is relevant to other reserves and other community components, is not clear. Small reserves, or management areas such as Killdeer, are only effective for conservation of small species, and small mammals are probably among the easiest species to protect. However, the suggestion that entire, nontarget subcommunities may be conserved in the many wildlife areas and reserves in the nation is encouraging.

Finally, the importance of any community component to other, more important or more charismatic, community members must not be underestimated. Certainly, the importance of the small mammals to the owls wintering at Killdeer cannot be overestimated. In addition, the members of the small mammal community play roles in seed dispersal, spore dispersal for mycorrhizal fungi (Maser *et al.* 1978), predation on insects, predation on seeds, and grazing (Rose and Birney 1985). As a result of these activities, the intact small mammal community may be of great importance to the maintenance of the structure of the remnant prairie community itself, and, thus, to the maintenance of local and global biological diversity.

ACKNOWLEDGEMENTS

We thank the reviewers and editors for helpful comments on the manuscript; Nelson Moore for bringing the eastern owl roost to our attention; and Bonnie Berger, Chris and Sherwin Hoagstrom, and Daryl Staton for helping with the dissection of the owl pellets.

LITERATURE CITED

Baker, R.H. 1968. Habitats and distribution. Pages 98-126. *In* J.A. King (ed.). Biology of *Peromyscus* (Rodentia). American Society of Mammalogists Special Publication Number 2.

Brayton, A.M. 1882. Report on the mammals of Ohio. Report of the Geological Survey of Ohio 4:1-185.

Colinvaux, P. 1986. Ecology. John Wiley and Sons, New York.

Cusick, A.W., and K.R. Troutman. 1978. The prairie survey project: A summary of data to date. Ohio Biological Survey Information Circular Number 10.

Diersing, V.E. 1980. Systematics and evolution of the pygmy shrews (subgenus Microsorex) of North America. Journal of Mammalogy 61:76-101.

Dobbins, R.A. 1937. Vegetation of the northern "Virginia Military Lands" of Ohio. Doctor of Philosophy Dissertation, Ohio State University, Columbus.

Getz, L.L. 1961a. Factors influencing the local distribution of *Microtus* and *Synaptomys* in southern Michigan. Ecology 42:110-119.

Getz, L.L. 1961b. Hunting areas of the long-eared owl. The Wilson Bulletin 73:79-82.

Getz, L.L. 1985. Habitats. Pages 286-309. *In* R.H. Tamarin (ed.). Biology of New World *Microtus*. American Society of Mammalogists Special Publication Number 8.

Gordon, R.B. 1969. The natural vegetation of Ohio in pioneer days. Bulletin of the Ohio Biological Survey, New Series 3:1-113.

Gottschang, J.L. 1981. A guide to the mammals of Ohio. Ohio State University Press, Columbus.

Hall, E.R. 1981. The mammals of North America. John Wiley and Sons, New York.

Hooper, E.T. 1968. Classification. Pages 27-74. *In* J.A. King (ed.). Biology of *Peromyscus* (Rodentia). American Society of Mammalogists Special Publication Number 2.

Jones, J.K., Jr., D.M. Armstrong, R.S. Hoffman, and C. Jones. 1983. Mammals of the Northern Great Plains. University of Nebraska Press, Lincoln.

Jones, J.K., Jr., and E.C. Birney. 1988. Handbook of mammals of the North-Central States. University of Minnesota Press, Minneapolis.

Kirkland, G.L., Jr., A.M. Wilkinson, J.V. Planz, and J.E. Maldonado. 1987. *Sorex* (*Microsorex*) *hoyi* in Pennsylvania. Journal of Mammalogy 68:384-387.

Klatt, B.J., and L.L. Getz. 1987. Vegetation characteristics of *Microtus ochrogaster* and *M. pennsylvanicus* habitats in east-central Illinois. Journal of Mammalogy 68:569-577.

Kotler, B.P. 1985. Owl predation on desert rodents which differ in morphology and behavior. Journal of Mammalogy 66:824-828.

Kurten, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York.

Long, C.A. 1974. *Microsorex hoyi* and *Microsorex thompsoni*. American Society of Mammalogists. Mammalian Species 33:1-4.

Longland, W.S., and S.H. Jenkins. 1987. Sex and age affect vulnerability of desert rodents to owl predation. Journal of Mammalogy 68:746-754.

Maser, C., J.M. Trappe, and R.A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799-809.

Miller, C.I., and L.D. Ford. 1988. Managing for nature conservation: from genes to ecosystems. BioScience 38:456-457.

Purdue, J.R., and B. W. Stiles. 1987. Changes in the mammalian fauna of Illinois and Missouri during the late Pleistocene and Holocene. Pages 144-174. *In* R.W. Graham, H.A. Semken, Jr., and M.A. Graham (eds.). Late Quaternary Mammalian Biogeography and Environments of the Great Plains and Prairies. Illinois State Museum Scientific Papers, Volume 22.

Rose, R.K., and E.C. Birney. 1985. Community ecology. Pages 310-339. *In* R.H. Tamarin (ed.). Biology of New World *Microtus*. American Society of Mammalogists Special Publication Number 8.

Sears, P.B. 1926. The natural vegetation of Ohio, II. The prairies. Ohio Journal of Science 26:128-146.

Semken, H.A. 1984. Holocene Mammalian biogeography and climatic changes in the eastern and central United States. Pages 182-207. *In* H.E. Wright, Jr. (ed.). Late-Quaternary Environments of the United States: The Holocene. University of Minnesota Press, Minneapolis.

Sokal, R.R., and F.J. Rohlf. 1987. Introduction to biostatistics. W.H. Freeman and Company, New York.

Transeau, E.N. 1935. The prairie peninsula. Ecology 16:423-437.

Zakrzewski, R.J. 1985. The fossil record. Pages 1-51. *In* R.H. Tamarin (ed.). Biology of New World *Microtus*. American Society of Mammalogists Special Publication Number 8.

SEASONAL ACTIVITY OF SNAKES ON A SAND PRAIRIE

Dwight R. Platt
Bethel College, North Newton, Kansas 67117

Abstract. Snakes were caught in drift fence traps throughout the season of activity on a 32 ha sand prairie in Harvey County, Kansas, from 1966 through 1974. In these nine seasons, 128,281 trap station days yielded 6,412 captures of the six most common species of snakes: *Pituophis melanoleucus sayi, Coluber constrictor flaviventris, Thamnophis sirtalis parietalis, Thamnophis radix haydeni, Heterodon nasicus,* and *Heterodon platirhinos*. Seasonal activity patterns, although variable from year to year, had a bimodal pattern with a period of low activity in late July or late August. Increases in snake activity resulted from increases in population size due to recruitment of new snakes or from increases in activity of individual snakes. Activity patterns were related to food abundance and reproductive activity.

Key Words. snakes, seasonal activity, sand prairie, Kansas

INTRODUCTION

Snakes are important predators in many prairie communities. They differ from most mammalian and avian predators in having lower and more flexible metabolic demands. Snakes are most active at optimum times for foraging and reproduction but may remain inactive for parts of the summer. Seasonal activity patterns have been considered important characteristics of the ecological niches of snakes and have been studied for more than 60 years (Brimley 1925, Conant 1938, Klimstra 1958). However, most studies have not differentiated variations in snake activity due to changes in population size from those due to changes in activity of individual snakes.

Gibbons and Semlitsch (1987), in a review of more recent studies, reported two distinct patterns in seasonal activity of temperate zone snakes: unimodal patterns with peak activity sometime between late spring and late summer and bimodal patterns with peaks of activity in spring and in fall. However, they also pointed out that determining general patterns is difficult, because the literature contains few geographic comparisons of the same species or local comparisons of a number of species in the same habitat. The present report describes a nine-year study of the seasonal activity of six species of snakes on a sand prairie in south central Kansas. Data from the nine years are combined to detect general patterns in seasonal activity.

METHODS

The study area, Sand Prairie Natural History Reservation, is a 32 ha (80 acre) grassland on wind-blown sand in the Hutchinson Dune Tracts of western Harvey County, Kansas. It is managed as a natural area by the Biology Department at Bethel College. The upland grass communities are dominated by little bluestem (*Andropogon scoparius* Michx.). The unflooded lowlands have dense tallgrass communities dominated by switchgrass (*Panicum virgatum* L.), sand bluestem (*Andropogon hallii* Hack.), indiangrass [*Sorghastrum nutans* (L.) Nash], and prairie cordgrass (*Spartina pectinata* Link). The depressions between dunes are flooded in wet seasons, forming temporary to semi-permanent ponds and marshes.

From 36 to 120 stations with live traps were operated continuously from late April or early May to late October or early November from 1966 through 1974, except that trapping was partially or completely stopped for a few weeks in August in some years. A trap station consisted of a low metal drift fence with a funnel trap fitted on each end, modified from those described by Fitch (1951). A total of 128,281 trap station days was completed in the nine years of study. A trap station day is the use of one trap station for 24 hours.

Many earlier studies did not standardize or quantify capture effort. Since our traps did not attract snakes but merely intercepted moving snakes, capture rates were calculated as a quantitative index of snake activity. Few snakes were caught before the first of May or after the end of October. Each month from May to October was divided into approximately 15-day trapping periods. For each trapping period capture rates were calculated as the number of captures per 1,000 trap station days (TSD), using the total captures and trapping effort in that trapping period in all nine years. Proportions of sexes or age groups in the sample indicated which groups were more active.

Gibbons and Semlitsch (1982) discussed the use of drift fences with pitfall traps to quantitatively sample populations, and many of their comments apply to the trapping methods used in this study. Not all of the population was equally susceptible to capture, since young snakes of some species escape through the 6 mm mesh of the traps. The data collected pertain to the trappable portion of the population.

RESULTS AND DISCUSSION

A total of 6,412 captures was made of the six species of snakes included in this report: bullsnake (*Pituophis melanoleucus sayi*), 683 captures; eastern yellowbelly racer (*Coluber constrictor flaviventris*), 942 captures; red-sided garter snake (*Thamnophis sirtalis parietalis*), 2,179 captures; western plains garter snake (*Thamnophis radix haydeni*), 2,147 captures; western hognose snake (*Heterodon nasicus*), 373 captures; and eastern hognose snake (*Heterodon platirhinos*), 88 captures.

Bullsnake

Total capture rates of bullsnakes had a bimodal seasonal pattern with a moderate peak in June, a low value in late July, and a high peak in late September (Figure 1). However, there was yearly variation in the pattern. Peak summer activity was in June in six of nine years, but in early May, late May, and late July in the other three. Activity was lowest in late July in four years, but in early July or in August in five years. The fall peak in activity was more consistent, being in late September in seven of nine years.

"Adult size" (Figure 1) includes snakes identified as one year old or older on the basis of size. Bullsnakes hatch in mid-August at approximately 350 mm snout-vent length (SVL) and grow to more than 500 mm SVL by late October (Platt 1984). From late August to late October, adult snakes were identified as those exceeding the hatchling size range. From May to early August adults included all that were greater than 850 mm SVL, the average length at one year (Platt 1984). These larger snakes were more constant in activity through spring and summer, showing some decline in activity in late July (Figure 1). The increase in capture rates of adult size snakes from late July through August was due to the recruitment of first-year snakes into the adult size category. After mid-August the adult size category represented the population included in total captures (adult plus first-year) earlier in the summer. Their activity gradually declined through the fall.

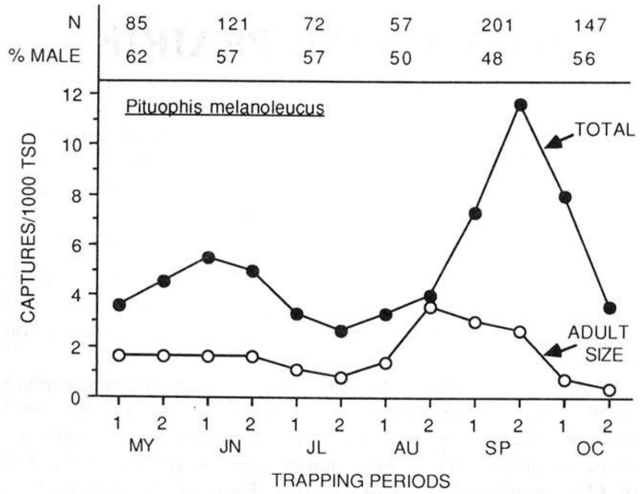


FIG. 1. Capture rates of bullsnakes in half-month trapping periods from May to October averaged over nine years (1966 to 1974). ''N'' is sample size or total captures in month in nine years. ''Adult size'' includes snakes one year or older based on size. ''TSD'' is trap station days.

The fall peak in total captures resulted from the recruitment of hatchlings, which increased the size of the population. These hatchlings were active later in the fall than the older snakes. The peak in June resulted from the activity of first-year snakes that became active later in spring than larger snakes (Figure 1).

The percentages of males in early spring samples of bullsnakes were higher than in later samples (Figure 1), but the difference was not significant (comparison of May sample to July-August sample: Chi-square = 2.45, P = 0.1-0.2). Gibbons and Semlitsch (1987) reported that male snakes are more active in spring when they search for females for mating. However, our research showed little difference between adult and first-year bullsnakes (May: adults 59% males and first-year 65% males; June: adults 62% males and first-year 55% males). Adult females were more active than males in midsummer (July: 38% males), while the percentage of males was higher in the first-year sample (July: 66% males). There was no evidence of increased male activity in the fall. Fitch (1970) reported only spring mating for this snake.

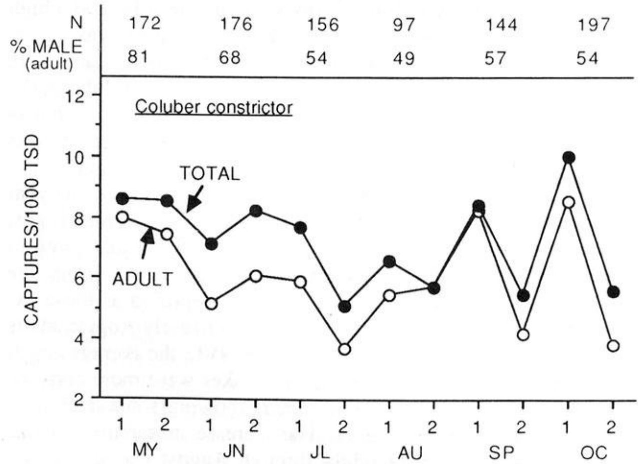


FIG. 2. Capture rates of eastern yellowbelly racers in half-month trapping periods from May to October averaged over nine years (1966 to 1974). ''N'' is sample size or total captures in month in nine years. ''Adult'' includes snakes with adult color pattern. ''TSD'' is trap station days.

Eastern Yellowbelly Racer

Total capture rates of racers had a bimodal seasonal pattern with high numbers in May decreasing to low numbers in late July and August and with high but irregular numbers in the fall (Figure 2). However, in three years capture rates remained high in July and August.

The adult snakes were identified by color pattern which changes gradually from the blotched juvenile to a uniform bluish-gray dorsum at the end of the first year. Young are hatched in late August at approximately 200 mm SVL but are not normally caught in traps until they are more than 300 mm SVL. The total population was often larger than the trappable population that was being sampled.

Few hatchlings were caught in fall, so the high capture rates resulted from high activity of older snakes (Figure 2). Fall is an optimum foraging time because of the abundance of large grasshoppers and crickets, common food items for racers. The decrease in activity in late September occurred in five of nine years, but its meaning is not obvious.

The high capture rate in May resulted in part from high activity of males searching for females (sex proportions in May sample compared to July-August: Chi-square = 56.63, P < 0.001). There was no increase in percentage of males in fall samples (Figure 2). Fitch (1970) reported only spring mating for this species.

Garter Snakes

Total capture rates of both species of garter snakes had large seasonal variation (high activity three to seven times low activity) in a bimodal pattern, with peaks in early July and late September or early October and low captures in late August (Figures 3 and 4). However, the plains garter snake had higher activity in early July and less activity in fall.

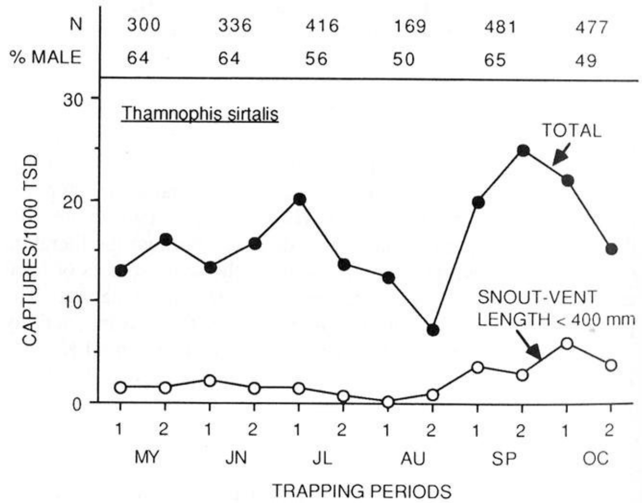


FIG. 3. Capture rates of red-sided garter snakes in half-month trapping periods from May to October averaged over nine years (1966 to 1974). ''N'' is sample size or total captures in month in nine years. ''TSD'' is trap station days.

Young garter snakes are 140-179 mm SVL at birth, but few are caught in traps until they are 310-350 mm SVL. Snakes less than 400 mm SVL have recently entered the trappable population. In the red-sided garter snake, some grew to that size by early September, and the high capture rates for this size group were in the fall (Figure 3). Plains garter snakes may be born later and grow more slowly, as young snakes were not caught in substantial numbers until October and were still caught at high rates the following June (Figure 4). Some small snakes were caught throughout the trapping season in both species. Because of variable growth, particularly in different years, first-year snakes cannot be identified in a multi-year sample.

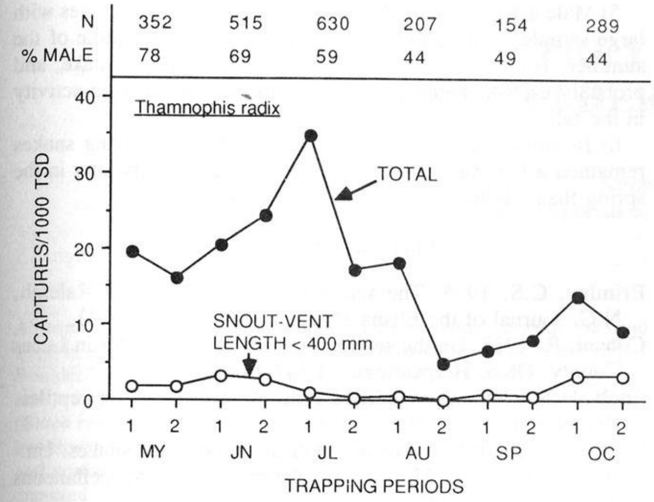


FIG. 4. Capture rates of western plains garter snakes in half-month trapping periods from May to October averaged over nine years (1966 to 1974). "N" is sample size or total captures in month in nine years. "TSD" is trap station days.

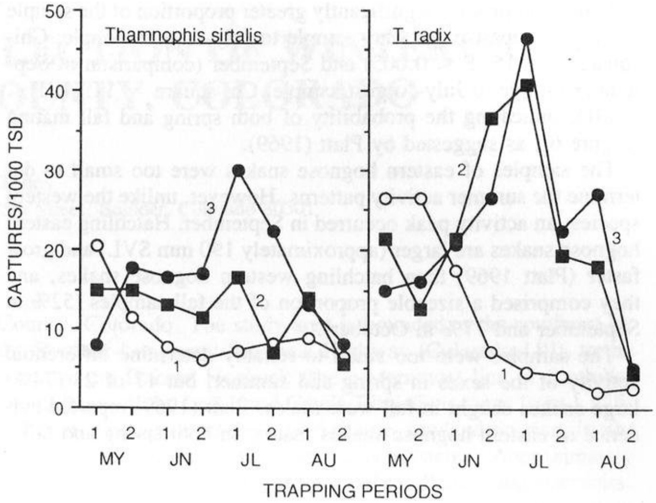


FIG. 5. Capture rates of red-sided garter snakes and western plains garter snakes in three summers (1966, 1967, 1972) with low frog populations (1), in three summers (1968, 1970, 1974) with moderate frog populations (2), and in three summers (1969, 1971, 1973) with very high frog populations (3). "TSD" is trap station days.

The higher percentages of males in samples of red-sided garter snakes from May (comparison of May sample to July-August sample: Chi-square = 11.45, $P < 0.001$), June, and September (comparison of September sample to July-August sample: Chi-square = 22.57, $P < 0.001$) indicate increased male activity and probably both spring and fall mating (Figure 3). Fitch (1970) reported that this species mated in spring and fall. The percentage of male plains garter snakes is significantly higher in May (comparison of May sample to July-August sample: Chi-square = 74.11, $P < 0.001$) but not in fall. Although it has been suggested that these snakes may mate in fall (Fitch, 1970), there is no evidence of fall mating in this study.

The increased activity of red-sided garter snakes in fall resulted from the recruitment of young snakes, causing a larger trappable population, and from increased activity of larger snakes, particularly males. Plains garter snakes showed less activity in fall in this study, because most young snakes were not trappable, and male activity was not increased.

In both garter snakes, the capture rates in early July were variable from year to year (Figure 5). In 1969, 1971, and 1973, precipitation was high, ponds and marshes were flooded for much of the summer, and leopard frog (*Rana blairi*) populations were high (frog captures mid-May to mid-July averaged 1,339 captures per 1,000 TSD). In those years, activity of garter snakes was high in early July when young frogs were metamorphosing and most abundant on the uplands. In 1966, 1967, and 1972, most ponds had dried out by mid-July, and frog populations were low (frog captures averaged 65 per 1,000 TSD). Garter snake activity declined during the summer and was low in early July. The years 1968, 1970, and 1974 were intermediate, with moderate frog populations, but not many on the uplands (frog captures averaged 105 per 1000 TSD). Garter snake activity was high in early July, but less extreme than in the years with abundant frogs. The high activity of garter snakes in early July in most years resulted from increased populations due to immigration (from adjoining lands with less frog habitat) and from increased activity of foraging individuals.

Hognose Snakes

Activity of western hognose snakes was relatively constant from late May to late September, except for a period of low activity in late July (Figure 6). In the years 1959 to 1963, when western hognose snakes in a similar sand prairie habitat were more abundant, the period of low activity was in late August, and less activity occurred in the fall (Platt 1969).

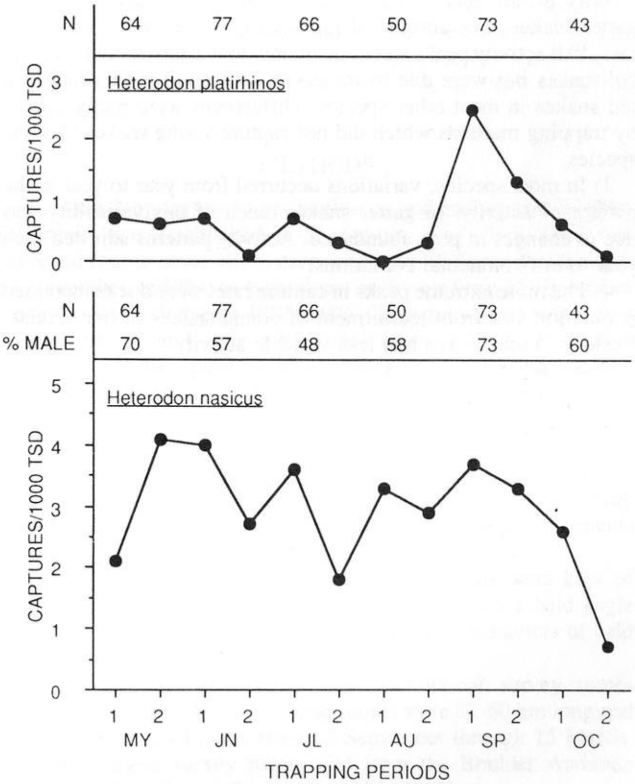


FIG. 6. Capture rates of eastern hognose snakes and western hognose snakes in half-month trapping periods from May to October averaged over nine years (1966 to 1974). "N" is sample size or total captures in month in nine years. "TSD" is trap station days.

Young western hognose snakes are small (approximately 150 mm SVL) at hatching, are seldom caught, and grow slowly. They are recruited into the trappable population over a long period. Snakes less that 250 mm SVL were 10% of the samples caught in September and October, 15% of the sample caught in June, and 2-3% of the samples caught in other months.

Males comprised a significantly greater proportion of the sample in May (comparison of May sample to July-August sample: Chi-square = 8.15, $P < 0.005$) and September (comparison of September sample to July-August sample: Chi-square = 11.71, $P < 0.001$), indicating the probability of both spring and fall mating (Figure 6), as suggested by Platt (1969).

The samples of eastern hognose snakes were too small to determine the summer activity patterns. However, unlike the western species, an activity peak occurred in September. Hatchling eastern hognose snakes are larger (approximately 190 mm SVL) and grow faster (Platt 1969) than hatchling western hognose snakes, and they comprised a sizeable proportion of the fall samples (52% in September and 77% in October).

The samples were too small to reliably determine differential activity of the sexes in spring and summer, but 17 of 23 (74%) large snakes caught in fall were males. Platt (1969) reported evidence of eastern hognose snakes mating in both spring and fall.

CONCLUSIONS

The following general conclusions can be drawn from a comparison of activity patterns of the six species:

1) Different patterns of activity occurred in different species in the same local habitat. These patterns were often related to food abundance and/or reproductive activity.

2) The five species for which there was sufficient data had some modification of a bimodal activity pattern, with a period of low activity in late July in three species and late August in the two garter snakes. The amount of fall activity varied in different species. Fall activity peaks were due mainly to the activity of hatchling bullsnakes but were due to increased activity of both young and old snakes in most other species. Differences were partly caused by trapping methods which did not capture young snakes of some species.

3) In most species, variations occurred from year to year in the pattern of activity. In garter snakes much of this variability was due to changes in prey abundance. Activity patterns adjusted each year to environmental conditions.

4) The more extreme peaks in capture rates were due to increased population size from recruitment of young snakes or immigrants. Resident adult snakes had less variable activity.

5) Male activity was higher in the spring in the five species with large samples, and female activity increased in the middle of the summer. The red-sided garter snake, western hognose snake, and probably eastern hognose snake also had increased male activity in the fall.

6) In bullsnakes and probably in other species, young snakes remained active longer in the fall but resumed activity later in the spring than adults.

LITERATURE CITED

Brimley, C.S. 1925. The seasonal catch of snakes at Raleigh, N.C. Journal of the Elisha Mitchell Society 41:100-103.

Conant, R. 1938. On the seasonal occurrence of reptiles in Lucas County, Ohio. Herpetologica 1:137-144.

Fitch, H.S. 1951. A simplified type of funnel trap for reptiles. Herpetologica 7:77-80.

Fitch, H.S. 1970. Reproductive cycles of lizards and snakes. University of Kansas Museum of Natural History Miscellaneous Publication 52:1-247.

Gibbons, J.W., and R.D. Semlitsch. 1982. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimleyana 1982:1-16.

Gibbons, J.W., and R.D. Semlitsch. 1987. Activity patterns. Pages 396-421. *In* R.A. Seigel, J.T. Collins, and S.S. Novak (eds.). Snakes: Ecology and evolutionary biology. Macmillan Publishing Company, New York.

Klimstra, W.D. 1958. Some observations on snake activities and populations. Ecology 39:232-239.

Platt, D.R. 1969. Natural history of the hognose snakes *Heterodon platyrhinos* and *Heterodon nasicus*. University of Kansas Publications Museum of Natural History 18:253-420.

Platt, D.R. 1984. Growth of bullsnakes (*Pituophis melanoleucus sayi*) on a sand prairie in south central Kansas. Pages 41-55. *In* R.A. Seigel, L.E. Hunt, J.L. Knight, L. Malaret and N.L. Zuschlag (eds.). Vertebrate ecology and systematics—A tribute to Henry S. Fitch. University of Kansas Museum of Natural History Special Publication 10.

POPULATIONS AND PREY SELECTION OF WINTERING RAPTORS IN BOULDER COUNTY, COLORADO

Stephen R. Jones
Boulder County Nature Association, 3893 75th Street, Boulder, Colorado 80301

Abstract. Wintering raptor populations were monitored between 1983 and 1988 in a 35 km² study area centered 8 km north-northeast of the city of Boulder, Colorado. Raptors congregated around active prairie dog (*Cynomys* sp.) colonies. Golden eagles (*Aquila chrysaetos*), ferruginous hawks (*Buteo regalis*), and red-tailed hawks (*Buteo jamaicensis*) were observed hunting and capturing prairie dogs. Bald eagles (*Haliaeetus leucocephalus*) and northern harriers (*Circus cyaneus*) participated in the competition for captured prey. Thirteen occurrences were noted of bald eagles stealing captured prairie dogs from ferruginous hawks. A bubonic plague outbreak killed most of the prairie dogs within the study area in 1986, corresponding with a > 60% decline in numbers of wintering bald eagles, ferruginous hawks and red-tailed hawks. A bald eagle winter roost that had been occupied by 40 eagles prior to the plague outbreak was abandoned the following winter.

Key Words. raptors, prairie dog, ferruginous hawk, bald eagle, red-tailed hawk, Colorado

INTRODUCTION

Explorers and settlers of the High Plains were astonished by the abundance of black-tailed prairie dogs (*Cynomys ludovicianus*) and the variety of wildlife that congregated around prairie dog colonies. Francis Parkman (1949), who crossed the High Plains in 1846, noted that prairie dog colonies along the Platte River "teemed with wildlife." Hal Borland (1956), whose family homesteaded in eastern Colorado in 1910, said the local prairie dog town appeared to have ". . . attracted half the hawks and coyotes and badgers in the county."

These early reports notwithstanding, the importance of prairie dogs as a food source for predators, particularly raptors, has not been determined. Grossman and Moore (1987) said that predation appears to have a minor impact on black-tailed prairie dog colonies in Wind Cave National Park, South Dakota. Campbell and Clark (1981) and Clark *et al.* (1982), who studied prairie dog-raptor associations in Colorado, Wyoming, Utah, and New Mexico, reported that golden eagles (*Aquila chrysaetos*), ferruginous hawks (*Buteo regalis*), and Swainson's hawks (*Buteo swainsoni*) hunted prairie dogs, but their research found no evidence of predation by red-tailed hawks (*Buteo jamaicensis*) or great horned owls (*Bubo virginianus*). Several observers suggested that red-tailed hawks are not large enough to effectively prey on prairie dogs (Bent 1937, Longhurst 1944, King 1955). On the other hand, Blumstein (1986) found prairie dog remains in pellets collected from three of four red-tailed hawk nests located within 1 km of active prairie dog colonies in Boulder County, Colorado. D'Ostilio (1954) reported that prairie dogs were the third most common prey item found in golden eagle nests in central Colorado, and Imler (1937) found evidence of predation on prairie dogs by bald eagles (*Haliaeetus leucocephalus*) wintering in western Kansas.

This study investigated raptor-prairie dog associations in Boulder County, Colorado, over a five-year period. The goals were to determine the extent of predation on prairie dogs by various raptor species and to note how fluctuations in prairie dog populations corresponded with fluctuations in wintering raptor populations.

STUDY SITE

The study was conducted within a 35 km² area centered approximately 8 km north-northeast of the city of Boulder in Boulder County, Colorado. The study area is bounded to the southeast by the Boulder-Longmont Diagonal Highway (Colorado 119), to the west by the Dakota Hogback (the easternmost line of foothills) and to the north by Left Hand Creek. Elevations range from 1,675-1,793 m. The area contains mixed prairie, lowland riparian, foothills shrub and sedge-cattail wetland ecosystems. Approximately 120 ha of wetlands occur around several small lakes and reservoirs. Prior to a bubonic plague outbreak in 1985-86, 17 active prairie dog colonies, which varied in size from 5 ha to 100 ha, occupied an estimated 8.2% of the study area. Land uses include agricultural grazing, rural residential, idle land, and agricultural cropland. About 80% of the land within the study area is privately owned; the remainder is undeveloped park land owned and managed by the City of Boulder.

Great horned owls, burrowing owls (*Athene cunicularia*), and red-tailed hawks nest within the study area. A pair of Swainson's hawks nested 3 km to the south during the summers of 1986 and 1987. A golden eagle eyrie, located in the foothills 2 km west of the study area, has been active since 1882 (Jollie 1943, Figgs and Lederer 1986).

METHODS

A 19 km long survey route, beginning and ending near Boulder Reservoir, was established in September 1983. This route was surveyed four to seven times each year from 15 September through 14 November and five to eight times each year from 15 November through 14 March during 1983-1988. The survey route was driven at 40 km/hour, and stops were made every 3.2 km. As raptors were sighted, their position was marked on a seven and one-half minute topographic map. Raptors that could not be identified were not included in the data base.

Between November 1982 and January 1984, pellets and bone fragments were collected from beneath wooden fence posts at Boulder Valley Ranch, a 5 km² wildlife preserve within the study area that is owned by the city of Boulder. Teeth and jaw fragments were analyzed to identify prey species.

Throughout the study period, anecdotal records were kept of raptor-prey interactions. Seven trips were made to a bald eagle roost along Left Hand Creek to observe hunting behaviors of bald eagles and ferruginous hawks.

During 1986-87, volunteers drove additional survey routes throughout Boulder County. These routes were 22-60 km long and were surveyed 5-13 times from 15 September through 15 March. Data from these survey routes and from the Boulder Audubon Christmas Bird Counts (Kaempfer 1986, 1987) were compared to data collected within the study area. Estimates of prairie dog populations along these survey routes were derived from the Boulder County Health Department's 1987 census of prairie dog colonies in Boulder County (Boulder County Health Department 1987). From 1984 to 1988, visual estimates were made of the size of prairie dog colonies within the study area.

RESULTS AND DISCUSSION

Raptor Migration Patterns

The fall raptor migration in Boulder County begins in early September and reaches its peak in early October (Boulder Audubon

Society 1987). Migrating raptors ride the thermals that rise up over the eastern foothills of the Rocky Mountains. Freeman Hall, who counted migrating raptors in Boulder County from 1982-88, observed as many as 30 raptors per hour from an observation point 3 km north of the study area during late September and early October (F. Hall, personal communication).

Arrival times for wintering raptors probably are related to a number of factors, including the availability of prey along the migration route and seasonal weather patterns (Craighead and Craighead 1956). Red-tailed hawks, sharp-shinned hawks (*Accipiter striatus*), and Cooper's hawks (*Accipiter cooperii*) reach peak numbers in September and October, while ferruginous hawks, rough-legged hawks, and bald eagles usually arrive later (Boulder Audubon Society 1987).

Mean raptor density per trip, per month was compiled for the Boulder Reservoir survey route from 1983-88 (Table 1). Red-tailed hawks were the first raptors to arrive in the study area in large numbers. During September, October, and November, they comprised 45% of all raptors observed. The highest number of red-tailed hawks observed on a single survey was 21 on 28 September, 1985. During most years, ferruginous hawks began to appear in the study area in October with mean ferruginous hawk density reaching a peak in November. Ferruginous hawks were relatively abundant during the winter months of December, January, and February, when they comprised 30% of all raptors observed. The highest number of ferruginous hawks observed on a single survey was 17 on 24 November 1985. Bald eagles usually arrived in the study area in November and stayed through February. The highest number of bald eagles observed on a single survey was 8 on 3 February 1985. Small numbers of rough-legged hawks and northern harriers were present throughout the study period. The highest number of rough-legged hawks observed on a single survey was 4 on 17 February 1985. The highest number of northern harriers observed on a single survey was 4 on 1 January 1984.

Species diversity (mean number of sightings within a given month) was greater during the winter months of December, January, and February (8.0 per month) than during the fall months of September, October and November (6.7 per month). During the winter months red-tailed hawks and ferruginous hawks comprised 51% of all raptors observed. During the fall months these species comprised 67% of all raptors observed.

Prey and Habitat Selection

Association of raptors with prairie dog colonies was examined by plotting the location, by habitat, of all raptors observed along the survey route from 1983-1987 (Table 2). Habitats were divided into 3 categories: "wetland," including marshes, lakes and reservoirs, "prairie dog colony," and "other." Raptors were placed in the "wetland" and "prairie dog colony" categories if they were initially sighted perched or soaring within the given habitat or within 50 m of its margins. All other raptors were placed in the "other" category.

Aggregations of ferruginous hawks, red-tailed hawks, and bald eagles were frequently observed in the vicinity of prairie dog colonies. During the winters of 1984-85 and 1985-85, 13 instances were noted of bald eagles taking prairie dogs from ferruginous hawks. Kleptoparasitism of ferruginous hawks by red-tailed hawks (4 instances) and by northern harriers (1 instance) was also observed throughout the study period.

Table 3 compares the size of prairie dog colonies and the number of perches within each colony or within 50 m of each colony with the total number of raptors sighted within each colony. Only prairie dog colonies immediately adjacent to the survey route were included. The data were analyzed using the correlation coefficient (r) and the true range of the correlation coefficient (ρ) at the 0.95 confidence interval. Correlations for which the range of ρ includes zero are not statistically significant. The correlation between number of perches and number of raptors ($r = 0.94$, $0.75 < \rho < 0.98$) was stronger than the correlation between prairie dog colony size and number of raptors ($r = 0.85$, $0.48 < \rho < 0.96$). All of the 5 prairie dog colonies where bald eagles were sighted ranked high in number of perches. Four of these colonies (Table 3: 34-1, 34-2, 34-3 and 34-4) were situated within 2 km of the bald eagle roost on Left Hand Creek.

Possibilities for observer error must be taken into account in these calculations. Since raptors perched on trees or telephone poles are probably easier to see than those soaring in the air or perched on the ground, observations from a survey route that passes on the periphery of prairie dog colonies may tend to overestimate the importance of perches. Observations from the survey route may tend to underestimate the importance of prairie dog colony size, since some raptors perched in large prairie dog colonies may be at the limit of observer visibility.

Pellets and bone fragments collected from within 1 m of the base of wooden fence posts at Boulder Valley Ranch yielded jawbone fragments and teeth of 37 black-tailed prairie dogs, 34 voles (*Microtus* sp.), 11 cottontail rabbits (*Sylvilagus* sp.), 10 mice (*Peromyscus* sp.), 2 birds, 1 muskrat (*Ondatra zibethicus*), and 1 domestic cat (*Felis domestica*). These fenceposts were used as perches by golden eagles, bald eagles, ferruginous hawks, red-tailed hawks, rough-legged hawks, and great horned owls. Pellet

Table 1. Mean number of raptors per trip by month on Boulder Reservoir survey route.[1]

Species	*Sept. (11)*[2]	*Oct. (11)*	*Nov. (11)*	*Dec. (8)*	*Jan. (8)*	*Feb. (7)*	*Mar. (1)*
	number/trip						
Northern harrier	0.30	0.43	0.50	0.75	0.75	0.22	0.00
Rough-legged hawk	0.20	0.43	0.80	0.75	1.16	1.89	1.00
Ferruginous hawk	0.30	1.78	4.50	2.25	3.25	3.56	1.00
Red-tailed hawk	4.40	4.43	4.60	1.38	2.75	2.00	1.00
Bald eagle	0.00	0.00	0.70	1.63	0.50	2.56	0.00
Golden eagle	0.30	0.50	0.20	0.13	0.25	0.56	0.00
Prairie falcon	0.00	0.07	0.00	0.00	0.00	0.22	0.00
American kestrel	1.60	2.64	1.20	0.75	1.08	1.11	0.00
Short-eared owl	0.00	0.00	0.00	0.13	0.42	0.00	0.00
Total	7.10	10.27	12.50	7.77	10.16	12.12	3.00

[1]Total number of raptors counted over the 5-year interval divided by total number of trips for given month.
[2]Number of trips per month.

analysis cannot present a true quantitative picture of prey consumed, since bones of smaller prey may be totally digested by some raptors, and the manner of pellet collection and analysis invariably biases the results (Errington 1932). Nevertheless, the number of black-tailed prairie dog remains found among these pellets and bone fragments suggests a high incidence of predation.

Population Trends

Between 1983 and 1985, when the prairie dog population within the study area was slowly expanding (Table 5), numbers of red-tailed hawks, ferruginous hawks, and bald eagles increased dramatically (Table 4). During the winter and spring of 1986, a bubonic plague outbreak killed most of the prairie dogs within the study area (Boulder County Health Department 1987). After the plague incident, numbers of red-tailed hawks, ferruginous hawks, and bald eagles declined sharply, whereas numbers of rough-legged hawks remained constant.

The observed decline in numbers of selected raptors within the study area after the winter of 1985-86 is confirmed by Boulder Audubon Christmas Count results for 1985 and 1986 (Kaempfer 1987). Bald eagle sightings fell from 36 on the 1985 Christmas Count (all within the study area) to 5 on the 1986 count (3 within the study area). Buteo sightings fell from 91 on the 1985 count (45 within the study area) to 78 on the 1986 count (27 within the study area).

During the winters of 1984-85 and 1985-86, bald eagles roosted within the study area in a cottonwood grove along Left Hand Creek. The creek was almost dry during the winter months, but the roost was situated in the midst of several active prairie dog colonies. As many as 40 bald eagles were observed flying into this roost on winter evenings. After the bubonic plague outbreak of 1985-86, the roost was abandoned. No bald eagles were observed at this roost during the winters of 1986-87 and 1987-88.

Mean raptor density and prairie dog density were computed for 5 additional survey routes in Boulder County. These routes were surveyed between 15 September and 15 March 1986-87 (Table 5). Mean density of ferruginous hawks was highest along the 2 survey routes (Marshall and South County) with the highest prairie dog densities. Prairie dog densities for all routes in 1986-87 and for the Boulder Reservoir survey route in 1984-85, 1985-86 and 1986-87 were plotted against mean raptor density for each route. A positive correlation existed between prairie dog density per survey route and mean raptor density per survey route ($r = 0.93$, $0.60 < \rho < 0.98$); between prairie dog density and mean ferruginous hawk density ($r = 0.93$, $0.60 < \rho < 0.98$); and between prairie dog density and mean red-tailed hawk density ($r = 0.91$, $0.55 < \rho < 0.97$). A significant positive correlation did not exist between prairie dog density and mean bald eagle density ($r = 0.68$, $-0.05 < \rho < 0.93$); or between prairie dog density and mean rough-legged hawk density ($r = 0.25$, $-0.52 < \rho < 0.78$).

The absence of a significant correlation between prairie dog density and mean bald eagle density suggests that the bald eagles overwintering in the study area during 1984-85 and 1985-86 may have been attracted to the area by factors other than high prairie dog density. These factors could include the presence of numerous lakes and marshes, the availability of suitable perching and roosting sites, and the abundance of other prey species. Since kleptoparasitism can be a primary means of prey acquisition by wintering bald eagles (Brockman and Barnard 1979, Griffin, 1981, Stallmaster and Gessaman 1984), the density of ferruginous hawks in the vicinity of prairie dog colonies may also influence bald eagle selection of prairie dog colonies as foraging sites. Mean ferruginous hawk densities for the South County and Marshall survey

Table 2. Raptor sitings (%) by habitat,[1] 1984-1987

Species	*Siting Location* Wetland[2]	Prairie Dog Colony	Other	*N*
	%	%	%	
Northern harrier	50	30	20	10
Rough-legged hawk	27	33	40	33
Ferruginous hawk	8	66	26	123
Red-tailed hawk	14	38	48	116
Bald eagle	6	34	60	68
Golden eagle	0	25	75	8
Prairie falcon	0	40	60	5
Short-eared owl	100	0	0	5

[1]Soaring or perched in the given habitat or within 50 m of its boundaries.
[2]"Wetlands" includes cattail and sedge marshes, lakes and reservoirs.

Table 3. Prairie dog colony attributes and total sightings of selected species, 1984-1987.

Colony Number	*Area (ha)*[1]	*Perches*[2]	*Red-tailed hawk*	*Ferrug. hawk*	*Rough-legged hawk*	*Bald eagle*	*Total*
			number of sightings				
6-1	6	6	3	6	1	0	10
4-1	8	5	0	0	0	0	0
34-1	8	18	6	4	2	5	17
3-1	9	0	0	0	0	0	0
30-1	11	7	2	1	0	0	3
34-2	11	18	1	7	1	2	11
34-3	13	21	3	11	0	2	16
34-4	15	16	5	8	2	4	19
31-1	28	0	2	1	1	0	4
5-1	45	14	6	10	0	1	17
31-2	100	40	13	21	4	0	38

[1]Maximum area of each colony, 1984-87.
[2]Number of telephone poles or trees taller than 5 m within each colony or within 50 m or its boundaries.

routes during 1986-87 (0.07 km and 0.11 km) were considerably lower than mean ferruginous hawk densities for the Boulder Reservoir survey route during 1984-85 and 1985-86 (0.18/km and 0.26/km).

This study did not examine the proportion of prairie dogs in raptor diets. Through analysis of pellets collected from roost sites and detailed field observations of foraging raptors, future studies may be able to ascertain more precisely the extent of predation on prairie dogs by raptors. Another issue needing further study is the relation of prairie dog colony attributes such as size, location, and density to wintering raptor population density. Identification of prairie dog colony attributes that correspond with high wintering raptor population densities may become an important management tool for preserving or enhancing wintering raptor habitat on the High Plains.

LITERATURE CITED

Bent, A.C. 1937. Life histories of North American birds of prey. United States National Museum Bulletin, Volume 1.

Blumstein, D.T. 1986. The diets and breeding biology of red-tailed hawks in Boulder County: 1985 nesting season. Boulder County Nature Association Publication No. 5.

Borland, H. 1956. High, wide, and lonesome. J.B. Lippincott Company, Philadelphia and New York.

Boulder Audubon Society. 1987. Boulder County wildlife inventory.

Boulder County Health Department. 1987. Inventory of prairie dog colonies in Boulder County, Colorado.

Brockman, R.J., and C.J. Barnard. 1979. Kleptoparasitism in birds. Animal Behavior 37:487-514.

Campbell, T.M., and T.W. Clark. 1981. Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie dogs in Wyoming. American Midland Naturalist 105:269-276.

Clark, T.W., T.M. Campbell, D.G. Socha, and D.E. Casey. 1982. Prairie dog colony attributes and associated vertebrate species. Great Basin Naturalist 42:572-582.

Craighead, J.J., and F.C. Craighead. 1956. Hawks, owls, and wildlife. Stackpole Company, Harrisburg, Pennsylvania.

D'Ostilio, D.O. 1954. Nesting status and food of the golden eagle in northern Colorado. Master of Arts Thesis, University of Colorado, Boulder.

Errington, P.L. 1932. Technique of raptor food habits study. Condor 34:75-86.

Figgs, M., and N. Lederer. 1986. Status of nesting golden eagles in Boulder County and adjacent areas of the Front Range in Colorado. Boulder County Nature Association Publication Number 2.

Griffin, C.R. 1981. Interactive behavior among bald eagles wintering in north-central Missouri. Wilson Bulletin 93:259-264.

Grossman, J., and T. Moore. 1987. A prairie dog companion. Audubon 89:52-67.

Imler, R.H. 1937. Bald eagle pellets in Kansas show rabbits as principal food. Condor 39:37-38.

Jollie, M.T. 1943. The golden eagle: its life history, behavior and ecology. Doctor of Philosophy Thesis, University of Colorado, Boulder.

Kaempfer, B. 1986. Boulder Audubon Society Christmas bird counts. American Birds 40.

Kaempfer, B. 1987. Boulder Audubon Society Christmas bird counts. American Birds 41.

King, J.A. 1955. Social behavior, social organization and population dynamics in a prairie dog town in the Black Hills of South Dakota. Contributions in Laboratory Vertebrate Biology, University of Michigan Number 67.

Longhurst, W. 1944. Observations on the ecology of the Gunnison prairie dog in Colorado. Journal of Mammalogy 25:4-36.

Parkman, F. 1949. The Oregon Trail. The Modern Library, New York.

Stalmaster, M.V., and J.A. Gessaman. 1984. Ecological energetics and foraging behavior of overwintering bald eagles. Ecological Monographs 54:407-428.

Table 4. Mean density (number of sightings/trip) of raptors along Boulder Reservoir survey route, 1983-1987.

Species	*1983-84*	*1984-85*	*1985-86*	*1986-87*	*1987-88*
	number of sightings/trip				
Red-tailed hawk	2.3	4.2	5.6	2.4	1.5
Ferruginous hawk	1.5	3.4	4.9	1.1	1.2
Rough-legged hawk	0.5	1.0	1.1	1.0	0.6
Northern harrier	1.5	0.3	0.9	0.0	0.1
Golden eagle	0.1	0.8	0.4	0.1	0.1
Bald eagle	0.0	1.5	2.1	0.1	0.1

Table 5. Mean density of raptors (number/kilometer) along all survey routes.[1]

Survey route	*Year*	*Prairie dog density*[1]	*Red-tailed hawk*	*Ferrug. hawk*	*Rough-legged hawk*	*Bald eagle*	*Total*
			number/kilometer				
Boulder Res.	1984-85	7.59	0.22	0.18	0.05	0.08	0.53
Boulder Res.	1985-86	8.24	0.29	0.26	0.06	0.11	0.72
Boulder Res.	1986-87	0.03	0.13	0.06	0.05	0.01	0.25
Table Mt.	1986-87	0.97	0.08	0.00	0.02	0.02	0.12
N. St. Vrain	1986-87	1.67	0.09	0.06	0.05	0.05	0.25
Lagerman Res.	1986-87	0.44	0.09	0.04	0.05	0.06	0.24
South County	1986-87	3.72	0.13	0.07	0.11	0.01	0.32
Marshall	1986-87	3.36	0.11	0.11	0.08	0.01	0.31

[1]Percent of land occupied by active prairie dog colonies within 2.6 km^2 land sections intersected by survey route.

BREEDING BIRD POPULATIONS OF A FLOODPLAIN TALLGRASS PRAIRIE IN KANSAS

Calvin L. Cink
Biology Department, Baker University, Baldwin City, Kansas 66006

and

Peter E. Lowther
Field Museum of Natural History, Roosevelt Rd at Lakeshore Drive, Chicago, Illinois 60605

Abstract. Breeding birds were censused yearly from 1974-1988 on a 10.1 ha floodplain tallgrass prairie, a portion of the Baker Wetlands Research Area on the south edge of Lawrence, Kansas. Dickcissels (*Spiza americana*) were the most abundant species, with densities about six times greater than in the Flint Hills tallgrass prairie (149 territorial males/km^2 *vs.* 25/km^2). This may be due to availability of moisture and associated density of grass stems and insect production. The bird community in the floodplain prairie however, is less diverse (5 species *vs.* 10 species). Grasshopper sparrows (*Ammodramus savannarum*) were the second most abundant species in Flint Hills upland prairie, but were absent from floodplain prairie. Red-winged blackbirds (*Agelaius phoeniceus*) which are rarely censused in upland prairie were the second most abundant species in floodplain prairie. Population densities were relatively stable over 15 years with exceptions due to different land use patterns in the vicinity of the study plot and burning or mowing of the prairie prior to the nesting season.

Key Words. population ecology, bird densities, birds, tallgrass prairie, mowing, burning, Kansas

INTRODUCTION

The value of long-term ecological studies is becoming more and more apparent (Callahan 1984), yet a tradition of short-term studies has developed in avian research (Wiens 1984). Research on birds in grassland ecosystems is no exception. Even studies on International Biological Program (IBP) grassland sites tended to emphasize short-term data (Wiens 1974). The population structure of grassland bird communities needs to be monitored over many years to evaluate the impact of environmental changes.

The majority of studies on tallgrass prairie birds deal with upland prairies. This may stem from the fact that few floodplain prairie sites of any size remain. These prairies, with their fertile, deep soils, were among the first to be plowed by early settlers. Although limited in size and extent, the ecology of remaining floodplain prairies should be studied.

The purposes of this paper are to document a long-term (15 year) study of breeding bird populations on a virgin floodplain tallgrass prairie in Kansas, to compare these composition and densities to midwestern prairies in upland or floodplain habitats, and to relate population fluctuations to mowing or burning.

STUDY AREA AND METHODS

The Baker Wetlands Research Area is located on the south edge of Lawrence, Kansas in northeastern Kansas (Figure 1). A portion of the 232.9 ha area was cultivated, and most was grazed until 1958 (Boyd 1980). Virgin prairie containing flora and fauna typical of lowland meadow were found in only two small areas totalling about 20 ha (Figure 1). These prairies were designated as a National Natural Landmark by the Department of the Interior and National Park Service in 1969. The largest of these prairies (14.2 ha) was first censused for breeding birds in the summer of 1974 (Cink 1974).

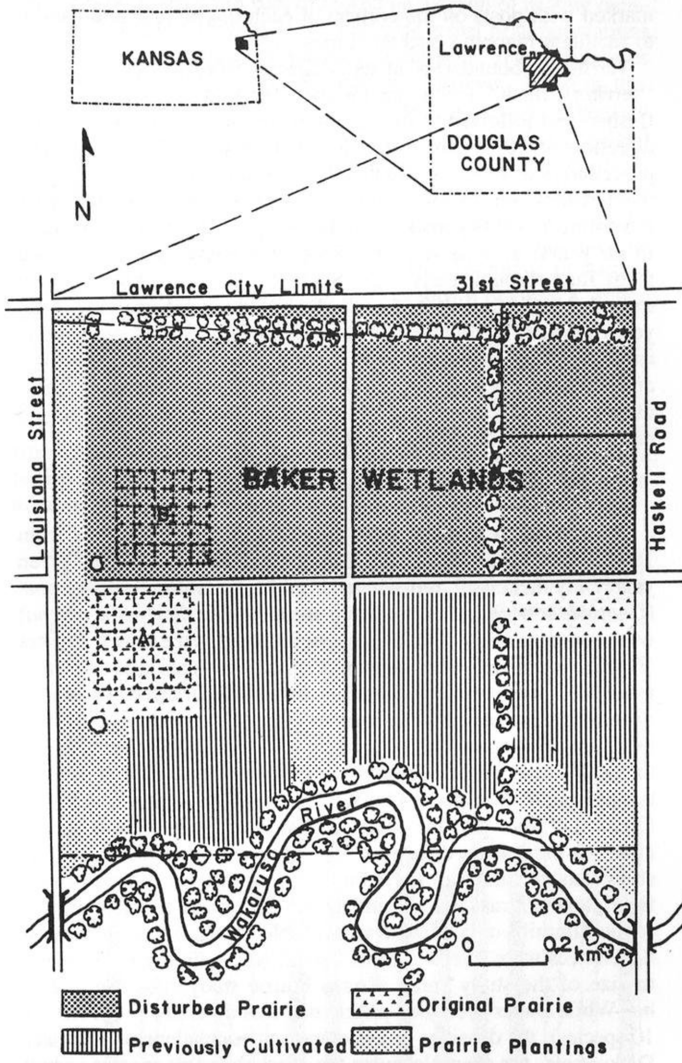


FIG. 1. Location of the Baker University Wetlands Research Area. The grid labelled A is the 10.1 ha census plot in floodplain tallgrass prairie. The grid labelled B is the 10.1 ha census plot in tallgrass prairie-shrub succession.

Küchler (1974) described this prairie as a "Freshwater Marsh (Spartina)" from the dominant grass, prairie cordgrass (*Spartina pectinata* Link.) which often reaches 2 m in height at midsummer and provides well over 70% of the canopy cover. Other dominant grasses include indiangrass [*Sorgastrum nutans* (L.) Nash], big bluestem (*Andropogon gerardii* Vitman), and switchgrass (*Panicum virgatum* L.). The water table is near the surface (6-12 cm) and allows for tall growth of these grasses. Some low depressions allow expanses of sedge (*Carex frankii* Kunth.) and rushes [*Eleocharis obtusa* (Willd.) J. A. Schult. and *Juncus torreyi* Cov.). Forbs are common and prominent only at midsummer. They include several species of sunflowers (*Helianthus annuus* L., *H. mollis* Larn. and *H. maximiliani* Schrad.), compassplant (*Silphiuml aciniatum* L.), dogbane (*Apocynum cannabinum* L.), showy milkweed (*Asclepias syriaca* L.), thickspike gayfeather (*Liatris pycnostachya* Michx.), and a variety of others. A ditch passing diagonally across the southern one-third of the study area contains a few peachleaf willows (*Salix amygdaloides* Anderss.), and the northern boundary is accentuated by a ditch with buttonbush (*Cephalanthus occidentalis* L.). A 10.1 ha portion of the prairie was marked with posts on the corners of each 0.4 ha in a grid pattern to facilitate mapping bird territories.

Territorial boundaries of each species were mapped with the "territory flush" technique (Wiens 1969). A singing male was flushed and followed to its landing point, and these positions and direction of movement were plotted on a scaled field map. The procedure was repeated usually about 20 times until the outline of the territory was readily apparent. Aggressive encounters with territorial neighbors made boundaries especially well delineated. In all years, at least six censuses of 3-4 hours each were made from June through early July. Since 1981, census periods were extended into late July and early August. In about one-half of the years studied, additional efforts were made to find as many nests as possible to document their success. In some years, nestlings and their parents were banded for identification. Vegetation measures of percent cover and stem density were sampled with 30 randomly located quadrats (1 m^2).

RESULTS AND DISCUSSION

A total of 13 species were censused on the study area from 1974-1988 (Table 1), but the average was five species any given year. Only dickcissel, red-winged blackbird, common yellowthroat (*Geothylpis trichas*), and eastern meadowlark (*Sturnella magna*) were censused every year. Some species, such as the brown thrasher (*Toxostoma rufum*), were censused infrequently, because they were associated with woody vegetation that only persisted when fires or mowing did not occur in a given year. The species of birds that breed on the floodplain tallgrass prairie in this study were similar to those found in a floodplain tallgrass prairie of similar vegetational composition studied by Wilson (1983) in southwestern Iowa (Table 1). Note that the total density for both areas was similar although the Kansas data were for a 15-year period while the Iowa study was for one year. Differences in avifaunas occurred between floodplain tallgrass prairies and more xeric upland tallgrass prairies of the Flinthills only 110 km west (Table 2). Clearly some of these differences were a reflection of habitat, and others may be related to size of the study areas. Konza Prairie study sites were 12-38 ha. While Baker Wetlands prairie had less diversity (7 species *vs.* 10 species), the densities of its component populations were greater. Dickcissels, for example, were the most abundant species in both prairies, but densities were about 6 times greater in floodplain tallgrass prairie. This difference may be attributed to moisture differences and associated density of vegetation and arthropod abundance. Zimmerman (1971) observed that dickcissels were present in higher densities in oldfield communities than on Konza prairie. Upland tallgrass prairie may not be preferred habitat, at least in males (Zimmerman and Finck 1983). A similar pattern was seen for red-winged blackbirds. They were 50 times more abundant in floodplain prairie than in upland prairie. The structure of the vegetation or abundance of preferred arthropod foods may have been the critical difference in habitat selection for this species.

Table 1. Bird species composition and densities (number/km²) of two midwestern tallgrass prairies.

Species	Bird density	
	Kansas	Iowa[1]
	-----number/km²-----	
Dickcissel (*Spiza americana*)	138	87
Red-winged blackbird (*Agelaius phoeniceus*)	59	76
Common yellowthroat (*Geothlypis trichas*)	69	49
Sedge wren (*Cistothorus platensis*)	30	71
Grasshopper sparrow (*Ammodramus savannarum*)	0	22
Eastern meadowlark (*Sturnella magna*)	tr	tr
Ringnecked pheasant (*Phasianus colchicus*)	tr	tr
Northern bobwhite (*Colinus virginianus*)	tr	tr
American goldfinch (*Carduelis tristis*)	tr	tr
Mourning dove (*Zenaida macroura*)	tr	0
Northern cardinal (*Cardinalis cardinalis*)	tr	0
Brown-headed cowbird (*Molothrus ater*)	tr	0
Bell's vireo (*Vireo bellii*)	tr	0
Brown thrasher (*Toxostoma rufum*)	tr	0
Eastern kingbird (*Tyrannus tyrannus*)	0	tr
American kestrel (*Falco sparverius*)	0	tr
Total number of species	13	11
Density of all species combined	316	331

[1]Data from a 1-year study (Wilson, 1983); Kansas data represent 15-year summary, tr = fewer than 0.5 birds/km².

Table 2. A comparison of bird species and densities (number/km²) from two Kansas tallgrass prairies.

Species	Bird density	
	Baker Wetlands	Konza[1]
	-----number/km²-----	
Dickcissel (*Spiza americana*)	149	25
Redwinged blackbird (*Agelaius phoeniceus*)	59	1
Common yellowthroat (*Geothlypis trichas*)	50	0
Eastern meadowlark (*Sturnella magna*)	10	14
Grasshopper sparrow (*Ammodramus savannarum*)	0	20
Upland sandpiper (*Bartramia longicauda*)	0	6
Mourning dove (*Zenaida macroura*)	0	6
Brown-headed cowbird (*Molothrus ater*)	tr	6
Eastern kingbird (*Tyrannus tyrannus*)	0	6
Common nighthawk (*Chordeiles minor*)	0	5
Brown thrasher (*Toxostoma rufum*)	5	0
Bell's vireo (*Vireo bellii*)	5	0
Henslow's sparrow (*Ammodramus henslowii*)	0	3

[1]Konza Prairie Research Natural Area, data from Knodel (1980) represent an average of 4 census plots; Baker Wetlands data are for the same census year, tr = fewer than 0.5 birds/km².

Some species found at Konza were not found on the floodplain prairie. This included the grasshopper sparrow, upland sandpiper (*Bartramia longicauda*), and Henslow's sparrow (*Ammodramus henslowii*). The latter two species possess critical area requirements (Samson 1980). It is possible that the area of virgin prairie in the Baker Wetlands was too small to fulfill the requirements for viable populations of these two species. The small size of the area, coupled with the fact that there were no islands of similar grassland habitat nearby, may also contribute to the absence of these birds. It was more likely that habitat differences such as vegetation structure were more important for grasshopper sparrows. Minimum area seems less important for this species. Common yellowthroats that occurred in high densities in floodplain prairie were not observed by Knodel (1980) but were observed in low frequency on other sites at Konza (Zimmerman and Finck 1983). Moist environments appeared to be an important component of habitat selection for this species. Differences in total densities between the two study areas, though not indicated in the table, were similar in magnitude to those found for the dickcissel alone (277 territorial males/km² for floodplain prairie and 97 males/km² for upland prairie).

Densities have remained nearly constant between 275-300 territorial males/km² on the Baker Wetlands prairie over the 15 year study (Figure 2). This represented a difference of only 2-4 birds/10 ha. Three peaks represent a departure from this pattern (1978, 1982, and 1986-88). A difference in the timing of censuses was partly responsible for these peaks. Beginning in 1981, censuses were made into late July, and sedge wrens (*Cistothorus platensis*) were recorded. This species may have been missed in cursory observations in late July previously because the prairie was mowed in July and no habitat was available. The density of wrens was particularly high in 1988 (69/km²) and increased the total density for the area to its highest point in 15 years.

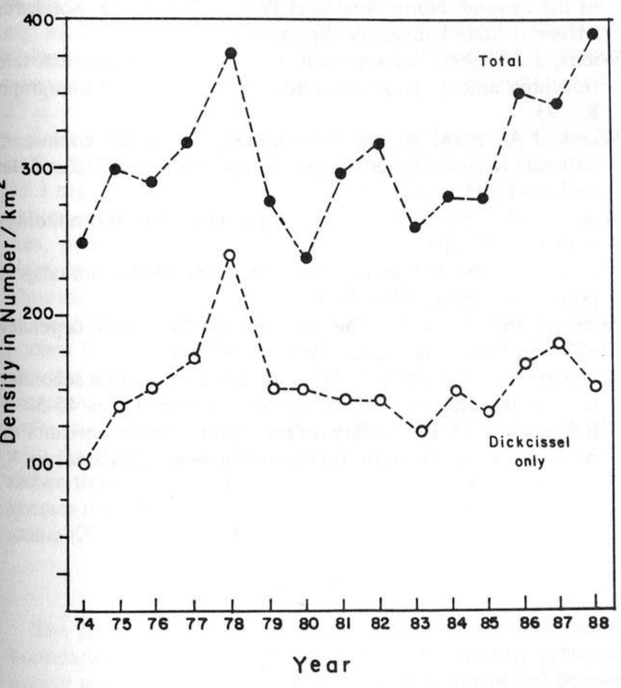


FIG. 2. Breeding densities of birds on floodplain tallgrass prairie. Solid circles represent total densities. Open circles represent densities of dickcissels.

To further evaluate densities among all 15 years, dickcissels alone were examined. The peak for 1988 disappeared, but the peak for 1978 remained. The small peak for 1982 was due to increases in common yellowthroats and red-winged blackbirds, and without their influence the peak disappears. Management practices may have influenced dickcissel numbers. Prior to 1983, mowing of the prairie in July or August was a normal practice. Mowing may have had pronounced influence on the birds breeding the following season by removing the standing vegetation. This removal might mean a later time of territorial settlement for returning males and less dense cover for early nest building. Both have been documented for dickcissels on the study area (Cink, unpublished data). It may also be that standing vegetation from previous years provided more singing posts for territorial males, and more males could be supported on the same area of grassland. When mowed and unmowed years are superimposed on a graph of nesting densities of dickcissels (Figure 3), it does appear that peak populations occurred after a buildup of standing vegetation. Yearly decreases after mowing were not always present, however. Mowing that occurred on adjacent grassland to the north may have influenced the largest peak in density (1978). This partially grazed grassland was not mowed or burned for at least seven years prior to 1977. During this period of succession, it became dominated by rough-leaved dogwood (*Cornus drummondii* C. A. Mey.). A 10.1 ha plot of this habitat (Figure 1) was censused at the same time as the prairie plot (Cink and Paul 1975). The difference in species diversity and density between the plots is shown in Table 3. When the shrub succession plot and surrounding area were cut in 1977, returning birds were forced into other areas. Evidence from banding suggests that some shrub succession plot birds established territories in the tallgrass prairie plot in 1978. Territories in 1978 were on the average 40 m² smaller in 1978 than years before or since. This suggests that the resident population condensed their territories to make room for new birds. Levels of aggression were notably higher in 1978 than other years.

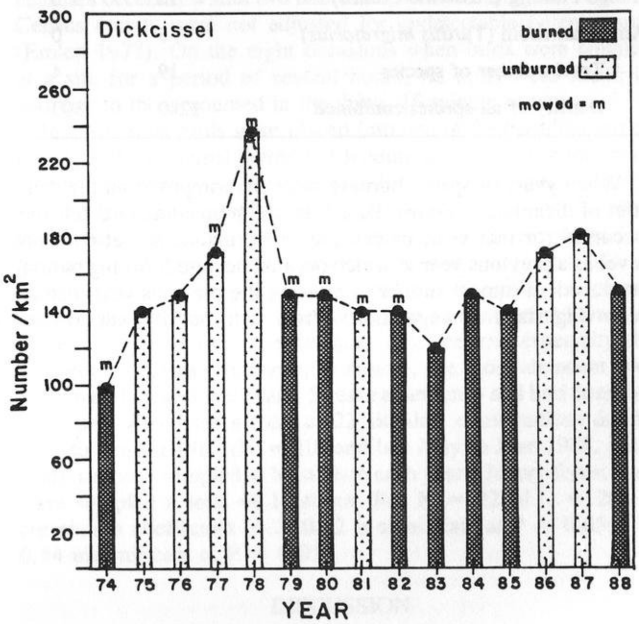


FIG. 3. Yearly pattern of mowed and unmowed prairie, and of burned and unburned prairie superimposed on the breeding densities of dickcissels at Baker Wetlands. Summer mowing occurred in July and spring burns occurred in April.

Table 3. Bird species and densities (number/km²) in adjoining floodplain tallgrass prairie and prairie-shrub succession. Data from adjoining 10.1 ha plots censused the same year.

Species	*Bird density*	
	Succession plot	*Mowed & Burned*
	------- number/km² -------	
Red-winged blackbird (*Agelaius phoeniceus*)	230	70
Dickcissel (*Spiza americana*)	210	140
Common yellowthroat (*Geothlypis trichas*)	180	50
Eastern meadowlark (*Sturnella magna*)	70	40
Bell's vireo (*Vireo bellii*)	85	0
Mourning dove (*Zenaida macroura*)	70	0
Yellow-billed Cuckoo (*Coccyzus americanus*)	60	0
Brown-headed Cowbird (*Molothrus ater*)	60	0
American goldfinch (*Carduelis tristis*)	50	0
Willow flycatcher (*Empidonax traillii*)	40	0
Yellow warbler (*Dendroica petechia*)	40	0
Orchard oriole (*Icterus spurius*)	40	0
Common grackle (*Quisculus quiscula*)	35	0
Black-billed cuckoo (*C. erythropthalmus*)	30	0
Brown thrasher (*Toxostoma rufum*)	30	0
Gray catbird (*Dumetella carolinensis*)	20	0
Northern bobwhite (*Colinus virginianus*)	15	0
Indigo bunting (*Passerina cyanea*)	10	0
American robin (*Turdus migratorius*)	5	0
Total number of species	19	4
Density of all species combined	1280	300

When years of spring burning were superimposed on the densities of dickcissels (Figure 3), a decrease in breeding bird densities occurred for that year, or densities were maintained at the same level as a previous year in which burning occurred. Spring burning produced an impact similar to mowing the previous year, namely removing standing vegetation. When stem density was lowered and potential song posts lost, the habitat suitability may have been lowered. Settlement on territories averaged two weeks later in years of burns. Less potential nesting cover was available and predation seemed to be higher. All these could have combined to lower the densities of nesting birds on this prairie. The pattern of burning and mowing was such that it was often difficult to separate the effects of the two on subsequent numbers of territorial males.

ACKNOWLEDGEMENTS

Our thanks to Roger Boyd and Tom Bragg for their comments on the manuscript. Thanks also to our colleagues over the years who have provided much needed field assistance, particularly J. T. Paul, C. T. Stahmann-Lowther, D. E. Seibel, P. Sepahi, M. C. Braun, M. K. Smith, G. Kramos, J. Bigler, and J. Fahrnow.

LITERATURE CITED

Boyd, I.L. 1980. Progress in establishing and maintaining prairie in the Baker Wetlands. Pages 231-233. *In* C.L. Kucera (ed.). Proceedings of the Seventh North American Prairie Conference. Southwest Missouri State University, Springfield.

Callahan, J.T. 1984. Long-term ecological research. Bioscience 34:363-367. Cink, C.L. 1974. Breeding bird census 100. Floodplain tallgrass prairie. American Birds 28:1031-1032.

Cink, C.L., and J.T. Paul. 1975. Breeding bird census 106. Floodplain tallgrass prairie-shrub succession. American Birds 29:11.

Knodel, J.J. 1980. Breeding bird censuses in the Flint Hills of Kansas. American Birds 34:69-70.

Küchler, A.W. 1974. A new vegetation map of Kansas. Ecology 55:586-604.

Samson, F.B. 1980. Island biogeography and the conservation of prairie birds. Pages 293-299. *In* C.L. Kucera (ed.). Proceedings of the Seventh North American Prairie Conference. Southwest Missouri State University, Springfield.

Wiens, J.A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs 8:1-93.

Wiens, J.A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. American Midland Naturalist 91:195-213.

Wiens, J.A. 1984. The place of long term studies in ornithology. Auk 101:202-203.

Wilson, B.L. 1983. Breeding bird census 96. Floodplain tallgrass prairie. American Birds 37:80.

Zimmerman, J.L. 1971. The territory and its density dependent effect in Spiza americana . Auk 88:591-612.

Zimmerman, J.L., and E.J. Finck. 1983. Success in a secondary habitat: the dickcissel in the tallgrass prairie. Pages 47-50. *In* R.Brewer (ed.). Proceedings of the Eighth North American Prairie Conference. Western Michigan University, Kalamazoo.

CORRELATIONS BETWEEN INSECTS AND BIRDS IN TALLGRASS PRAIRIE RIPARIAN HABITATS

Lawrence J. Gray
Department of Biology, Ottawa University, Ottawa, Kansas 66067

Abstract. Previous observations in riparian habitats of Kings Creek, Konza Prairie Research Natural Area, Kansas indicated that emerging aquatic insects represent a concentrated source of food for insectivorous birds, particularly the flycatcher and gleaner guilds. This hypothesis was tested by concurrent measurements of net insect emergence (total emergence minus adults returning to the stream) and densities of birds at six sampling sites from June to August 1987 and May to June 1988. Significant positive correlations with emergence were found for flycatchers (r = 0.93) and gleaners (r = 0.91), the two insectivore guilds containing the majority of individuals along Kings Creek. Observations also showed that flycatcher and gleaner populations rapidly respond to temporal changes in insect emergence.

Key Words. fly catcher, gleaner, bird, aquatic insect, tallgrass prairie, stream, Kansas

INTRODUCTION

Streams in the prairie and desert regions of western North America support riparian ecosystems that are of critical importance as habitats for local and regional avifaunas (Knopf *et al.* 1988). In addition to providing cover and water, these habitats provide a concentrated source of insects as food for avian insectivores. Along desert streams, this insect food appears to consist mainly of emerging aquatic insects, such as midges and mayflies. Jackson and Fisher (1986), for example, found that the annual biomass of emerging aquatic insects from Sycamore Creek, Arizona, was over 23 g/m².

Emergence biomass from Kings Creek, a tallgrass prairie stream in the Konza Prairie Research Natural Area (KPRNA), averages 20.3 mg/m²/day in the summer (Gray, unpublished). Field observations during previous summers had suggested that certain species, particularly flycatchers, were found in greater abundance along those stream reaches with the highest rates of emergence. Thus the objective of this study was to determine if riparian habitats of tallgrass prairie streams, like desert streams, serve as an important feeding area for insectivorous birds by testing the hypothesis that insectivore densities should be positively correlated with emergence biomass.

Previous studies of birds in the KPRNA primarily have dealt with typical grassland species (Zimmerman 1982, Finck 1984) rather than riparian species. Published information on riparian species is confined to a listing of seasonal occurrence and breeding status (Zimmerman 1985).

METHODS

The Kings Creek catchment (1,637 ha) lies entirely within the boundaries of KPRNA. The headwaters are typically ephemeral, except near springs and seeps, whereas intermittent and perennial reaches occur downstream. Riparian vegetation in the headwaters is composed of shrubs, small trees, grasses, and sedges. A relatively abrupt transition to a gallery forest of oak (*Quercus* L. spp.), hackberry (*Celtis* L. spp.), and elm (*Ulmus* L. spp.) occurs along lower stream reaches (Gurtz *et al.* 1982). In this study, three sampling sites were along third- and fourth-order channels in the prairie/shrub vegetation type, and three sites were located in fourth- and fifth-order channels bordered by gallery forest. Two of the prairie/shrub sites had flow during April and May but then dried completely by late June. The other four sites had flow until late June; discharge then declined until only isolated pools remained in July and August. No scouring floods occurred at any site. Discharge was measured by using a meter stick, stopwatch, and fluorescein dye.

Aquatic insect adults emerging from the stream were collected in traps constructed from inverted 15-liter plastic buckets similar in design to that used by Jackson and Fisher (1986). Each trap collected adults emerging from an area of 452 cm². Traps were emptied each 24-hour period using an aspirator. The number of traps placed at each site varied from 10 to 25, depending on flow conditions and habitat area. Adults were preserved in 80% ethanol, sorted by taxon, and dried at 80 C for 24 hours before weighing on an analytical balance.

Aquatic adults returning to the stream were collected by isolating a short section of channel with two drift nets (1.0 mm mesh) for a 24-hour period. Returning biomass was calculated by dividing the biomass collected in the downstream net by the channel area between nets. Net emergence equalled trap biomass minus returning biomass. Net emergence/m² was multiplied by the square meters of wetted area in 100 linear meters of channel to compensate for variations in total stream area.

Birds were censused by recording all sightings within an area of 0.2 ha for 15 minutes. For a given site and date, three replicate censuses were taken along a 250 m reach of stream channel. All censuses occurred within two hours after sunrise during fair weather. Census counts were not adjusted for undetectable (silent) birds (Emlen 1977). On the eight occasions when birds were counted at a site for a period of several hours, no birds were found in addition to those counted in the three, 15-minute censuses.

Insectivorous birds were placed into one of four feeding guilds based on the principal method of feeding as observed in the field. Gleaners actively search vegetation for stationary prey, whereas flycatchers wait for active prey (usually flying insects) to enter their field of view before moving from a perch. Sweepers feed on flying insects during flight, often ranging over a large area. Woodpeckers excavate deeply in wood and bark. Emphasis is placed here on the gleaners and flycatchers. The census method was not suitable for measuring the densities of sweepers, especially the common nighthawk (*Chordeiles minor*), the most abundant species. Woodpeckers were rare. Stream emergence and bird densities were determined for a total of 22 site-date combinations during June to August 1987 (N = 10) and late May to June 1988. Each study site was sampled at least once each year. Gallery forest sites were sampled a total of 12 times. For N = 22 (d.f. = 20), a correlation coefficient (r) > 0.42 is significant at P = 0.05; r > 0.54 insignificant at P = 0.01.

DISCUSSION

The emergence of aquatic insects from Kings Creek shows wide spatial and temporal variability (Gray, unpublished). For the sampling dates in this study, daily emergence varied from 0 to 21 g/100 m. Emergence is strongly dependent on stream flow. When stream channels dry to isolated pools, daily emergence biomass is 10 to 100 times less than that when stream flow is stable.

The most common insects emerging from Kings Creek were midges (Diptera: Chironomidae), mayflies (Ephemeroptera), and stoneflies (Plecoptera). These groups comprised 53%, 27%, and

10% of total emergence biomass, respectively. Midges and mayflies emerged throughout the spring and summer, whereas stoneflies primarily emerged in May.

Flycatchers included the eastern wood-pewee (*Contopus virens*), great crested flycatcher (*Myiarchus crinitus*), eastern phoebe (*Sayornis phoebe*), eastern kingbird (*Tyrannus tyrannus*), and western kingbird (*Tyrannus verticalis*). Eastern wood-pewees and great crested flycatchers were the most abundant species at the gallery forest sites, whereas kingbirds predominated at the prairie/shrub sites. Flycatcher densities were strongly correlated with net stream emergence (Figure 1). Among individual insect taxa, flycatchers were highly correlated with chironomid emergence (r = 0.85) and, to a lesser extent, stoneflies (r = 0.43). The correlation with mayflies (r = 0.40) was not significant.

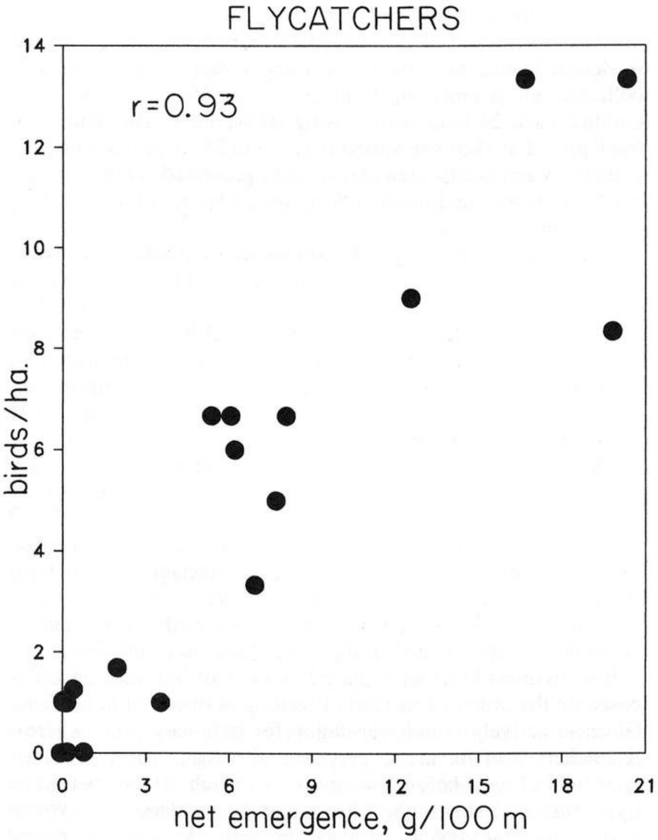


FIG. 1. Correlation between net emergence of aquatic insects from Kings Creek and the density of flycatchers. Net emergence equals total emergence biomass minus that returning to the stream and is given for a 100-m reach of channel to account for variations in wetted area at the various sites.

Common gleaners at gallery forest sites, in order of abundance, were the black-capped chickadee (*Parus atricapillus*), house wren (*Troglodytes aedon*), tufted titmouse (*Parus bicolor*), Louisiana waterthrush (*Seiurus motacilla*), and Bewick's wren (*Thryomanes bewickii*). The common yellowthroat (*Geothlypis trichas*) was the main gleaner at prairie/shrub sites. Total gleaner densities were strongly correlated with total stream emergence (Figure 2). The abundance of gleaners was highly correlated with stoneflies (r = 0.70), chironomids (r = 0.69), and mayflies (r = 0.49).

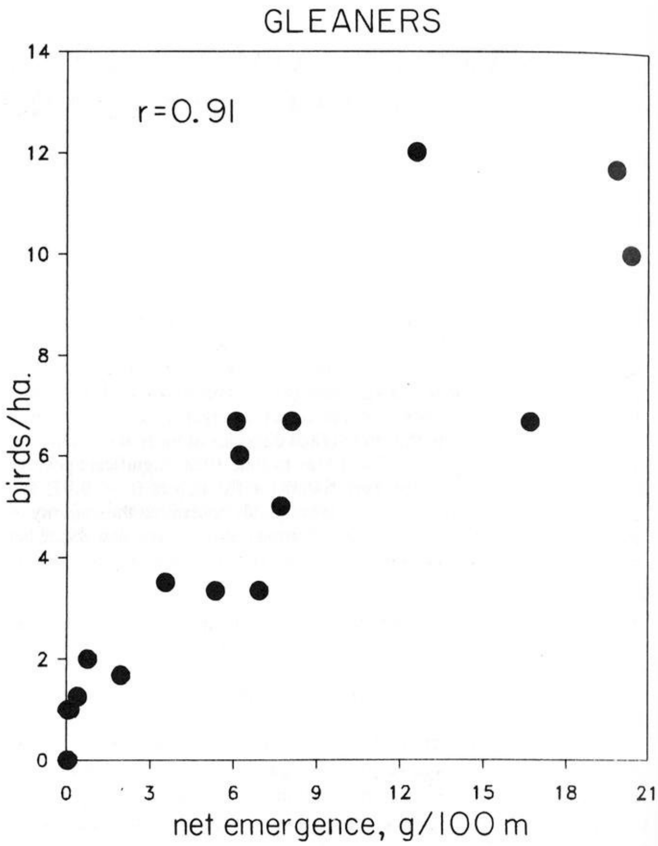


FIG. 2. Correlation between net emergence of aquatic insects from Kings Creek and the density of gleaners.

Correlations between specific insect taxa and the two insectivore guilds reflect the activity level of the insects and feeding behavior of the birds.In addition to resting on riparian vegetation, chironomids form mating swarms during the morning and late afternoon, and thus are exposed to predation by flycatchers. Eastern wood-pewees and eastern phoebes were observed feeding on chironomid swarms on several occasions. Mayflies and stoneflies spend most of the daylight hours resting on low vegetation near the stream channel. Most of the feeding activity of gleaners observed occurred in this habitat. The significant correlation between flycatchers and stoneflies may reflect some feeding on riparian vegetation by flycatchers. Stoneflies may be easier to detect than other insects against the background of vegetation because of their dark coloration and relatively large size (10-13 mm total body length).

A further indication of the importance of stream insects to flycatchers and gleaners is shown in Figure 3. At one of the gallery forest sites during 1987, discharge decreased from 100 l/sec in June to 20 l/sec in July. By August, only isolated pools remained. Total densities of flycatchers and gleaners declined in proportion to decreases in stream insect emergence. In August, nearly all of the birds had moved downstream to reaches that still had flow.

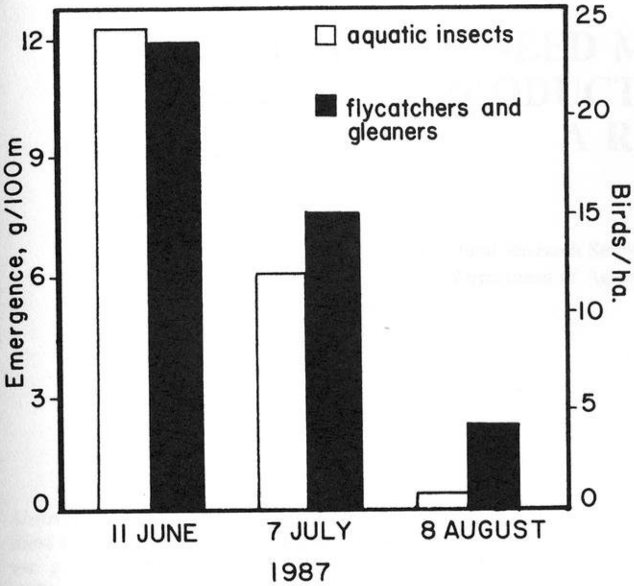


FIG. 3. Reduction in the combined densities of flycatchers and gleaners at a gallery forest site in response to decreases in aquatic insect emergence. Stream discharge declined from 100 l/sec on 11 June to 0 l/sec by 8 August.

Until the diets of insectivorous birds in riparian habitats of the Konza prairie can be analyzed in more detail, the contribution by stream insects is unknown. Although other factors are undoubtedly influencing the distribution of gleaners and flycatchers (e.g., competition, availability of nest sites, etc.), the strong correlations between bird densities and insect emergence, and field observations of feeding behavior, suggest that these birds are dependent to some extent on stream insects. Thus riparian habitats of tallgrass prairie streams, like that of desert streams, appear to be a concentrated source of insect food for riparian insectivores.

ACKNOWLEDGEMENTS

K. Johnson assisted with the field work, and E. Finck provided advice in the design of the bird census method. This research was supported by National Science Foundation Grant BSR-8704333 and the Division of Biology, Kansas State University, Manhattan.

LITERATURE CITED

Emlen, J.T. 1977. Estimating breeding season bird densities from transect counts. The Auk 94:455-468.

Finck, E.J. 1984. Male dickcissel behavior in primary and secondary habitats. Wilson Bulletin 96:672-680.

Gurtz, M.E., G.R. Marzolf, K.T. Killingbeck, D.L. Smith, and J.V. McArthur. 1982. Organic matter loading and processing in a pristine stream draining a tallgrass prairie/riparian forest watershed. Contribution No. 230, Kansas Water Resources Research Institute, Manhattan.

Jackson, J.K. and S.G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. Ecology 67:629-638.

Knopf, F.L., R.R. Johnson, T. Rich, F.B. Samson, and R.C. Szaro. 1988. Conservation of riparian ecosystems in the United States. Wilson Bulletin 100:272-284.

Zimmerman, J.L. 1982. Nesting success of Dickcissels (*Spiza americana*) in preferred and less preferred habitats. The Auk 99:292-298.

Zimmerman, J.L. 1985. The birds of Konza Prairie Research Natural Area, Kansas. Prairie Naturalist 17:185-192.

BLUESTEM SEED MIDGE INFLUENCE ON SEXUAL REPRODUCTION OF BIG BLUESTEM: A REVIEW

K.P. Vogel
Agricultural Research Service, U.S. Department of Agriculture,
Department of Agronomy, University of Nebraska

and

G.R. Manglitz
Agricultural Research Service, U.S. Department of Agriculture,
Department of Entomology, University of Nebraska, Lincoln, Nebraska 68583

Abstract. A Cecidomyiid midge (*Contarinia wattsi* Gagne') has been identified as a significant parasite of big bluestem [*Andropogon gerardii* Vitman var. *gerardii*] by adversely affecting the production of viable seeds. The midge was first identified from specimens collected from big bluestem racemes in 1983 in eastern Nebraska. Subsequent collections and studies have shown that it is widespread in the Great Plains, and that it can reduce seed yields of big bluestem by over 40%. The midges apparently over winter as diapausing larvae in disarticulated spikelets, emerge as adults at the time of early panicle emergence, and lay their eggs near developing caryopses. The larvae feed on the developing caryopses, pupate, and develop into adults within the florets. The adults emerge without leaving a trace. Up to three generations may occur per year with generation intervals of 13 to 16 days. The bluestem midge, in turn, is parasitized by a wasp that remains unidentified.

Key Words. big bluestem, *Andropogon gerardii, Contarinia wattsi*, cecidomyiid, midge, seeds, prairie insects, Nebraska

INTRODUCTION

Big bluestem (*Andropogon gerardii* Vitman var. *gerardii*) is one of the dominant grasses of the tallgrass prairie. Consequently, it has been the object of numerous botanical, ecological, management, and genetic studies. However, limited information is available on the effect of insects on its life cycle. Carter *et al.* (1988) recently reported that a Cecidomyiid seed midge (*Contarinia wattsi* Gagne') could reduce seed yields by over 40%. This midge, referred to as the bluestem seed midge, was first identified from specimens collected from big bluestem racemes grown in eastern Nebraska in 1983 (Carter *et al.*, 1988). The purpose of this report is to summarize the research that has been done to date on the bluestem seed midge and to describe the bluestem seed midge's effect on the sexual reproduction of big bluestem. Methods of studying the bluestem seed midge will be described.

Contarinia wattsi was first reared from racemes of little bluestem [*Schizachyrium scoparium* (Michx.) Nash] collected in New Mexico by Dr. J. G. Watts and was classified and named by Dr. R. J. Gagne' (1966). Gagne' (1966) also described another species (*Contarinia halliicola* Gagne') that was reared from racemes of sand bluestem [*Andropogon gerardii* var. *paucipilus* (Nash) Fern.] collected in New Mexico by J.G. Watts. Watts and Bellottii (1967) reported that *Contarinia wattsi* damaged 20% of the seed crop of little bluestem, while *Contarinia halliicola* and the larvae of another insect destroyed 30 to 60% of the sand bluestem seed crop in New Mexico.

The research that led to the discovery of the bluestem seed midge was initiated because of very low seed yields in big bluestem breeding nurseries and seed production fields that could not be attributed to weather or production practices. Insects were suspected because of previous research on the effect of the bromegrass seed midge (*Contarinia bromicola* Marilovski & Agafonova) on smooth brome (*Bromus inermis* Leyss.) seed yields in the Great Plains and in other areas where it is grown (Neiman and Manglitz 1972). At that time, the authors were not aware of the reports by Gagne' (1966) and Watts and Bellottii (1976). Both midges belong to the class of insects commonly known as "gall midges".

The life cycle of the bromegrass midge, in contrast to that of the bluestem midge, is well known and was described by Neiman and Manglitz (1972). Diapausing larvae of the bromegrass seed midge overwinter in fallen florets on or in the top few centimeters of the soil. A cold period followed by a warmer, moist period of at least six weeks is necessary to break larval diapause. The emergence of the adults of the overwintering generation is delayed until about the time of smooth brome panicle emergence. The adult midges live only one or two days and do not feed (Agafonova 1962). The adults mate and the female then lays eggs on the interior surface of the palea of the smooth brome floret. The larvae hatch, migrate to, and feed on the developing ovary which stops the development of the flower including stamens. The larvae pupate at the feeding site when they reach maturity and within two to three days, a new generation of adults emerge to repeat the process. Three generations of bromegrass midges have been reported to occur during a single season. The last larvae of the last generation feed on fertilized ovaries and developing caryopses and, instead of pupating, develop a cocoon and enter diapause. A wasp [*Tetrastichus* sp. (Hymenoptera:Eulophideae)] can parasitize all stages of the bromegrass midge with parasitism rates as high as 90%.

A midge (*Contarinia sorghicola* Coq.) of sorghum [*Sorghum bicolor* (L.) Moench] is first in importance of all sorghum insect pests on a worldwide basis (Young and Teetes 1977). Although it occurs on an annual grain crop, its biology is similar to the bromegrass midge (Walter 1941). A single sorghum seed midge can lay 28 to 144 eggs and, in Texas, it may have up to 13 generations per year (Walter 1941). Midges also have been reported to parasitize timothy (*Phleum pratense* L.) in Finland (Raatikainen *et al*. 1967).

MATERIALS AND METHODS

Different methods can be used to collect and study midges in native or planted stands of big bluestem. The procedures that have been used and their relative merits are briefly summarized below. These methods can be used on both natural grasslands or planted fields and pastures of big bluestem.

The most precise, but also the most difficult, method used to study the bluestem seed midge is hand dissection of inflorescences. Because of the small size of big bluestem florets and seed this is a tedious procedure, and only a limited number of samples can be dissected. The adult midge can be collected with sweep nets during its brief life cycle. Since the insect spends most of its life cycle in the larval or pupal stage, its presence in big bluestem stands may not be detected by using sweep nets.

Populations of midges infesting big bluestem can be monitored during the growing season by sampling raceme-bearing culms from big bluestem plants in the study site, transporting them to a laboratory, and placing them in water-filled flasks. The flasks containing racemes are then placed in opaque insect rearing cages. Insects emerging from the racemes are collected in clear glass vials (light traps) which are inserted into the sides of the cages. Racemes can be collected weekly to monitor the midge life cycle and midge numbers. This procedure was used in the initial study on the big bluestem seed midge by Carter *et al.* (1988).

Light traps (Figure 1) can also be used to collect midges from big bluestem seed. Moistened seed is placed on top of vermiculite or pearlite in sealed, opaque containers in a refrigerator at 4 C for approximately six weeks. The seed container is then removed from the refrigerator, placed on a laboratory bench, and vented with a light trap in its side. The seed needs to be kept moist. Viable seeds will germinate and produce seedlings within two to four weeks after being removed from the germinator. These seedlings can be removed when the seed is remoistened. The midges will emerge from the diapausing larvae inside the grass floret about six to eight weeks after the seed germinates. If the weight of seed and its per seed unit weight or the number of seeds that are placed in a container is known, then estimates of the degree of infestation of the seed by midges can be made. This method can also be used to determine the area of distribution of the midge. In addition to seed, litter from grasslands following seed shattering can also be used in the seed light traps. Hand dissection, sweep nets, and both the raceme and seed light traps can also be used to assay for the presence of any parasites of the midges.

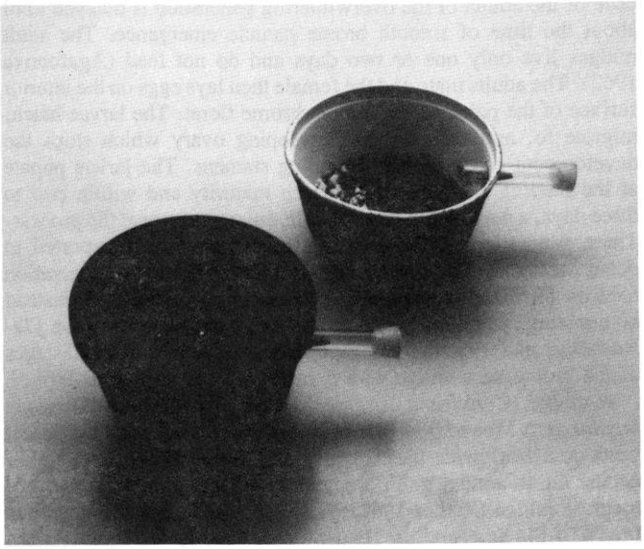


FIG. 1. A light trap for collecting midges emerging from big bluestem seed.

RESULTS AND DISCUSSION

Carter *et al.* (1988) reported that the number of bluestem seed midges that emerged from big bluestem racemes in insect rearing cages at weekly intervals indicated that at least three generations of the midge occurred in eastern Nebraska. Generations were indicated by peaks in midge numbers that occurred at about 13- to 16-day intervals (Figure 2). The first generation adults (Figure 3) are believed to emerge from diapausing larvae (Figure 4) at about the time of panicle emergence. Second and third generation midge adults left no evidence of their former presence in the floret making damage assessment difficult (Carter *et al.* 1988).

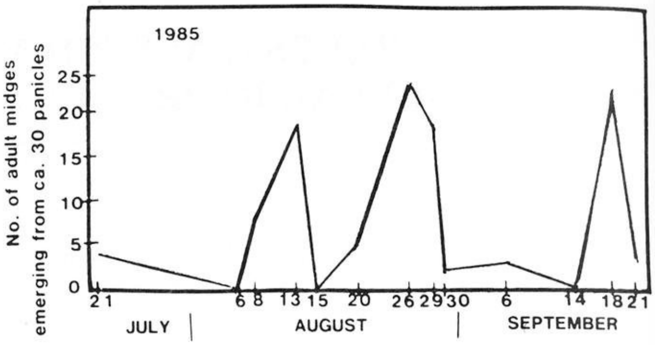


FIG. 2. The emergence of adult midges from field collected racemes of big bluestem during 1985 at Mead, Nebraska (from Carter *et al.* 1988).

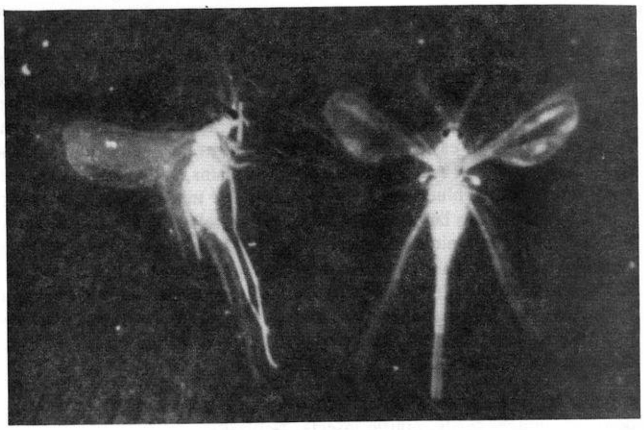


FIG. 3. The bluestem seed midge female (actual length is approximately 3 mm).

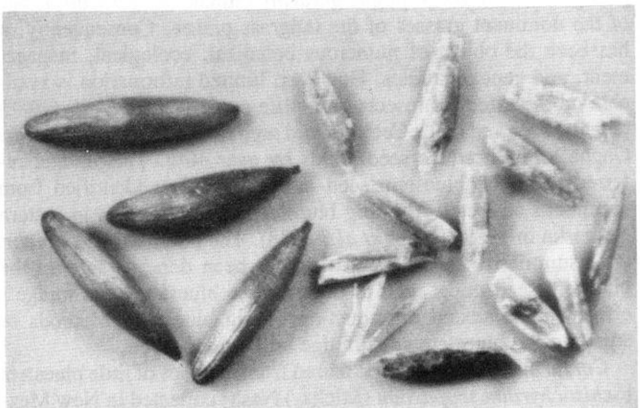


FIG. 4. Caryopses of big bluestem (left) and diapausing larvae of the bluestem midge (right).

Hand dissection of florets during the growing season demonstrated that the percentage of infested florets increased during the season, indicating an increase in the midge population during the growing season (Carter *et al.* 1988). Hand dissection of seed samples from two different seed production nurseries in eastern Nebraska indicated that the midge can substantially reduce seed yields (Table 1). The florets with small or no caryopses could have been damaged by previous generations of the midge. Carter *et al.* (1988) dissected both the pedicellate and sessile spikelets, because Boe *et al.* (1983) reported that pedicellate spikelets in big bluestem seed production fields may be fertile. Since many of the pedicellate spikelets do not set seed, Carter *et al.* (1988) estimated that the midge reduced seed yields in a 'Pawnee' big bluestem seed field by at least 40% in 1985. Boe (1988) reported that the percentage of mature big bluestem florets that contained diapausing midge larvae was as high as 27% for sessile spikelets and 3% for pedicellate spikelets in South Dakota. Cornelius (1950) reported finding larvae of an insect in 13% of the florets of big bluestem examined in 1945. He was not able to identify the insect, but, from his description, it was probably the bluestem seed midge.

Table 1. Seed development and presence of midges in two seed fields of big bluestem cultivars in eastern Nebraska in samples collected 21 September 1985 (from Carter *et al.* 1988).

	Field	
Floret categories	*'Pawnee'*	*'Kaw'*
	--------%--------	
Normal seed	23	41
Small seed	12	34
No seed	47	18
Midge	18	7

In 1987, many farmers and ranchers attempted to harvest big bluestem seed from native grasslands in northern Nebraska because of the high seed price and what appeared to be a good seed crop based on the number of racemes. However, the amount of harvestable big bluestem seed on many of these grasslands was negligible because of empty florets. Since other factors that could have limited seed set were favorable, it is believed that the bluestem midge was responsible for the almost complete loss of this seed crop.

Midges have been reared from seed of the big bluestem cultivars 'Pawnee' and 'Kaw' and the sand bluestem cultivar 'Goldstrike' harvested in eastern Nebraska and from 'Champ' harvested in central Nebraska. Thus the bluestem seed midge appears to be widespread throughout the Central Great Plains, and it could have a substantial impact on commercial seed production in some years. Its economic impact on big bluestem seed production is substantial, since seed prices often exceed $10/kg and can be as high as $50/kg.

Bluestem seed midges have been collected from both burned and unburned grass seed production fields and breeding nurseries. The 'Pawnee' big bluestem field studied by Carter *et al.* (1988) (Table 1) had been burned every spring for over ten years and still had substantial numbers of midges. Controlled studies on the effect of burning on midge numbers are needed.

Wasps, which are midge parasites, were collected along with midges from grass seed fields in 1987 in Saunders and Cass counties in Nebraska. The parasites are unclassified but appear to be *Tetrastichus* sp. (Hymenoptera:Eulopideae). The number of parasites increased during the growing season as did the number of midges (Table 2). In order for the parasites to develop, midge larvae need to be present. Hence, midge and parasite numbers represent the number of caryopses damaged by that generation of the midge. Diapausing larvae of the midge and presumably of the parasitic wasp were obtained by hand dissection from seed harvested from the Cass County field.

Table 2. Big bluestem seed midges and midge parasites collected in laboratory light traps from 25 big bluestem racemes from Saunders and Cass Counties, Nebraska collected during the first week of August and September 1987.

Location	*August*		*September*	
	Midge	*Parasite*	*Midge*	*Parasite*
	------------	Number	------------	
Saunders Co.	7	1	37	43
Cass Co.	7	1	31	22

SUMMARY

The bluestem seed midge appears to be a significant parasite of big bluestem, and it has the capability to greatly reduce the production of viable seed. The discovery of the midge parasite indicates that a biological control mechanism exists. The damage to big bluestem seed production by the bluestem seed midge is likely determined by relative numbers of midges and parasites. It is assumed that the parasite's life cycle is closely matched to that of the bluestem midge which, in turn, is matched to that of big bluestem. Precipitation and other climatic factors affect seed production of big bluestem. These factors combined with the parasitism of the bluestem seed midge determine the extent of sexual reproduction of big bluestem by seed. Although it is assumed that the life cycle of the bluestem seed midge is similar to that of the bromegrass and sorghum midge, no information is available on overwintering of the bluestem seed midge in natural grasslands, mating and egg laying processes of the adults, life span and mobility of the adults, feeding behavior of the larvae, and many other aspects of the bluestem seed midge's life cycle and biology.

Midges have also been reared from indiangrass and little bluestem seed produced in Nebraska by G. R. Manglitz. Because of the great similarities between species of midges, it is not known whether the midges from the different species of grass are all the same or belong to two or more species. It is apparent that an insect complex affecting seed production exists for several important prairie grasses.

LITERATURE CITED

Agafonova, Z.Y. 1962. Development of the midge *Stenodiplosis bromicola* Mar. et Ag. (Diptera: Itonididae), in relation to peculiarities of brome biology (*Bromus inermis* Leyss. and *riparius* Rehm.) Entomological Review. 41:11-21.

Boe, A.A. 1988. Biological aspects of seed production in big bluestem. Pages 37-43. *In* J.R. Johnson and M.K. Beutler (eds.). Proceedings Northern Great Plains Grass Seed Symposium, Pierre, South Dakota.

Boe, A.A., J.G. Ross, and R. Wynia. 1983. Pedicellate spikelet fertility in big bluestem from eastern South Dakota. Journal of Range Management 36:131-132.

Carter, M.R., G.R. Manglitz, M.D. Rethwisch, and K.P. Vogel. 1988. A seed midge pest of big bluestem. Journal of Range Management 41:253-254.

Cornelius, D.R. 1950. Seed production of native grasses under cultivation in eastern Kansas. Ecological Monographs 20:3-29.

Gagne', R.J. 1966. The neartic species of *Contarinia* which infest grasses (Diptera:Cecidomyiidae). Proceedings of the Entomological Society of Washington 68:318-321.

Neiman, E.L., and G.R. Manglitz. 1972. The biology and ecology of the bromegrass seed midge in Nebraska. Nebraska Agricultural Experiment Station Research Bulletin 252.

Raatikainen, M., O. E. Savas, and A. Tinnila. 1967. Contarinia Kanervoi Barnes (Dipt. Itonididae), bionomics, damage, and control. Annales Agriculturae Fenniae 6:145-158.

Walter, J.G. 1941. The biology and control of the sorghum midge. United States Department of Agriculture Technical Bulletin 778.

Watts, J.G., and A.C. Bellotti. 1967. Some new and little known insects of economic importance on range grasses. Journal of Economic Entomology 60:961-963.

Young, W.R., and G. L. Teetes. 1977. Sorghum entomology. Annual Review of Entomology 22:193-218.

DESIGNING WITH PRAIRIE: A HEIDEGGERIAN HERMENEUTICAL ANALYSIS

Evelyn A. Howell and Dave Egan
Department of Landscape Architecture, 25 Agriculture Hall, 1450 Linden Drive,
University of Wisconsin-Madison, Madison, Wisconsin 53706

Abstract. Landscape architects have been advocating the use of native species in designs for over 100 years. This Heideggerian hermeneutical analysis of the work of authors from 1919 to 1929 yields several underlying themes regarding the use of native species: 1) biological conservation (preservation), 2) possession (control of human-ordered world), 3) promotion of national and regional identity, 4) spirituality, and 5) aesthetics. The prairie-inspired designs of Jens Jensen, Darrel Morrison, and John Diekelmann illustrate the ways in which the emphasis placed on these themes and different assumptions about ''prairie'' influence the resultant plantings. Jensen's works are meant to evoke the relationship of people to a higher power, Morrison's are concerned with the visual impact of prairie and the feelings this evokes, and Diekelmann's are meant to unveil the phenomenon of nature and the associated interrelated play of human existence.

Key Words. design, history, landscape architects, landscape architecture, natural landscaping, prairie

INTRODUCTION

Designers often approach natural landscaping without an explicit idea about what it is they are trying to achieve or an historical perspective about what others have done. Most landscape architects have been inspired by nature, if only to react against its perceived characteristics. The forms of their works are influenced by these perceptions or conceptual models whether or not they are consciously expressed. As a way to enable designers to understand the background of professional practice, this hermeneutical analysis attempts to elucidate the assumptions of early practitioners as expressed in their writings. In addition, an examination of the work of three landscape architects, who have clearly expressed the motivations behind their prairie designs, is described to explain how the assumptions and perceptions of designers influence their work. The following discussion is a synthesis of these preliminary efforts to understand what it is to design with prairie.

METHODS

The method used for this analysis was two-fold. First, selected natural landscaping texts published between 1919 and 1929 were analyzed using Heideggerian hermeneutics. This time period was chosen because a review of other sources (Hubbard and Kimball 1917, Robinette 1973) suggested that much attention was given to the natural landscape during this period. The purpose of hermeneutics is understanding (Heidegger 1962, Palmer 1969, Tesch 1987). The process involves reading and discussing the texts so that themes emerge.

The second part of the study examined the work of three landscape architects, Jensen, Morrison, and Diekelmann, in light of these themes. Articles by and about these practitioners were examined. In addition, an interview with John Diekelmann was transcribed and analyzed as a text.

Examination of Themes Pertaining to the Use of Native Plants in Design

The use of plants native to a region is not a new idea in landscape architecture. It has been advocated and accomplished in the United States for over 100 years. A review of the literature in the first two decades of the Twentieth Century reveals botanists (including members of the then relatively new field of ecology), landscape architects, and horticulturists all discussing the potential use of native plants. Five themes that weave through this literature have been identified. These are similar to ideas used by advocates of natural landscapes in the 1980s (Dyas 1975, Küchler 1973, Otto 1983).

The themes include:
1) Biological conservation (preservation)
2) Possession (control of human-ordered world)
3) Promotion of national and regional Identity
4) Spirituality
5) Aesthetics

Biological Conservation (Preservation)

The authors were alarmed by the changes evident in their lifetime which they attributed to the pressures brought about by increasing urbanization, industrialization, and the automobile:

> ''These beauties of our wild lands are free to the finder, but yearly they become more scarce. The green groves have passed from many a hillside; field crops now grow where we used to gather the wild phlox and the painted cup, and farther apart are the wild ladyslipper or moccasin flower. Less frequently than formerly can we gather armfuls of our Turk's cap lily.''
>
> Toole 1923 p. 5

> ''The great destructive agent to our native flowers is civilization and the operations that go with it. Cutting the forest, draining and plowing the meadows, building houses, roads, and railroad tracks, the smoke of cities, and the travel of feet—all these wipe our wild flowers out of existence. The only complete remedy would be for us to give up our civilized ways.''
>
> Hamblin 1922 p. 2

Alfred C. Hottes (1925) described another source of destruction:

> ''Some believe that they love nature. They have a fast car, which they pack to overflowing with persons disinclined to walk, the women prepare too much to eat, and after arriving at the spot they lie about on the grass and talk of every-day things—of the price of lots, and business conditions, and newspaper reports—blind to the beauties around them.''
>
> ''Others of these 'nature-lovers' set the example to their friends by destroying what they can see, remarking as they pull and break the plants, 'These flowers are so beautiful I am sorry we can't stay longer to take all of them.'''
>
> ''If it be Dogwood time, they ruin the trees as high as they can reach to break the branches. If it be a shaded, marshy spot, they step full force upon an orchid, because they have their eyes on the path which will take them from the place as quickly as possible.''
>
> Hottes 1925, pp. 163-164

The solutions proposed by the writers we reviewed include the preservation of species through landscape gardening, genetic improvement (Toole 1923, Hamblin 1922, Wilder 1919), restoration (Hamblin 1922), the creation of public and private nature reserves, and other protective measures *in situ* (Jensen 1921 and 1927) and *ex situ* (Durand 1923). It is interesting to note that most authors writing in the period did not or would not consider the possibility that the expansion of development and hence "progress" should be slowed.

Possession (Control of Human-Ordered World)

This is a curious or ironic theme in some ways, describing the human desire to dominate nature even in the name of preservation. Note that the passage by Toole (1923) quoted above ends with a lament that opportunities to harvest (possess) wildflowers were becoming more scarce. Preservation, in the form of natural landscaping, was seen by several authors as the best way to ensure a continuing supply (Toole 1923, Hamblin 1922). Toole (1923) appears to be primarily interested in preserving species for his nursery business.

Another aspect of this theme is the very fact that as native plants were becoming rare they became more "valuable." Therefore, their possession in a garden conferred status and power on the owner:

> "And while it is true that many of us do not begin to suspect the treasure trove contained in this flower gifted country of ours, we are making strides toward that knowledge, and each year longer lists of rare native plants appear in the collector's catalogues, and more gardening folk go afield in their own neighborhoods to seek out and establish in their gardens plants that have hither to gone unnoticed."
>
> Wilder 1919, p. 39

Similarly, in an era in which the "new look" was naturalistic, natives provided raw materials for the development of new varieties, which is another manifestation of the human desire to control nature:

> "With seedlings, there is a chance for variation and through selection one can plan for bringing out new varieties. Such opportunities are manifest in the phloxes, Jacob's ladder, the native asters, black-eyed Susan, wild lilies, pleurisy root and others. I have derived much satisfaction from this work with some of the kinds."
>
> Toole 1923 pp. 7-8

Others felt that by removing plants from their natural environment they could be improved and made more "worthy" (Toole 1923):

> "It is a common but mistaken impression that wild plants are inherently scraggly and unattractive in form. The fact is that if they are relieved of the intense competition that prevails in the wild and given room to develop in a congenial location, they quickly make luxurious growth, become compact and shapely and produce larger and better flowers in greater profusion.
>
> Durand 1923 p. 6

Promotion of National and Regional Identity

This theme has several aspects. One is a desire to preserve a regional American heritage. Jensen expresses the idea that the natural environment of the midwestern United States produced unique and desirable cultural characteristics and that it should be turned to for "new inspiration, for freshness, for vigor, and strength of mind" (p. 146):

> "Few who have been born and bred on the prairies are happy amongst the hills, with the vision shut in, and deprived of the beauty and expanse of the far distant horizon. Its influence on the imagination and the character of the prairie man and woman is already evident, whether in arts, in poetry, in politics, or in masters of industry, and one cannot foretell the growth of intellect due to the character molding by the prairie landscape. Masters like Louis Sullivan, Frank L. Wright, Walter Griffin, Vachel Lindsay and Carl Sandburg are all of mid-America growth."
>
> Jensen 1927 p. 130

A second aspect is a kind of American "nativism" and/or "chauvinism" based on reaction to our involvement in World War I. The title of two works from this period, one a book (Roberts and Rehmann 1929) and the second an article (Wilder 1919), is "American Plants for American Gardens". This phrase aptly describes the nativism and chauvinism that formed the basis of the arguments used by several authors to promote natural landscaping. "Nativism" means the idea of protecting the interest of native inhabitants against those of immigrants, "chauvinism" is the exhibition of zealous patriotism:

> ". . . many who give honored space to the splendid phloxes, the soft-toned physostegias, gayfeathers, and Michaelmas daisies, the evening primroses, lungworts, heucheras, mallows, penstemons, shooting stars, and many more of our established garden favorites, have no notion that they are entertaining good Americans who, but a short while since, have nodded their greetings from roadsides and meadows in various sections of our homeland."
>
> Wilder 1919 p. 39

> "Perhaps now that we are experiencing a better appreciation of things American than we have in the past, patriotism may incline us to wish to know more about our native shrubs."
>
> Toole 1923 p. 13

> "No remarks about American plants would be in any way adequate without mention of the vast numbers of native shrubs that are worthy to be grown among the best of the foreigners."
>
> Wilder 1919 p. 43

Spirituality

Several authors in the period express a profound emotional reaction to nature and the native species of which it is comprised. Several quote poetry, others philosophy; many describe scenes from nature in vivid terms. One of the dominant themes is that of spirituality. Two examples follow:

> "How are wild flowers most truly appreciated? The real enjoyment of nature depends upon ourselves. As Emerson says, "Nature reflects the color of the spirit." Go to the woods, according to your temperament, either in groups, alone, or with some congenial companion. Go whenever the spirit moves, at any time of the year, and there will be something to delight you, if you give yourself to the spirit of the place."
>
> Hottes 1925 p. 163

> "We marvel at their (native plants) various forms and the fitness of each to carry out the purpose given it by the Creator. Flowers speak more to our hearts than to our minds and intelligence, and it is in this that we are particularly interested at the present. We have toward favorite flowers an almost human affection. They become a part of our lives and by association come to have a symbolic meaning to us that early man never knew. This animism of flowers is bound to grow even more rapidly in the future, and have its peculiar phases among different peoples. The age of flower nymphs and flower fairies is passing, but still we can find the presence of something not to be seen by the human eye."
>
> Hamblin 1923 p. 87

Aesthetics

Aesthetics is also a way in which emotional reactions to native plants are discussed. All of the authors reviewed discussed this theme with two approaches being most common: 1) descriptions of the line, form, color, or texture of individual species and 2) descriptions of the effects achieved by the landscape as a whole (often expressed as "pictures"). For example, Hottes quotes naturalist Samuel Soville Jr:

> "In the half-light I knelt in the soft pine-needles and studied long the hollow purple pink shell (of *Cypripedium acaule*), veined with crimson, set between two other tapering petals of greenish-purple, while a sepal of the same color curved overhead. The whole flower swayed between two large, curved, grooved leaves".
>
> Hottes 1919 p. 165

Roberts and Rehmann (1929) describe native trees of the maple-hemlock-beech community as follows:

> "The hemlocks are tall evergreen trees with seal brown trunks, dropping branches and short flat needles. The maples are sturdy round-topped trees. Their trunks are furrowed and gray-brown, their strong branches are noticeably upright, their leaves are deeply lobed. The beeches are broad symmetrical trees. Their smooth trunks are steel gray, their horizontal branches are placed in widespread tiers, their slender buds and pointed leaves are arranged far apart on spray-like stems."
>
> Roberts and Rehmann 1929 p. 57

Herbert Durand (1923) in describing the approach one should take in establishing a natural garden writes:

> "The natural features of the place—such as the contours of the ground, the distant outlooks, the sky lines, desirable indigenous trees and shrubs—should be scrupulously preserved, so that by embellishing them and by guiding and encouraging Nature in their development, a series of delightful pictures will be created that are faithfully expressive of that simplicity, refinement and endless variety of form and color which characterize our American scenery."
>
> Durand 1923 pp. 3-4

Jens Jensen, whose work we will be discussing in some detail below, often referred to the color of natural scenery which he tried to emulate in his designs:

> "Those who have seen the rim of the oak forest, festooned with the delicate pink of the crab apple blossom, entwined in the silver and rosy buds of the oak, against the blue sky of May, must have been inspired by their color composition—a symphony of colors, so to speak."
>
> Jensen 1927 p. 130

These visual values of nature were apparently a strong selling point for natural landscaping.

All of these themes have been echoed in modern times. Two new ideas have emerged in the writings of recent natural landscaping advocates. The first is that of energy and resource conservation (Morrison 1981). The second is a phenomenological approach that explores how humans are in their comportment towards involvement in the natural world. The phenomenon of "dwelling as a coming-into-nearness" with the natural world is grounded in Heideggerian phenomenology and advocated by Diekelmann (1988a) among others.

Prairie-Inspired Designs of Jens Jensen, Darrel Morrison, and John Diekelmann

The diverse prairie designs and writings of three landscape architects, Jens Jensen, Darrel Morrison, and John Diekelmann, illustrate the way in which different assumptions about the nature of "prairie", and different emphases on the themes discussed above result in very different plantings. These assumptions and emphases were influenced in turn by the uses for which the sites were designed, plant material availability, the sophistication of knowledge about species requirements, and the cultural context in which these individuals worked. These three designers were selected because of an intellectual and, in some cases, a direct connection between them, and because they worked or are working in the upper Midwest.

Jensen, Morrison, and Diekelmann have several things in common in their approaches to prairie design. Most importantly: 1) they view the prairie as a community (as a whole) and not simply as a source of interesting plant materials; 2) they are motivated to create plantings for the benefit of people and the human spirit, not only to preserve species; and 3) there is more to the plantings than just copying nature, because the approach and process and the involvement and experience of people are paramount.

1. Jens Jensen

Jens Jensen designed public parks and gardens as well as private estates during the period 1888 to 1951. To Jensen, the spatial character of prairies (horizontal lines, flowing spaces) embodied the freedom of the human spirit:

> "To many, the prairie country is monotonous and uninteresting, but to us who have lived with it most of our lives it shows great breadth and freedom that works upon the imagination in many ways."
>
> Jensen 1927 p. 130

In nature one could see God's work:

> "The landscape unadulterated by man is a finer thing than that which man calls his work. It has something of a spiritual nature that is beyond man's ability. There is a mystery and a charm about it that leads one into a new realm of untold beauty, full of inspiration and a freshness and vigor that stimulates you to action. It is a different world—a world not of our making, that opens visions of depth and grandeur, with endless themes and forms for study, for spiritual enjoyment, and for a richer and broader life."
>
> Jensen 1927 p. 129

Landscape architects, using native species, translate this "prairie spirit" into a form which can be enjoyed in a human setting:

> "The real worth of the landscaper lies in his ability to give to humanity the blessings of nature's spiritual values as they are interpreted in his Art. The field is boundless, and there is no need of importing from foreign shores."
>
> Jensen 1939 p. 2

> "But in trying to make the garden natural, we must not make the mistake of copying Nature . . . Art idealizes; it is creative, and a reproduction is only a reproduction, no matter how fine and noble the model is. The landscape garden must have a dominant thought in it. To me, that feeling should be spiritual; it should be love for the great out-of-doors, for the world that God made."
>
> Jensen 1930b p. 169

The garden writer Wilhelm Miller describes Jensen's design for the Henry Ford Estate in Dearborn, Michigan as follows: "Of course

> the garden does not attempt to reproduce literally the broad, treeless prairie. No garden can do that because it would require too great a scale. It merely embodies. The open part or lawn suggests the freedom and flatness of the prairie, the irregular border of trees suggests the woods that line the every river. . . . The case is analogous to program music. Beethoven in his "Pastoral Symphony" did not try to imitate a storm. Music cannot do that, but music can arouse in us the emotions we have during a storm."
>
> Miller from Eaton 1964 p. 128

A similar approach can be seen in Jensen's design for Columbus Park, Chicago, Illinois, illustrated in Figure 1 and described in Table 1. Jensen did not use many true prairie species in this design, being mostly concerned with the placement of woody materials to create the open spaces that represented the freedom of the prairie in his conception. In part this may be a result of lack of knowledge about prairie grass cultivation, although Jensen was reputedly quite knowledgeable about native materials and also because this open space was designed for active use as a golf course. On the other hand, one could say that his attention was not on creating diversity; but on representing the spatial essence of the prairie.

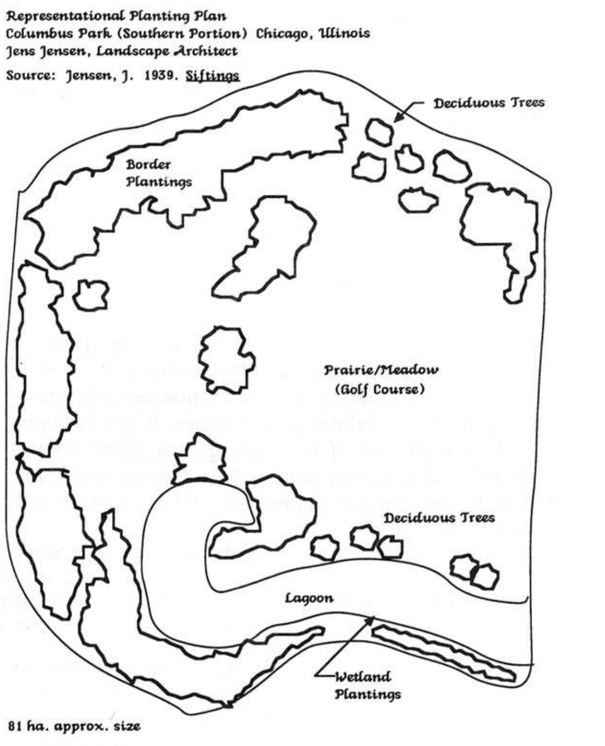


FIG 1. Representational planting plan for Columbus Park, Chicago, Illinois. Jens Jensen, Landscape Architect.

Table 1. Plantings[1] for Columbus Park, Jens Jensen, Landscape Architect.

Trees:	
Acer saccharum	Sugar Maple
Fraxinus sp.	Ash
Prunus sp.	Cherry
Quercus sp.	Oak
Tilia sp.	Linden
Ulmus sp.	Elm
Undergrowth Among the Trees:	
Cornus racemosa	Gray dogwood
Hamamelis virginiana	Witch hazel
Viburnum lentago	Sheepberry
Viburnum sp.	Viburnum
Border Plantings: Shrubs	
Cornus racemosa	Gray dogwood
Cornus stolonifera	Red dogwood
Crataegus sp.	Hawthorn
Hamamelis virginiana	Hazel
Physocarpus opulifolius	Ninebark
Prunus americana	Plum
Prunus virginiana	Chokecherry
Pyrus sp.	Crabapple
Rosa sp.	Prairie rose
Viburnum lentago	Sheepberry
Prairie Flowers in Open Spaces Bordering Meadow:	
Aster sp.	Asters
Dodecatheon meadia	Shooting star
Echinacea sp. or *Ratibida* sp.	Coneflower
Phlox sp.	Phlox
Solidago sp.	Goldenrod
Understory:	
Anemone sp.	Anemones
Claytonia virginica	Spring beauty
Erythronium	Dogtooth violet
Polemonium reptans	Jacob's ladder
Trillium sp.	Trillium
Viola sp.	Violet
Wetland Plantings:	
Cornus stolonifera	Red dogwood
Hibiscus palustris	Rose mallow
Juncus sp.	Rushes
Nuphar sp. or *Nymphaea* sp.	Water Lily
Ribes sp.	Yellow currant
Sagittaria sp.	Arrowhead
Sambucus sp.	Elderberry
Staphylea trifolia	Bladdernut
Typha sp.	Cattail

[1]From Jensen (1930a). In this text, species are listed by common name only. Identification of botanical taxa is based on the authors' knowledge of Jensen's work. See Great Plains Flora Association (1986) for appropriate authorities for the scientific names.

2. Darrel Morrison

Darrel Morrison, like Jensen, was interested in embodying an idea of prairie in design. His concept emphasizes aesthetics, what he calls the "visual essence" of prairie:

> ". . . there is not, and indeed there cannot be a single 'recipe' for design and implementation of a successful prairie planting. . . . Some may be aesthetically-oriented with a primary goal of recreating the 'visual essence' of prairie with tall grasses waving in the wind, interspersed with contrasting colors and textures of prairie forbs.
>
> Morrison 1981 p. 11

Morrison worked with prairie in the 1970s and early 1980s, designing home grounds and industrial sites. He was highly influenced by Jensen's designs and can be said to have taken Jensen's spatial concept and expanded on it by concentrating on the species composition of the open space.

Morrison's designs consist of selected groupings of species chosen to represent typical botanical compositions and what he understood to be the ecological structure of prairie, combined to create characteristic "scenes". These scenes are adapted to the purpose at hand. Plantings meant to be viewed at a distance are handled differently from more garden-like arrangements meant to be viewed up close (Howell and Morrison 1979).

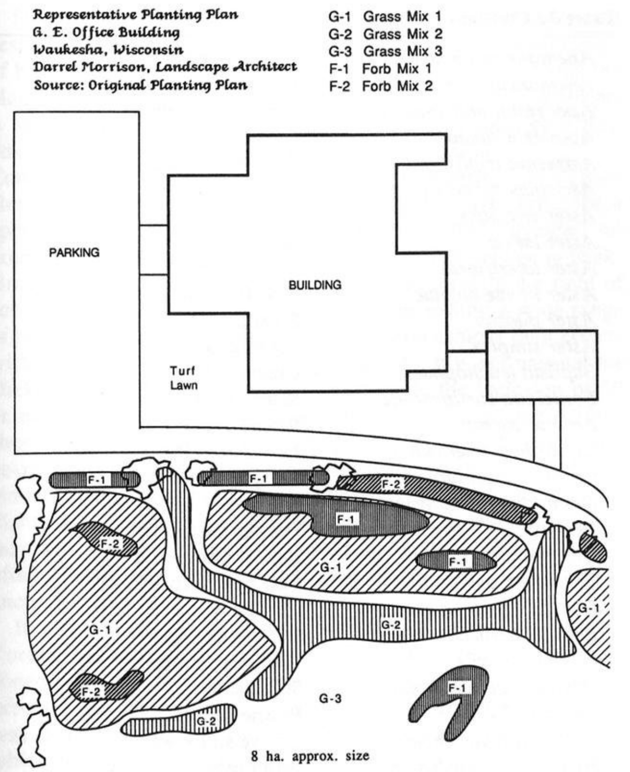


FIG 2. Representational planting plan for General Electric Office Building, Waukesha, Wisconsin. Darrel G. Morrison, Landscape Architect.

Table 2. Plantings[1] for General Electric Company, Darrel Morrison, Landscape Architect.

Grass Mixture 1:	
Bouteloua curtipendula	Sideoats grama 10%
Schizachyrium scoparium	Little bluestem 75%
Stipa spartea	Needlegrass 15%
Grass Mixture 2:	
Bouteloua curtipendula	Sideoats grama 10%
Schizachyrium scoparium	Little bluestem 70%
Sporobolus heterolepsis	Prairie dropseed 10%
Stipa sparea	Needlegrass 10%
Grass Mixture 3:	
Andropogon gerardii	Big bluestem 40%
Panicum virgatum	Switchgrass 15%
Schizachyrium scoparium	Little bluestem 15%
Sorghastrum nutans	Indiangrass 30%
Forb Mixture 1:	
Amorpha canescens	Leadplant
Baptisia leucantha	White false indigo
Echinacea pallida	Pale purple coneflower
Echinacea purpurea	Purple coneflower
Liatrus aspera	Rough blazingstar
Rudbeckia hirta	Black-eyed susan
Solidago rigida	Stiff goldenrod
Solidago speciosa	Showy goldenrod
Forb Mixture 2:	
Amorpha canescens	Leadplant
Lespedeza capitata	Prairie bush-clover
Monarda fistulosa	Bergamot
Ratibida pinnata	Gray-headed coneflower
Solidago rigida	Stiff goldenrod

[1]From original planting plan. See Great Plains Flora Association (1986) for proper authorities for scientific names.

Figure 2 and Table 2 illustrate one of Morrison's early prairie projects. The General Electric planting is meant to be viewed at a distance and represents a prairie scene in which color and texture contrasts created by the drifts of forbs among the grass background predominate. Morrison describes his approach as follows:

> ''Within the general category of species selection, an important consideration in ultimately achieving the appearance of prairie is the proportion of grasses to forbs. In the prairie stands studied by Weaver, he found grasses comprising 95 percent of the vegetational cover (Weaver, 1968). The importance of grasses is not only in quantitative terms, but also in terms of visual character of prairies. The linear form of the grass blades . . . , unify it visually. Further, this screen of narrow, predominantly vertical lines 'filters' the sometimes blatant flower colors and modifies the effect of coarse-textured leaves. Extending a bit further into the subjective evaluation of the effects of grasses on prairie aesthetics, there is the important element of movement displayed by them. This quality, perhaps more than any other is critical in imparting a 'prairie spirit' to a landscape (Morrison 1980).''
>
> Morrison 1981 p. 12

> ''A visual analysis of natural prairies from a distance often reveals a degree of 'zoning' of species, seen as 'bands' or 'drifts' of different colors or textures, blending or grading one into the next. Typically, these are not sharply defined, but in some cases, they may be quite apparent.''
>
> Morrison 1981 p. 12

The results are generally simplifications of natural stands, especially for plantings several acres in extent. To some extent this effect was part of Morrison's aesthetic concept, but it was probably also influenced by the pragmatics of working in an era in which large quantities of seed (especially of forbs) and large numbers of species were not available.

3. John Diekelmann

John Diekelmann was a student of Morrison and a reader of Jensen. His prairie designs have been implemented in the 1980s and involve residential sites. In landscaping with prairie, Diekelmann seeks to provide complex intellectual and emotional stimulations. He is concerned with ''the how'' or the ways in which one approaches the landscape. Thus the lived experiences of his clients—the way in which they dwell in his planned landscapes—as well as the practice of ''being-in-the-world'' (Heideggar 1962) as a landscape architect are integral parts of his approach. His work and writings are influenced by the German philosopher, Martin Heideggar, among others. Diekelmann describes the practice of landscape architecture as a return to a phenomenological understanding of the indigenous landscape as well as landscape architectural practices. He sets his conceptions apart from several of the themes advocated by others.

> ''If we look for a meaning in Nature, we could say that it has intrinsic worth in and of itself, independent of our subjugating it.''
>
> Diekelmann 1988b p. 42

> ''Let me then submit my interpretation of what natural landscape is taken to be and what it can be and why. For the most part natural landscaping is not:
>
> 1. The planting of weeds . . .
> 2. Neglect . . .
> 3. Chaotic. There is a dynamic order to ecosystems that we are only beginning to understand.
> 4. Jingoistic. Plants indigenous to a place are encouraged to inhabit it not because they are 'Americans' but because they have an intrinsic right to exist independently of us.
> 5. Subjugation. Plantings are controlled, but they are controlled through the understanding of the intrinsic Being of beings in relation to human culture.''
>
> Diekelmann 1988a pp. 6-7

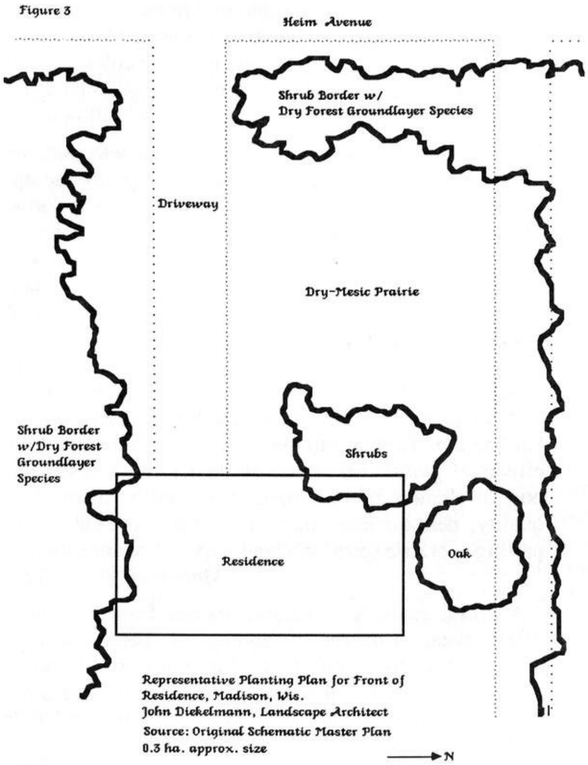


FIG 3. Representational planting plan for residence, Madison, Wisconsin. John Diekelmann, Landscape Architect.

Table 3. Plantings[1] for residence in Madison, Wisconsin, John Diekelmann, Landscape Architect.

Dominant:	
Rosa blanda	Thornless rose
Sorghastrum nutans	Indiangrass
Common:	
Asclepias syriaca	Common milkweed
Cacalia atriplicifolia	Indian plantain
Carex pensylvanica	Pennsylvania sedge
Coreopsis palmata	Stiff coreopsis
Dodecatheon meadia	Shooting star
Erigeron sp.	Fleabane
Erythronium albidum	White trout-lily
Eupatorium rugosum	White snakeroot
Euphorbia corollata	Flowering spurge
Geranium maculatum	Wild geranium
Helianthus divaricatus	Woodland sunflower
Hysterix patula	Bottle-brush grass
Monarda fistulosa	Bergamot
Potentilla simplex	Old-field cinquefoil
Ratibida pinnata	Gray-headed coneflower
Smilicena stellata	Starry false soloman's seal
Solidago altissima	Tall goldenrod
Solidago canadensis	Canada goldenrod
Solidago rigida	Hard-leaved goldenrod
Tradescantia ohiensis	Spiderwort
Veronicastrum virginicum	Culver's root
Occasional (ten stems or less):	
Achillea millefolium	Yarrow
Agrimonia sp.	Agrimony
Ambrosia psilostachya	Western ragweed
Amphicarpa bracteata	Hog peanut
Andropogon gerardii	Big bluestem
Anemone patens	Pasqueflower
Anemone quinquifolia	Wood anemone

Table 3. Continued

Anemone virginiana	Thimbleweed
Anemonella thalictroides	Rue-anemone
Apocynum androsaemifolium	Spreading dogbane
Aquilegia canadensis	Columbine
Arisaema triphyllum	Jack-in-the-pulpit
Asclepias tuberosa	Butterflyweed
Aster ericoides	Heath aster
Aster laevis	Smooth aster
Aster lateriflorus	Calico aster
Aster novae-angliae	New England aster
Aster pilosus	Frost aster
Aster simplex	Panicled aster
Baptisia leuchophaea	Cream wild indigo
Bouteloua curtipendula	Sideoats grama
Bromus kalmii	Brome grass
Ceanothus americanus	New Jersey tea
Convolvus sepium	Hedge bindweed
Desmodium canadense	Showy tick-trefoil
Desmodium glutinosum	Pointed-leaved tick-trefoil
Desmodium illinoense	Illinois tick-trefoil
Echinacea pallida	Pale purple coneflower
Elymus canadensis	Canada wild rye
Eryngium yuccifolium	Rattlesnake master
Galium boreale	Northern bedstraw
Gentiana quinquefolia	Stiff gentian
Geum triflorum	Prairie smoke
Heliopsis helianthoides	Ox-eye sunflower
Heuchera richardsonii	Alum root
Liatrus aspera	Rough blazingstar
Oenothera biennis	Evening primrose
Oxalis violocea	Violet wood-sorrel
Panicum sp.	Panic grass
Parthenocissus sp.	Virginia creeper
Pedicularsis canadensis	Lousewort
Phlox pilosa	Downy phlox
Polygonatum canaliculatum	Great solomon's seal
Quercus macrocarpa	Bur oak (saplings)
Rudbeckia hirta	Black-eyed susans
Sanguinaria canadensis	Bloodroot
Schizachyrium scoparium	Little bluestem
Silene stellata	Starry campion
Silphium laciniatum	Compass plant
Smilacina racemosa	False solomon's seal
Smilax lasioneura	Greenbriar
Solidago juncea	Early goldenrod
Soldago speciosa	Showy goldenrod
Thalictrum dasycarpum	Purple meadow-rue
Uvularia grandiflora	Large-flowered bellwort
Verbena urticifolia	White vervain
Vitis sp.	Wild grape
Zizea aptera	Heart-leaved golden alexander
Zizea aurea	Golden alexander

[1]See the Great Plains Flora Association (1986) for authorities for scientific names.

An example of a portion of one of Diekelmann's residential designs is illustrated by Figure 3 and Table 3. As Diekelmann (1988b) expresses it, his prairie designs:

> 1. Carefully match plants to environmental conditions.
> 2. Bring together as many species that are found in prairies as possible, as it is in diversity that the essence and therefore the meaning of the community lies.
> 3. Strictly within this framework (points 1 and 2), use a variety of studied visual relationships to highlight certain areas when possible or desirable because of the site's use.
> 4. Work with natural processes even if they change the composition, but allow for intervention to add propagules or remove exotics.
>
> Diekelmann 1988b p.35

Diekelmann's approach considers traditional visual aspects of aesthetics, but also goes beyond this to stress the ''experience'' of being in a plant community. To encourage ''dialogue'' with the planted landscape in a way that creates new meanings for people is seen by Diekelmann as a better approach to landscaping than other expressions that symbolize human dominance.

Considering the prairie landscapes of Jensen, Morrison, and Diekelmann as a group, several comparisons can be made. First, there appears to be an increased understanding of the ''science'' of prairies moving chronologically from Jensen to Morrison to Diekelmann. This is in large part because of advances in the field of ecology over this time. Second, the designs exhibit a wide range of botanical complexity. Jensen and Morrison achieve their effects with relatively few species (Tables 1 and 2). It is not unusual for Diekelmann, on the other hand, to advocate the inclusion of 50 or more species even on a small home site. Third, the designs show a range of obvious control by people. Some of Jensen's later designs, such as Springfield Gardens, and some of those by Diekelmann appear superficially to be out of control and without order. Plants are placed seemingly at random and left to reproduce where they will, rather than being confined to designated, clearly defined often ''balanced'' locations. These designs make some people uncomfortable.

In a sense, the works of these designers all reflect a search for ''order'' which evolved differently for each of them. Jensen was concerned with spirituality, seemingly in a reaction to what he perceived as the materialism of his day (Jensen 1921). Morrison was in part reacting to the environmental crisis of the 1970s in which energy and other natural resources were perceived as running out. Diekelmann was reacting to what he perceived as the increasing attempts of people to control nature and to the crisis of our increasing alienation from the biosphere.

If one wanted to characterize the works of each of these designers, one could say that Jensen's are meant to evoke the relationship of people to a higher power; Morrison's are concerned with the visual impact of prairie and the feelings this evokes; and Diekelmann's are meant to re-involve as with the flux and mystery of our relationship with indigenous landscapes.

CONCLUSIONS

Landscaping with indigenous plants is a means of expressing our relationships with the natural world. Advocates over many years have shared a belief in the value of natural elements in day to day life. However, notions as to what this ''value'' is are quite varied, and have led to different activities ranging from attempts to use ''improved'' natives in traditional garden settings to preserving intact communities.

The prairie-inspired designs of Jensen, Morrison, and Diekelmann, illustrate this concept. Their very different creations are studied evocations of individual reactions to experiencing prairie. They reflect the practices of the designers and the cultural contexts in which they arose. They are ''successful'' because they each have an underlying framework that can be communicated to those experiencing the plantings.

It is important that all of us who design with prairie adopt and explain our own ''frameworks'' so that our creations, too, can begin to communicate particular concepts. In this way, natural landscaping can begin to be seen, not just as a means of assembling indigenous plants in which any arrangement or grouping goes (a criticism that we have heard voiced on several occasions by the public and landscape professionals alike), but as sophisticated design expressions.

LITERATURE CITED

Diekelmann, J. 1988a. From place to placeness. Unpublished text of presentation at the Annual Meeting of the New Jersey Chapter of the American Society of Landscape Architecture. 28 January 1988.

Diekelmann, J. 1988b. Transcript of personal interview. 24 June 1988.

Durand, H. 1923. Taming the wildings. G.P. Putnam & Sons, New York.

Dyas, R.W. 1975. Landscape design with prairie plants. Pages 411-416. *In* M.K. Wali (ed.). Prairie: A multiple view. University of North Dakota Press, Grand Forks.

Eaton, L. 1964. Landscape artist in America: The life and work of Jens Jensen. University of Chicago Press, Chicago.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence.

Hamblin, S. 1922. Increasing native perennial flowers. Landscape Architecture Quarterly 8:1-18.

Hamblin, S. 1923. Man's spiritual contact with nature. The Gorham Press, Boston.

Heideggar, M. 1962. Being and time. J. Macquarrie and E. Robinson, translators. Harper and Row, New York.

Hottes, A.C. 1925. About wild flowers. Wisconsin Horticulture July: 162-165, 167, 169.

Howell, E.A., and D.G. Morrison. 1979. Approaches to the design of small prairie plantings. Unpublished manuscript.

Hubbard, H.V., and T. Kimball. 1917. An Introduction to the study of landscape design. Macmillan, New York.

Jensen, J. 1921. Wisconsin beautiful. The Country Magazine May:10-11.

Jensen, J. 1927. Landscape appreciation. Wisconsin Horticulture May:129-130, 146-147.

Jensen, J. 1930a. The naturalistic treatment in a metropolitan park. American Landscape Architect January:34-38.

Jensen, J. 1930b. Natural parks and gardens (as told to Egna B. Eskil). Saturday Evening Post March 8:18-19, 169-170.

Jensen, J. 1939. Siftings. Ralph Fletcher Seymour, Chicago.

Küchler, A.W. 1973. The prairie as an aesthetic experience and a tool for public enlightenment. *In* L.C. Hulbert (ed.). Proceedings of the Third Midwest Prairie Conference. Kansas State University, Manhatten.

Morrison, D. 1981. Utilization of prairie vegetation on disturbed sites. Transportation Research Record 882:10-17.

Otto, L. 1983. Through our windows an alternative to lawns. Pages 179-181. *In* C.L. Kucera (ed.). Proceedings of the Seventh North American Prairie Conference. Southwest Missouri State University, Springfield.

Palmer, R. 1969. Hermeneutics. Northwestern University Press, Chicago.

Roberts, E.A., and E. Rehmann. 1929. American plants for American gardens. The Macmillan Company, New York.

Robinette, G.O. 1973. Landscape education, volume 2. American Society of Landscape Architects Foundation, Washington, D.C.

Tesch, R. 1987. Emerging themes: The researcher's experience. Phenomenology and Pedagogy 5:230-241.

Toole, W., Sr. 1923. Native plants of Wisconsin: Suitable for cultivation. Wisconsin State Horticultural Society Bulletin, Madison.

Wilder, L.B. 1919. American plants for American gardens. Country life in America July:39-43.

AN ESSAY ON THE CONCEPT OF DEMONSTRATION ROOFTOP PRAIRIES

Patrick Horsbrugh
Environic Foundation International, Incorporated,
916 South Vincent Street, South Bend, Indiana 46617

Abstract. The concept of demonstration prairies on the roofs of industrial and commercial premises is recommended as a means of stimulating interest in prairie ecology and of providing educational facilities in urban areas. The economics of such rooftop locations for prairie studies and research depends upon the multiple use of land for seemingly incompatible activities. The use of selected vegetation as an integral part of the structure provides the opportunity for the prairie to invade the city, while potentially offering the benefits of effective insulation, microclimatic modification, and reductions in roof maintenance costs. This would be one method to meet the unchallenged thrust of urban expansion at the cost of rural productivity. The use of roof areas for demonstration prairie research in urban areas would reveal the economic, psychological, and aesthetic value of introducing ecological influences to the city.

Key Words. rooftop prairies, demonstration prairies, design, prairie education

INTRODUCTION

I believe that prairie preservation is now an ecological necessity required to relieve the stresses imposed upon all natural resources by the character of modern life. Commercial enterprise must provide some compensation for the consequences of the continuing urban trespass upon the natural and agricultural landscape. In particular, the relentless sacrifice of prairies to urban growth must be reduced and redeemed by deliberate design.

Prairie conservation is both an ethical obligation and an ecological necessity, and it should recognize the entire environment. The importance of species diversity must be emphasized as part compensation for the abrupt interface between the vital grassland biome and the urban environment.

As a regional planner and architect, I maintain that technological capabilities now permit the use of indigenous vegetation on and over any structure. My proposal for the establishment of demonstration rooftop prairies is based upon several economic benefits to be gained from the integration of vegetation in the design of industrial and commercial accommodation, whereby urban conditions can be improved by stimulating public interest in ecology.

I advocate the provision of demonstration prairies by using the roof areas of factories, warehouses, shopping centers, and structures of like size, resulting in the achievement of economies in four directions simultaneously. First, industrial and commercial rooftops are now large enough to offer practical demonstration and experimentation in prairie ecology under controlled conditions, permitting a double use of the same area of land surface. Second, improved summer and winter insulation can be achieved by the use of soil and grasses on the roof, producing substantial economy in energy consumption. Third, the photosynthetic effect of grass covered roofs will reduce thermodynamic extremes, thereby improving the microclimatic conditions of the urban areas. Fourth, any increase in areas of vegetation by the use of rooftops will promote the diversity of species among insects, reptiles, and birds.

Success in promoting ecological variety and in extending habitat depends upon the economic balance between the additional costs invested in the structure required to uphold the weight of prairie topsoil and in the consequential reduction in heating and cooling costs. The consistent cover will protect the roofing materials from the stress of constant expansion and contraction which would result in further economy in maintenance. There is, moreover, the inestimable social benefit of psychological well-being which the presence of vegetation will confirm amid the stresses of modern urban life. I am not aware of any such experimentation promoted either by industrialists or by prairie ecologists. I wish to explore the prospects for the combination of any such operation which should bring economic benefit to industry and commerce while providing research opportunities for the biologist. This association of seemingly inconsistent endeavors could bring improvement in urban conditions while promoting general educational advancement.

NEW DESIGN CONCEPT

This new design concept represents a drastic change from the current sterile, scaleless, and monotonous architectural style and urban planning practice. Architects seem unable to balance the provision of personal comfort and social confidence with structural magnitude. Vigorous actions will be required to restore the environmental vitality which only vegetation can provide. In consequence, a design program of "dressing" buildings with selected vegetation should be undertaken by professional architects and planners in the development of new design concept. In the name of cultural seemliness, arid architecture should be redeemed by a vital design where selected vegetation is used as an integral part of the structure.

ROOFTOP PRAIRIE COMPOSITION

Demonstration prairies should be established on the roofs of industrial and commercial structures wherever the area is sufficiently large to ensure assisted species self-sufficiency. Individuals involved in structural design and urban planning must recognize the problems arising from the destruction of habitat and those landscape characteristics which sustain species diversity. Rooftop area should be reviewed as potential sites for the cultivation of particular species of prairie grasses and forbs. The soil could be composed, root depth determined, humidity controlled, fire effects assessed, and the ecological balance between grasses and forbs planned, observed, recorded, and reviewed in great detail.

MULTIPLE LAND USES

The necessity for creating prairies on the roofs of industrial and commercial structures is founded upon ethical, environmental, and economical principles of conduct. When taken together, these principles form a triangle of influences which govern the conditions of life. I believe that the prevailing visual natural or man-made seemliness and lack of aesthetic quality represents a dependable alarm system. Degradation of the environment is an impelling signal of something amiss. It is a visual alarm. Ugliness is complementary to the noxious smell, irritating noise, or unpalatable taste. Some relief from this ugliness can be gained by the deliberate use of self sustaining native vegetation in the urban scene in the provision of that natural biological safeguard of variety of species so essential to social stability.

As an ethical principle, we can no longer afford to build for human convenience alone. We must accommodate other species while providing for our own requirements. We can no longer afford to do one thing at a time or to provide for only one purpose in one place. The economics of zoning by spacial monopoly in land uses is ecologically unsound in recognition of the evident benefits of variety.

It is ecologically unethical to allow the prairie landscape to become ever more industrialized. Planning for diversity is an ecological investment. By designing for multiple land uses which do not defy environment nor ecological ethics, economic return may be achieved from each surface and subsurface location and from thermal conditions resulting from such combinations.

Historic and modern examples of multiple land uses are many, and illustrate the combined effects of ethical judgment and environic consistency, resulting in economic benefit. The horizontal character of modern industrial and commercial structures is especially appropriate in permitting multiple uses in the same area, and deserves particular design consideration. The construction of subterranean accommodations have been created without imposition on the landscape above. The loess hills of Iowa may offer accommodation similar to that which has sustained successive cultures in central China for several thousands years. The agricultural productivity may be maintained without interruption from the activities below.

The deliberate remolding of the topography to provide accommodation with the advantage of the earth's consistent thermal properties is also recommended in prairie landscapes. While these design concepts became popular during the fuel crisis of the 1970s, the real value of this ancient concept of living in close harmony with the land. This has been demonstrated at Pawito on the Platte River escarpment south of Columbus, Nebraska by the distinguished planner Doyen Emiel Christensen.

ROOFTOP PRAIRIE ECONOMICS

Environmental considerations now determine that we can no longer treat the landscape as a market place commodity of fluctuating value. The landscape must be respected as the ultimate insurance of human survival. Structural and maintenance economy, however, take precedence over the ethical, cultural, and environmental implications in coordinating prairie ecology with urban vitality. Industrialists and investors must be convinced that the provision of rooftop demonstration prairies is justified by the resulting remuneration. The biologist, also, must be persuaded that the crisis in prairie ecology justifies practical planning beyond the protection of incidental areas of undisturbed prairies.

The economic equation of rooftop prairies depends upon the depth of topsoil required. Increased construction costs arise from the stronger purlins, beams, columns, and foundations needed to carry the earth load and for the water sprinkling system needed to sustain vegetation. An initial increase of 8 to 10% must be added to the basic investment in buildings in the prairie regions to provide for any changes in structural design. This increase may be redeemed over a decade by the reduction in roof maintenance costs resulting from the insulation of grass and earth reducing damage caused by the continuous expansion and contraction of the exposed roofing materials. This topsoil and plants can be expected to provide substantial savings in the cost of winter heating, summer cooling, and in the choice of conventional insulating materials. The economic equation of roof top cultivation includes the consequence of microclimatic modifications and the reduction of environic stress due to the reflection of heat from hard surfaces. New roofing materials are available which reduce the risks of leakage, are easier to apply, and will respond effectively to the demands of rooftop prairies.

EDUCATIONAL OPPORTUNITIES

Rooftop prairies should offer the prairie ecologist new educational opportunities to involve city dwellers. Industrial rooftops provide an experimental platform on which to demonstrate a variety of experiments under conditions of control and observation which would be difficult to achieve under field circumstances.

The most significant factor of the rooftop prairie is that of choice of soil and its natural or composed microbial composition. The experimental value of this composition includes irrigation control provided as an extension of the water system of the industrial or commercial investment. Rooftop prairie may be designed to maintain arid or marsh prairie biome, according to the climatic characteristics at variance with the location of the investment. Other variables could include species composition, plant densities, cover and biomass, fertilization, patterns, and climax chronology. The isolated rooftop prairie offers a mutual economy which should appeal to the industrialist and the biologist.

OTHER USES

These isolated rooftops would probably deny the effects of game and grazing large animals. But, the free arrival of other wildlife will be of special interest to those studying adaptability. The rooftop prairie should be of special interest to urban apiculturists. In addition to grasses, rooftop prairies could be planted with clovers, vetches, perennial mints, and leguminous plants native to the area. These would form bee pastures easily accessible to the urban enthusiast.

SUMMARY

In summary, the concept of establishing prairie landscaped should bring together three apparently incompatible objectives: 1) a professional and public interest in prairie ecology, 2) an improvement in the urban environment and microclimatic conditions, and 3) economies in structural maintenance and energy conservation. The threefold forces of ethics, environment, and economics are interactive in producing a much needed interest in prairie ecology and will advance the understanding of the benefits of the prairie as a basis of design and planning for the general improvement of the urban scene.

WRITING CONSTRUCTION SPECIFICATIONS FOR PRAIRIE LANDSCAPES: THE BASICS

Jon Bryan Burley
Landscape Architecture, Colorado State University,
Fort Collins, Colorado 80523

Abstract. Prairie landscaping is being incorporated into the construction industry. This means that designers of prairie landscapes must be able to communicate landscape specifications to landscape contractors. At present, the Construction Specifications Institute (CSI) format has been adopted by the construction industry as the organizing structure to communicate specifications. This paper describes the CSI specification structure and its application in preparing prairie landscaping construction specifications. The paper describes the importance of divisions zero, one, and two plus sections 02200, 02920, 02930, 02950, and 02970. In addition, the paper presents basic key principles in writing each specification section and the content of the section including: related work; submittals; product delivery, storage, and handling; job conditions; quality assurance; inspection; products; and execution. Suggestions concerning the appropriate wording of the specifications are also presented.

Key Words. landscape architecture, prairie, specifications, planting design

INTRODUCTION

Prairie landscaping emerged when prairie enthusiasts and landscape architects began creating prairies for more than just scientific research and landscape preservation. These prairie landscapes were created for residential, institutional, and commercial purposes. Morrison (1979) typifies recent prairie landscaping trends. From these efforts, prairie landscaping has emerged to become a significant part of the landscape construction industry. Many designers and new landscape contractors are participating in prairie landscaping. However, many of these participants are unfamiliar with current requirements for communicating construction specifications and implementing a design. This paper is written to inform landscape contractors who wish to install prairie landscapes and landscape designers who wish to write specifications for installing prairie landscapes concerning specification basics.

Construction specifications are typically used by designers to clarify standards, procedures, and products used by a contractor to build a project. Almost any construction project that requires the communication of specifications may require a construction specification document.

Presently, the Construction Specifications Institute (CSI), an interdisciplinary organization concerned with the advancement of construction technology, has developed a standard for communicating construction specifications. Until this format was developed, writing and reading construction specifications was extremely time consuming, because each architectural/engineering firm had its own format for writing specifications.

Landscape architects and contractors need to become competently familiar with this body of specification literature. Using the CSI format streamlines the specification writing and reading process plus assists in the comprehension and clarification of construction processes, procedures, and products.

The primary source for learning about specifications is the Manual of Practice (Construction Specifications Institute 1988). This book provides details about general construction specifications writing and organization of specifications. This book may be purchased by writing: The Construction Specifications Institute, 601 Madison Street, Alexandria, Virginia 22314-9970.

Specifications are written documents that accompany construction drawings. In addition, bidding requirements, contract forms, conditions of the contract, addenda, and contract modifications accompany the specifications and drawings. To avoid miscommunication, these items must be carefully coordinated. The drawings indicate the locations of materials, the dimensions of the construction work, and details illustrating the connections between construction materials. The specifications describe the physical qualities, chemical constituents, workmanship, and installation procedures associated with the construction materials.

The drawings and specifications must be consistent in terminology and should not repeat information (double describing). Double describing can lead to errors and confusion. Usually the errors are the result of changing either the drawing or specification without modifying the accompanying construction document. In the case of problems arising from conflicts associated with double describing, CSI recommends that neither the drawings nor specifications should be stated as having precedence. Instead, it is recommended that the conflict be brought to the attention of the landscape architect, and the landscape architect will make a written interpretation.

WRITING SPECIFICATIONS

Methods of Specifying

Four basic methods for writing specifications exist. Usually a specification document uses a combination of the four methods. The first method is a descriptive approach. This approach is tedious and does not mention actual brand names. By law some government documents require that brand names not be given when specifying products and procedures. The second method is the performance approach. This approach states the required results of the product or from a piece of equipment. The third approach is the reference standard method. For example a certain material can be installed according to a particular reference. While this approach is common in installing concrete or asphalt, it may not be common in prairie landscaping. However, as new books and procedures are developed and improved, standard reference material may be made available. When specifying several references, be careful that there is not duplication or conflict arising from the references. The fourth method is the proprietary approach. This approach lists specific products and materials to be used. Closed proprietary specifications require that only the identified product can be used. Open proprietary specifications allow the use of alternate products and alleviate some of the problems associated with overpriced sole source suppliers.

Specification Language

Certain communication approaches are preferred, and some communication languages to be avoided in the specification document. Essentially, the specifications should be clear, correct, complete, and concise. Various terms are avoided. These undesirable terms can cause a specification to become unclear. Table 1 gives a list of the common terms to be avoided. The specifications are written in an imperative mood. An example of the imperative mood is ''Apply seed with a Truax seeder.''

Table 1. A list of specification terms to be avoided (Construction Specifications Institute 1988).

Term
As allowed
As appropriate
As approved
As directed
As indicated
As necessary
As required
Hereinafter
Hereinbefore
Herewith
Wherein
Any
All
Such
etc.
As per
In a workmanlike manner
To the satisfaction of the Landscape Architect/ Architect/Engineer
Shall function as intended
As indicated

Organization

Specifications have a specific organization, which allows for a standard location for the contents of the specification information. Before the standards were implemented, each engineering/landscape architectural firm had its own specification writing preferences and habits. This meant chaos for the contractor. The contractor had to be acquainted with each design firm's own particular specification organization. The CSI system has reduced this chaos. The result has been that contractors are able to more efficiently understand the specifications and have increased the accuracy of their bids.

It was agreed at interdisciplinary meetings back in the 1960s that specifications should be placed into divisions. Each division contained broad categories of construction information that were similar in nature. Division 2 contains specifications relating to site work including site preparation, site demolition, earthwork, piped utilities, landscaping, paving, and surfacing. Therefore, landscape contractors should always examine Division 2 for information directly pertaining to landscape work.

Each Division is divided into sections, as listed in Masterformat (Construction Specifications Institute 1988). Landscaping is Section 02900 of Division 2. Other pertinent sections include Section 02100 Site Preparation and Section 02200 Earthwork. The landscaping section can be divided further into several sections including Section 02910 Shrub and Tree Transplanting; Section 02920 Soil Preparation; Section 02930 Lawns and Grasses; Section 02950 Trees, Plants, and Ground Covers; and Section 02970 Landscape Maintenance.

These sections are the current framework for the landscape section; however, they do not neatly incorporate prairie landscaping procedures. For example, Section 02930 addresses lawns and grasses including hydro-mulching, plugging, seeding, sprigging, sodding, and stolonizing of grasses. Yet prairie landscaping often includes the seeding or plugging of forbs. The present construction format seems to ignore the need to incorporate non-grass material in this section. This oversight may be corrected in the future. For the present, it is recommended that forb seeding and plugging be included in Section 02930.

Each section has a particular, universal outline for the content of the material placed in the section. This outline assists in the consistent location of similar information and keeps the information in a logical order.

Descriptions of Specifications Parts

Sections are divided into three parts. The first part is a general description that identifies specific requirements unique to the section. The second part addresses the products by describing in detail the quality of the item. The third part describes the execution of how the product is to be incorporated into the construction site.

Description of Part 1.

Products furnished but not installed under the section are listed in Part 1. For example, the contractor may supply plant materials that may be installed by the owner. In addition, products installed but not furnished under this section also are listed. These products may be plant material supplied by the owner but installed by the contractor. Part 1 of any section should list the sections related to the current section. Usually sections addressing earthwork, site preparation, plant material installation, and site maintenance are pertinent to prairie landscaping. However, each construction project is unique and may require the list of other important sections.

Many times on large construction sites, the exact area of land to be prepared or planted may not be known. Construction site damage and earth moving may produce variability. Thus, it may be difficult for a contractor to give an exact quote for implementing the construction documents. However, some site construction work can be identified as having an allowance. This means that, depending upon how much area is prepared or planted, the contractor will be given an allowance for a precise unit of measurement. Those items covered under allowances need to be listed, and the units of measurement need to be stated. Do not include cash amounts. Cash amounts are covered in other areas of the contract and bidding documents.

If certain portions of the section are part of a request for alternative bids, the alternatives need to be identified. For example, two types of seeding mixtures may be in the construction specifications. One mixture may be more expensive, while the other is an inexpensive mixture that minimally covers the site with essential plant materials. The contract documents in Division 1 may request that the contract give two prices or alternates.

References pertaining directly to the sections should be listed. For example, botanical names differ according to regional authorities. In North Dakota, Stevens (1963) may be considered an authority for the identification and botanical name for plant material; however, in Wisconsin, Curtis (1959) may be used as a reference. Each reference should be listed in Part 1. Occasionally, a term may require defining. That term should be defined in Part 1.

Requests for submittals in prairie landscaping are common. The requests ask for relevant data to be furnished by the contractor. The submittals may be product data, shop drawings, samples, quality control documents, test reports, warranties, and other notices. Requests may include a list from the seed supplier giving the quantity and botanical name of the seed supplied. In addition, the contractor may request to have tests performed that verify seed germination results, amount of weed seed, amount of inert material, and percent of pure live seed. These submittals are often related to quality assurance and may require the appropriate certificate or sample.

Part 1 also describes the delivery, storage, and handling of construction material. This is an important portion of the document. Plant material is a live product and must be treated and handled properly. The requirements must be stated clearly, such as if seed needs to be stored at a specific temperature, humidity, and light level; or if plugs, bare root plants, potted plants, or balled and burlapped plants require specific handling or storage, the requirements must be stated clearly.

Project and site conditions required for the installation of material and the protection of existing site features must be listed in Part 1. Often, grade stakes, site utilities, and pavement must be protected and kept clean. Special sequencing and scheduling requirements pertinent to other sections also are described. For example, the site preparation may include careful control and elimination of weed seeds in the topsoil. Until the weed seeds are eliminated, the seed planting cannot be accomplished. Special and extended warranties must be identified in Part 1. For example, seed germination failure may be guaranteed by mandating a second seeding application.

Description of Part 2.

A list of manufacturers or growers that are able to supply the products under the section are often given at the beginning of Part 2. This approach is especially important if a certain type of seed mixture or piece of equipment is to be used. The contractor needs to know where the material can be obtained.

The exact description of materials is listed in Part 2. This description is extremely important. For example, landscape drawings may only identify locations for application of seed mixtures A, B, and C. The specification then lists the contents of those seed mixtures. Special proportions for seed mixtures or soil material are also listed. If the material is inspected at the source, requests for verification or certificates should be identified in Part 2.

Description of Part 3.

A request may be made to verify the suitability of the site to receive the products before the work is executed. This request should be clearly stated. For example, weed seeds may still be on a site that was to receive a seeding mixture. However, if a certain percentage of weeds cover the site, the landscape is not ready to be planted. Actions specifically required to prepare a site or surface are stated in Part 3. In addition, special action that needs to be taken to protect other materials and surfaces requires listing.

The actual installation procedures are listed in Part 3. This means that the actions required to install the products and perform the work are presented. Each product will require its own list of actions. The procedures are presented in chronological order. During the installation, any tests or field quality control measures are described. The final actions to install the product are listed in Part 3. For example, some materials may require special cleaning and adjustment. In addition, some products may require special protection. Seeded areas may require barriers or signs to protect the material.

These three parts comprise the organization and presentation of information for each section. The parts allow a general overview, a list of products and installation instructions.

EXAMPLE SPECIFICATIONS

To conclude this paper, an example of a section specification is provided (Figure 1). Please note that this specification is simply an example to illustrate the structure and organization of a section specification. Each construction project has a unique client, site, and users. Therefore, the specification should reflect these characteristics. Universal, perfect specifications for every construction site do not exist. The specification should be tailored to fit special environmental conditions and design functions. In addition, the standards for prairie landscaping are still evolving. Specifiers may have their own particular approaches to constructing a project, and these approaches may vary according to regions.

FIG. 1. Example of a specification written for section 02930.

Section 02930- Seeding

Part I GENERAL

SUMMARY:

This section encompasses the furnishing of all labor, equipment and material to complete hydro-seeding work.

Allowances and Unit Prices: Amount hydro-seeded will be measured by acre seeded to the nearest one-thousandth acre.

RELATED WORK SPECIFIED ELSEWHERE:

Division 1 General Requirements
Topsoil in Section 02920
Landscape Maintenance in Section 02970

REFERENCES:

Stevens, O.A. 1963. Handbook of North Dakota Plants. North Dakota Institute for Regional Studies.

USDA. 1972. Plant Hardiness Zone Map. USDA, miscellaneous publication No. 814.

SUBMITTALS:

Grower's Certification: Data showing plant species supplied and location of origin.

Seed Data: Test reports showing purity, mix and germination.

Certificates: Manufacturer's certification of fertilizer and herbicide composition.

QUALITY ASSURANCE:

Labor: Work is performed with personnel experienced in the work required by this Section under the direction of a skilled foreman.

Substitutions: If specified product is not obtainable, submit to Landscape Architect proof of non-availability and proposal for use of equivalent.

Standards: Provide plants true to name, grown in a recognized nursery or seed farm in accordance with good horticultural practice. Nomenclature in accordance with Stevens (1963).

Provide healthy, vigorous stock, free from disease, insects, eggs, larvae and free of defects, injuries, abrasions or disfigurement.

Plant material will be from nurseries or seed farms that have been inspected by state or federal agencies and comply with the rules and regulations under the Federal Seed Act.

Less than 1.3% weed seed allowed in seed mixes.

Less than 66% non-weed seed impurities allowed in seed mixes

Collected material may be used when approved.

All plants shall be from stock which has been acclimated to the state of North Dakota. Plants which have been consistently grown and cultivated outside the state but within the boundaries shown on the Plant Hardiness Zone Map, USDA, miscellaneous publication No. 814, 1972 in Zones 2 and 3 shall be considered winter hardy in Fargo, North Dakota.

PRODUCT DELIVERY, STORAGE AND HANDLING:

Deliver products in original package labeled with manufacturer's name, product name, weight, certified analysis and instructions for use.

Protect seed from dehydration, contamination, freezing and heating during transportation and delivery.

Store seed in a dark room, 50 degrees F. to 60 degrees F., at 20% to 40% relative humidity.

Prior to planting, keep seed in area protected from mechanical and chemical damage.

JOB CONDITIONS:

Existing conditions: Perform plant installation after work affecting ground conditions are completed.

Site Utilities: Locations of utilities must be determined by contractor and work performed in a manner which will avoid damage to utilities.

Figure 1 (Continued)

Maintain grade stakes, benchmarks and monuments.

Site Maintenance: During work specified in this section, keep pavement, sidewalks and buildings clean and unstained. Keep work area in an orderly condition. Remove all litter from premises weekly. Remove all waste material from site.

When any detrimental conditions to plant growth are encountered, such as rubble fill, clay fill, adverse drainage conditions and obstructions, notify landscape architect before proceeding.

Protection: Restrict foot and vehicular traffic from seeded area to the end of the establishment period.

PART 2 PRODUCTS:

Upland Seed Mix: Seed mix containing the following species:
- Agropyron smithii
- Bouteloua curtipendula
- Bouteloua gracilis
- Chrysothamnus nauseous
- Lolium multiflorum
- Sarcobatus vermiculatus
- Schizachyrium scoparium
- Symphoricarpos occidentalis

Wetland Seed Mix:
- Distichlis stricta
- Elymus salinus
- Puccinellia distans
- Sporobolus airoides
- Suaeda depressa

Upland Fertilizer: Contained weight 10% slow release nitrogen, 10% phosphorus and 10% potash.

Wetland Fertilizer: Contained weight 10% slow release nitrogen, 0% phosphorus and 0% potash.

Water: Furnish all necessary hose, equipment, attachments and accessories for hydro-seeding. Water shall be clean and potable.

Cellulose Fiber Mulch

Tackifier

PART 3 EXECUTION:

UPLAND HYDRO-SEEDING:

Seeding to occur between April 16th to May 31st.

Apply upland fertilizer and upland seed mix together.

Apply upland fertilizer at a rate of 1000 pounds per acre.

Apply upland seed mix at:

Agropyron smithii	4 pounds per acre PLS
Bouteloua curtipendula	1 pound per acre PLS
Bouteloua gracilis	1/2 pound per acre PLS
Chrysothamnus nauseous	1/4 pound per acre PLS
Lolium multiflorum	1/2 pound per acre PLS
Sarcobatus vermiculatus	1/4 pound per acre PLS
Schizachyrium scoparium	1 pound per acre PLS
Symphoricarpos occidentalis	1 pound per acre PLS

Apply cellulose wood mulch and tackifier together.

Apply cellulose wood mulch and tackifier within two hours of applying upland fertilizer and upland seed mix.

Apply cellulose wood mulch at a rate of 1,500 pounds per acre.

Apply tackifier at a rate of 45 pounds per acre.

WETLAND HYDRO-SEED MIX

Seeding to occur between August 15th and September 15th.

Apply wetland seed mix and wetland fertilizer together.

Apply wetland fertilizer at a rate of 1000 pounds per acre.

Apply wetland seed mix at:

Distichlis stricta	1 pound per acre PLS
Elymus salinus	2 pounds per acre PLS
Puccinellia distans	2 pounds per acre PLS
Sporobolus airoides	1 pound per acre PLS
Suaeda depressa	2 ounces per acre PLS

LITERATURE CITED

Construction Specifications Institute. 1988. Manual of practice. Construction Specifications Institute, Alexandria, Virginia.

Construction Specifications Institute. 1988. Masterformat. Construction Specifications Institute, Alexandria, Virginia.

Curtis, J.T. 1959. Vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison.

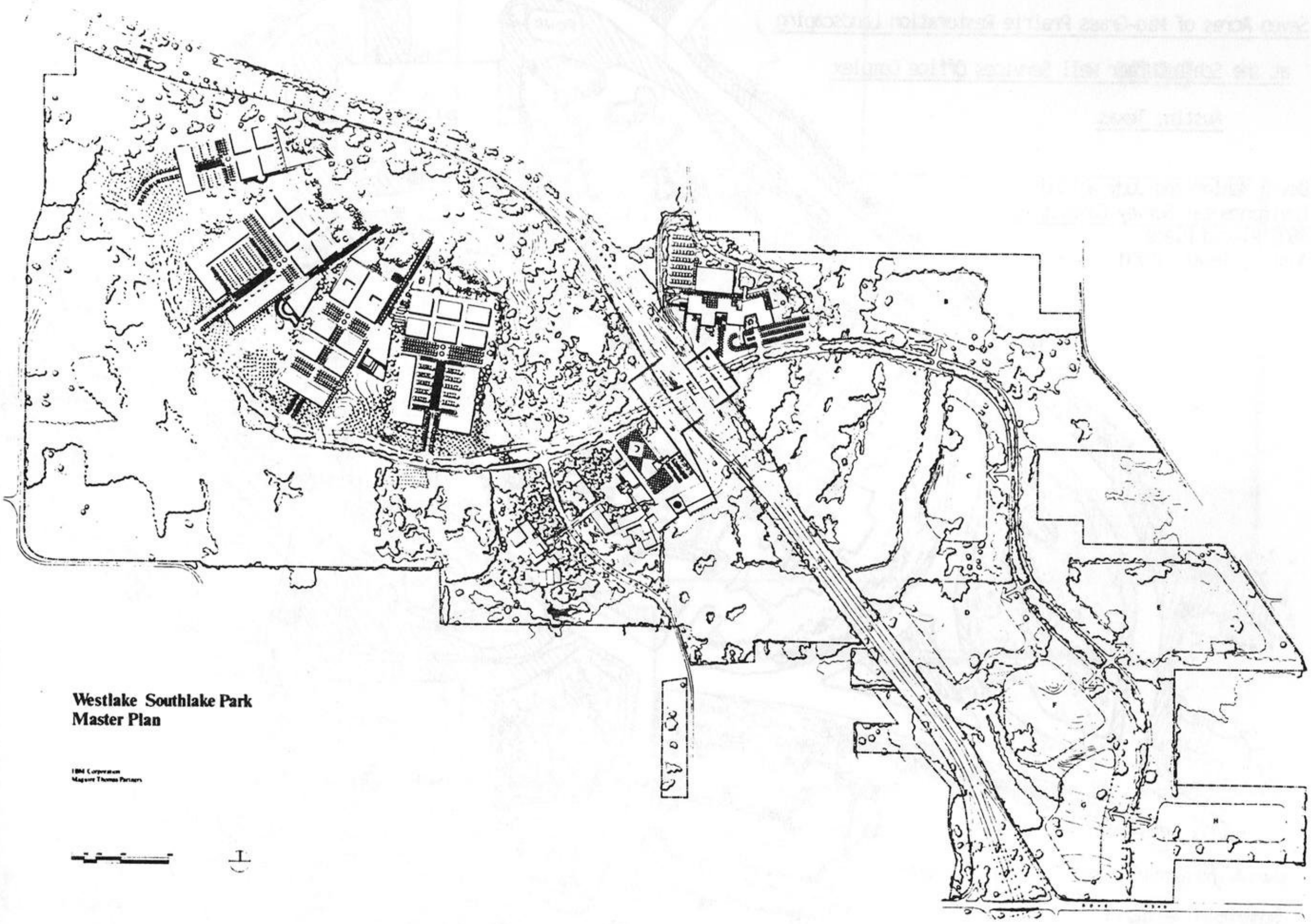
Morrison, D.G. 1979. Prairie grasses, monarch butterflies, rose hips. . .: the 'wild' moves in on the backyard. Landscape Architecture, March:141-145.

Stevens, O.A. 1963. Handbook of North Dakota plants. North Dakota Institute for Regional Studies, Fargo.

LANDSCAPE DESIGN AWARDS

Commercial/Industrial Honor Award

The Office of Peter Walker and Martha Swartz
San Francisco, California
Westlake/Southlake Master Plan



Jury's Comments:

"A huge project with imaginative concept in which prairie is a small but important part of project."

"Project may be too big conceptually for simply a prairie context, though it is really a fine example of sensitive corporate planning, incorporating prairie preservation/restoration."

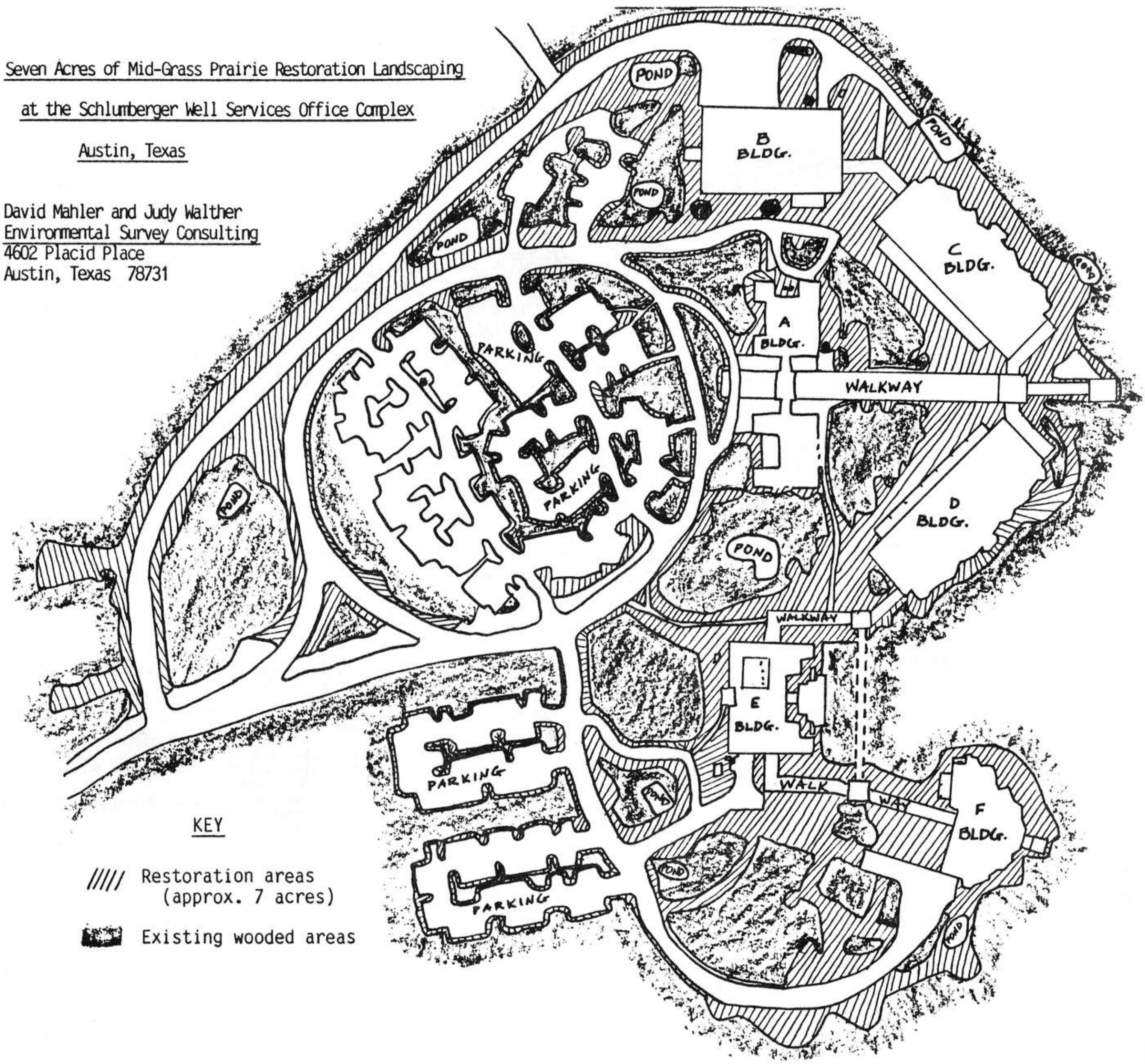
"The masterplan compacts development and restores a natural environment, while creating a liveable environment."

"Agriculture is an aesthetic context as well as a land use; prairie aspects center on restoring degraded pasture for upgrading landscape quality and sustainability."

Prairie in many areas apparently to be used as long-term temporary cover crop."

Commercial/Institution Merit Award

Environmental Survey Consulting, Austin, TX
David Mahler, July Walther
Robert J. Anderson Landscape Architect
Schlumberger Well Services, Inc., Austin, TX



Jury's Comments:

"Careful attention to detail and the site's intimate character returned it to the character of original prairie savannah."

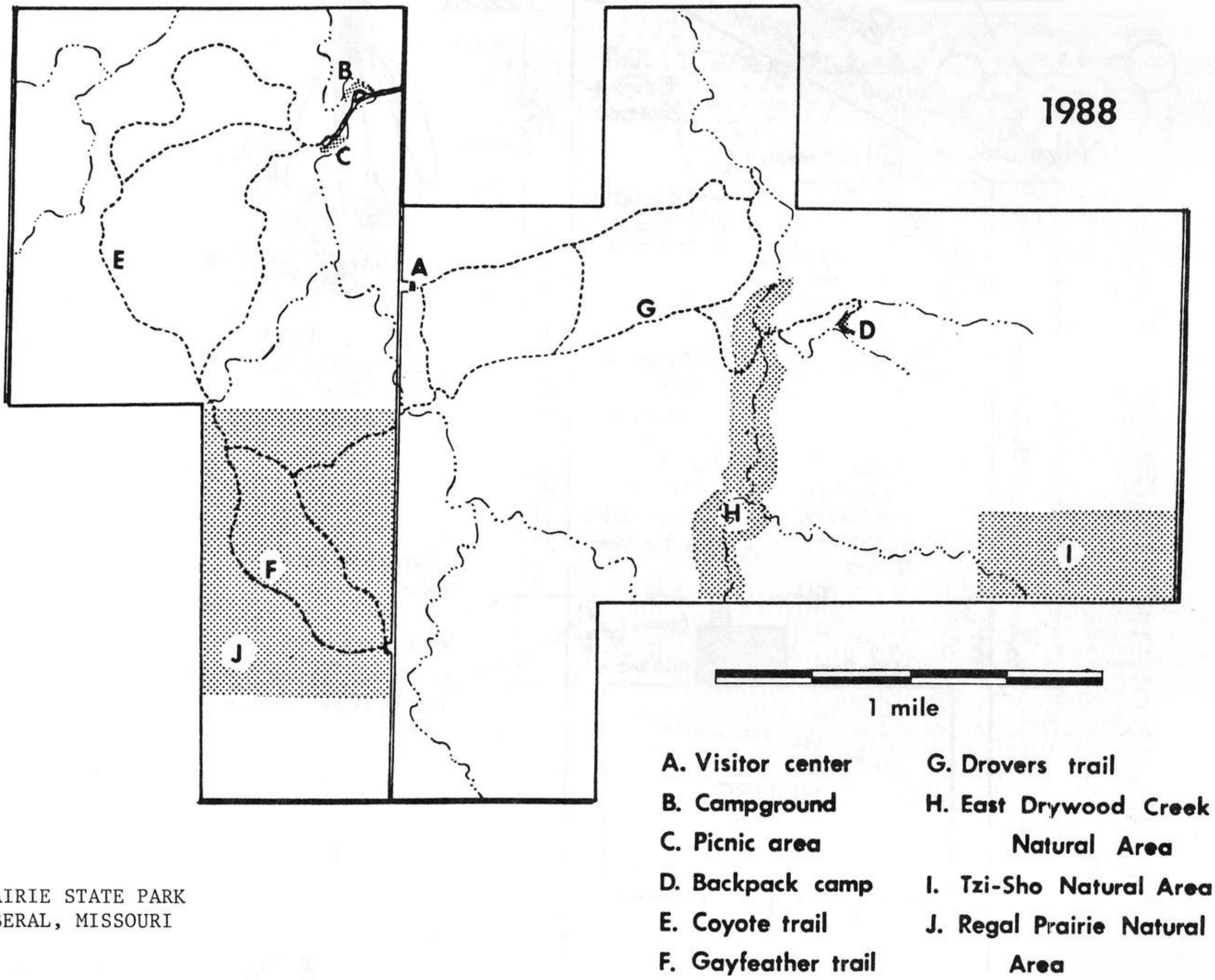
"Knowledge of the ecosystem and environment translates into tremendous success of planting, especially when integrated with maintenance. Design, installation and maintenance well integrated into an overall process. We applaud use of a range of sizes and planting methods (plants and seedlings) for native plant material in this environment. Immediate success in prairie plantings such as this are too often overlooked as a good public relations tool."

"Parking clustered in woods preserved existing vegetation and minimized site disturbance."

"Research, design, installation and maintenance were well-integrated into an overall process."

Public Landscape Honor Award

Missouri Department of Natural Resources
Division of Parks and Recreation
Prairie State Park Master Plan
Barton Company, MO



PRAIRIE STATE PARK
LIBERAL, MISSOURI

Jury's Comments:

"The planners understood the visual impact of man and his creations in a prairie landscape. Therefore, limiting the group usage is commendable and necessary to preserve the prairie and the prairie experience as is the foresight to remove traces of man's development to create the open sweep of a prairie. The change to 'experience' the prairie is great, even better than learning about or interpreting the prairie. Here you can *live* it."

"Research is reflected in plan documentation; management and preservation are also well-integrated. We applaud the explicit forethought accorded research and management. This coordination is commendable."

"The combination of private and public land acquisition looks like a difficult but key ingredient to overall success."

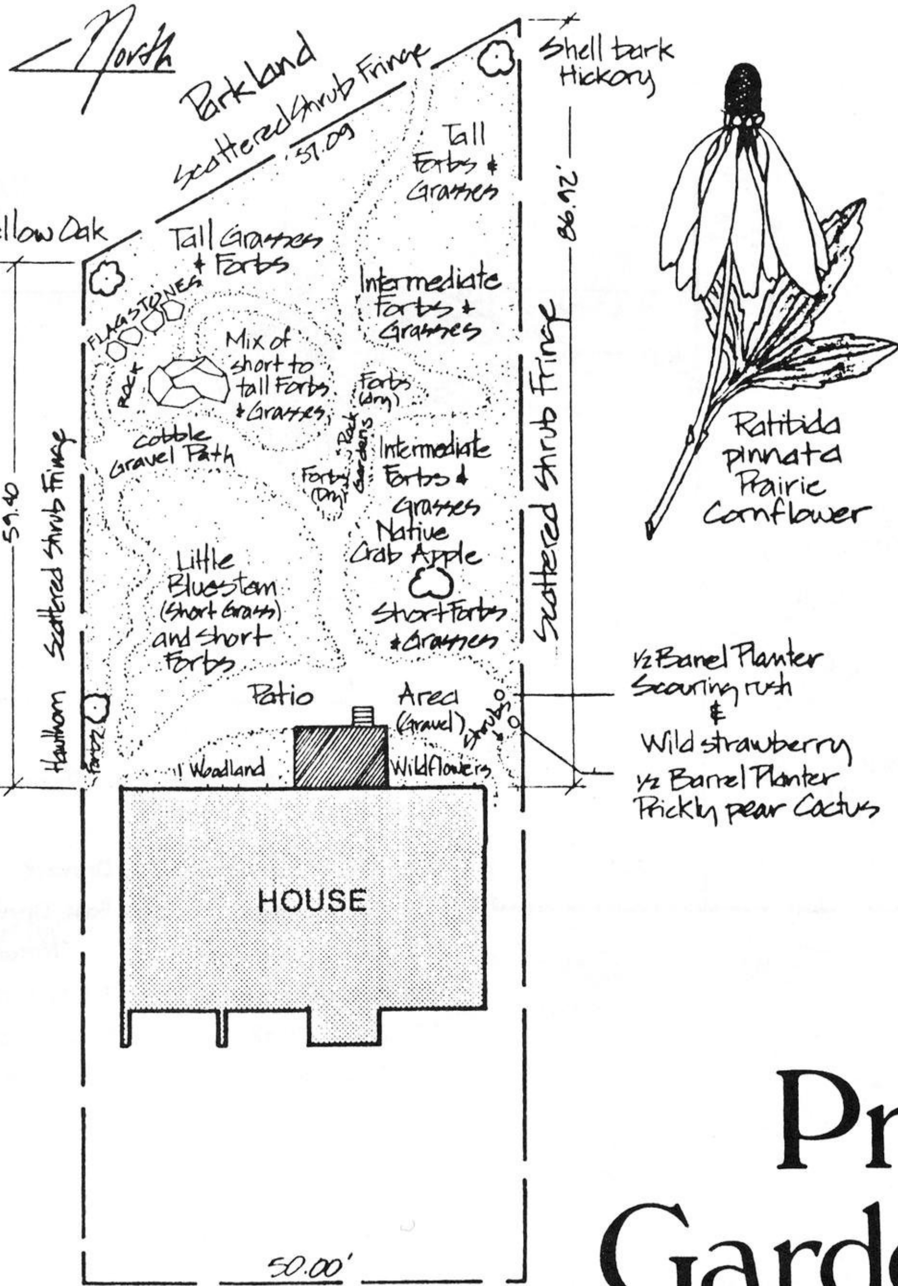
"Well-stated and carefully followed objectives."

"Submitted material apparently lacks documentation of process for accommodating physical design elements."

"We question the safety of bison/man interaction."

Student Honor Award

Laurence Lamb
Kitchener, Ontario, Canada
Prairie Fringe



Prairie Garden

Jury's Comments:

"We appreciate the realization that it is not 'low maintenance' to establish a prairie garden but obviously a great learning process, showing dedication to implementation."

"Hard to perceive the overall character of the project. Needed an eye level shot or aerial shot."

"The design created a prairie 'oasis' but a collection of prairie plants does not create a prairie; probably better understood simply as a prairie garden."

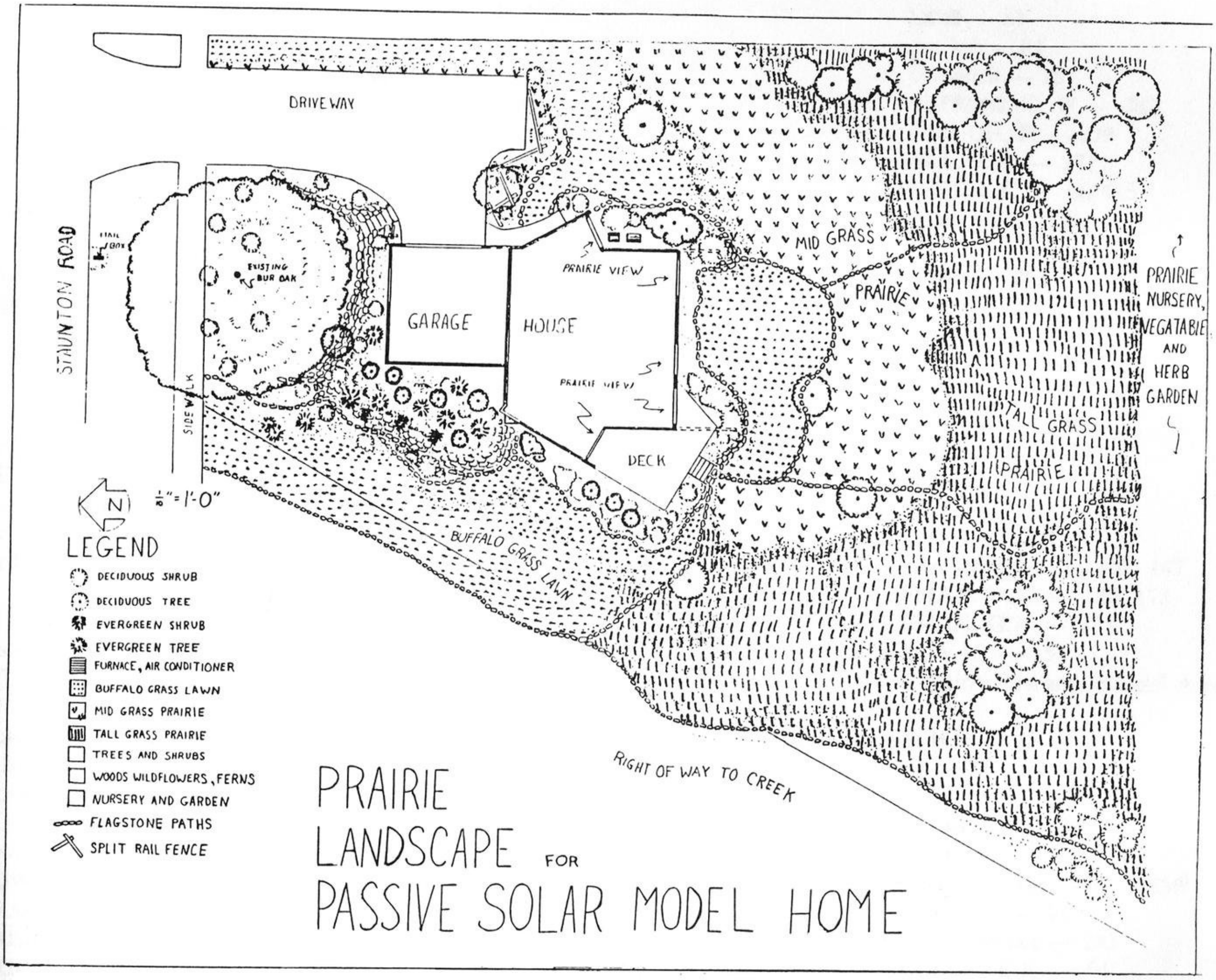
"234 species, 63 rare collection of plants - extreme north - 7 year's work; a major objective is to attract butterflies, but needs more explicit objectives."

"Mix is a prairie arboretum garden/collection - very positive."

"Use of boulder as focal point very important."

Non-Professional Honor Award

Patricia K. Armstrong
Napierville, IL
Prairie Sun



Jury's Comments:

"A lot of variety in material but well-placed in a small area. Good attention to detail throughout—stone paths, down spouts, etc. Unique 'foundation plantings' help to conceal utilities. Over-planting for dramatic early effect may need to be dealt with later. Excellent use of plants in their niches. Variety of plants well-contained within a space. Concept clear, well thought out, well executed. Plantings conceived to deal with climate, microclimate and screening. Nice layering of plant material."

List of Jury

Richard K. Sutton, ASLA, UN-L, Department of Horticulture
Deon Bahr, AIA, Principal, BVH Ltd.
Art Thompson, Jr., ASLA, Nebraska Department of Roads

INDEX TO AUTHORS AND KEY WORDS

The following index consists of the names of authors of the included manuscripts and the subjects indicated by key words submitted by the authors.

CONFERENCE FACILITATORS

Gilbert Adrian, Biology Department, Hastings College
Randy Baynes, Homestead National Monument
Thomas B. Bragg, University of Nebraska at Omaha
Rosalind K. Carr, Center for Great Plains Studies
Paul J. Currier, Platte River Whooping Crane Habitat Maintenance Trust
Michael I. Fritz, Nebraska Natural Heritage Program
Gary Garabrandt, Fontenelle Forest Nature Center
Richard W. Gray, Jr., Nebraska Department of Roads
Peter N. Jensen, Lincoln, Nebraska
Anthony Joern, School of Biological Sciences, University of Nebraska-Lincoln
Robert Kaul, School of Biological Sciences, University of Nebraska-Lincoln
Brent Lathrop, Twin Platte Natural Resources District
Jim Locklear, Nebraska Statewide Arboretum
Hal Nagel, Department of Biology, Kearney State College
Steve Rothenberger, Biology Department, Midland College
Ellen Scudder, Omaha, Nebraska
Wanda Schroeder, Soil and Water Conservation Society of America
Joe Springer, Department of Biology, Kearney State College
James Stubbendieck, Agronomy Department, University of Nebraska-Lincoln
Al Steuter, Niobrara Valley Preserve, The Nature Conservancy
David M. Sutherland, Department of Biology, University of Nebraska at Omaha
Richard K. Sutton, Department of Horticulture, University of Nebraska-Lincoln
Curtis Twedt, Nebraska Game and Parks Commission
Bill Whitney, Prairie/Plains Resource Institute
Richard Williams, Homestead National Monument
Gary Willson, National Park Service

SPONSORS

The Planning Committee of the Eleventh North American Prairie Conference Acknowledges the support of the following sponsors whose assistance substantially improved planning and conduct of the meetings.

Executive Corporate

Omaha World Herald Foundation
Nebraska Statewide Arboretum

Corporate

Horizon Seeds
Dr. William Laux
Lower Platte South Natural Resources District
John Osler
Papio Natural Resources District
Stock Feed Farms, Inc.
Upper Loup Natural Resources District

Organizational

Fontenelle Forest Association
National Audubon Society/Nebraska Audubon Council
National Park Service
Nebraska Association of Resource Districts
Nebraska Council of Chapters — Soil and Water Conservation Society
Nebraska Games and Parks Commission
Prairie/Plains Resource Institute
Soil and Water Conservation Society, Lincoln Chapter
The Nature Conservancy
University of Nebraska-Lincoln: Center for Great Plains Studies, Department of Agronomy, Department of Horticulture, Range Club, School of Biological Sciences.
University of Nebraska at Omaha: Department of Biology
USDA — Soil Conservation Service

ISBN 0-939870-00-3