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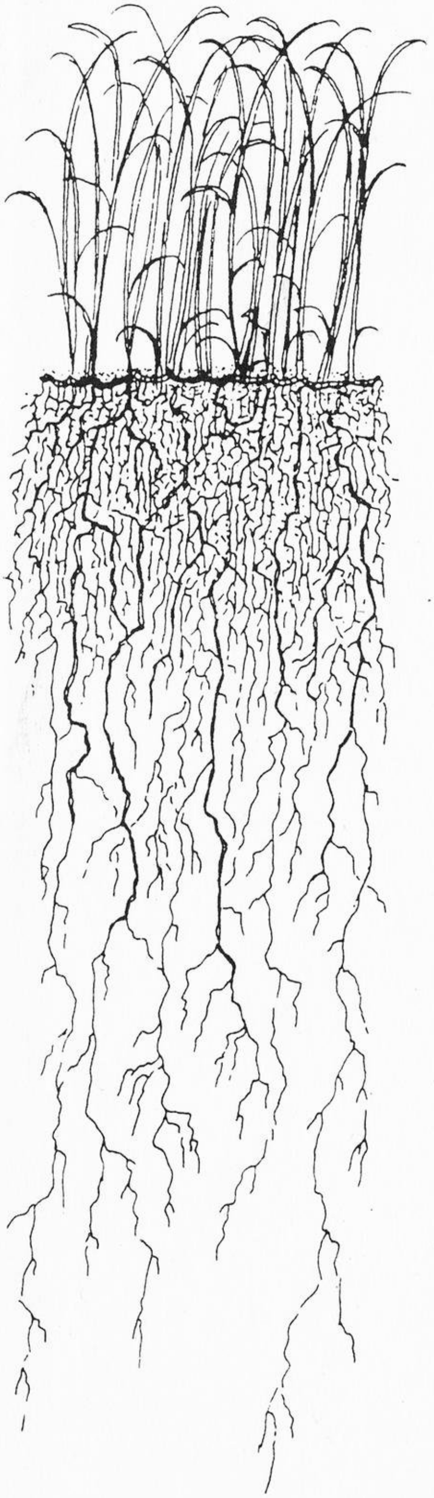

PRAIRIE BIODIVERSITY

Kansas State University
Manhattan, Kansas

David C. Hartnett, Editor

Fourteenth North American Prairie Conference: Prairie Biodiversity

Kansas State University
Manhattan, Kansas

July 12-16, 1994

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PREFACE

The Fourteenth North American Prairie Conference held on the campus of Kansas State University represented a wide range of interests in the ecology, history, management, and preservation of prairies. The theme of this conference was "Prairie Biodiversity" and many of the papers presented and included in this volume contributed to the understanding and preservation of biological diversity in prairies at multiple levels.

During the past decade, scientists and environmental conservationists have directed their attention to the preservation of biodiversity. This has been prompted by the recognition that species are being lost from natural ecosystems at an alarming rate due to human activities, and that this loss has significant consequences. Biodiversity is not simply species numbers. Rather, it refers to the variety of growth forms, species, habitat types, and genetically distinct individuals (genotypes) present within natural ecosystems. The preservation of biodiversity is important because this variety of organisms is necessary to provide essential ecosystems "services" such as the production of oxygen, decomposition and nutrient cycling, and the natural regulation of plant, consumer, and pathogen populations. Diversity is also important because native plants and animals provide an essential genetic resource for the development of foods, medicines, fibers, biological pest control agents and other important resources for our expanding human population. Biodiversity provides aesthetic benefits since we appreciate and enjoy the diversity of environments and life forms in the prairies and other natural ecosystems around us.

As we focused on prairie biodiversity, it is also worth noting that prairies have recently been instrumental in providing important empirical tests of long-standing ecological theories and debate over the relationship between diversity and ecological stability. Recent studies in Minnesota remnant prairies, grasslands of Yellowstone National Park, and the Konza Prairie in the Kansas Flint Hills have documented clear positive relationships between plant species diversity and stability in the productivity and composition of grassland plant communities.

Much current research is aimed at understanding the patterns of prairie biodiversity and its controlling processes. For example, long-term research on the Konza Prairie in northeast Kansas is assessing how grazing, fire, and climatic variability influence the diversity of plant, insect, bird, and mammal populations. These long term studies have shown us that plant, insect, and mammal species diversity are highest when prairie fire frequencies are intermediate (every 4 to 6 years), that bird diversity increases with decreasing fire frequency, and that grazing by bison increases plant diversity. A new long-term study on Konza is comparing the effects of native and introduced ungulate grazers (bison and cattle) on components of tallgrass prairie biodiversity. The Nature Conservancy is currently supporting a regional study examining patterns and controls on prairie biodiversity across the eastern Great Plains. This study involves four preserves in The Nature Conservancy system including the Cross Ranch (North Dakota), Niobrara Valley Preserve (Nebraska), The Tallgrass Prairie Preserve (Oklahoma), and Konza Prairie (Kansas).

Grassland ecosytems throughout the world, and agricultural ecosystems based on productive grassland soils, provide the majority of food resources worldwide. In addition, grasslands make a significant contribution to total global biodiversity. As exemplified by many of the papers included here, active research plays a vital role in enhancing our understanding and appreciation of the prairie and its biodiversity.

We are greatly indebted to the conference chair Dr. John Zimmerman for his leadership and hard work in developing the program agenda, field trips, and other arrangements. We also thank each of the members of the local organizing committee for their varied efforts. Numerous individuals from several institutions provided thorough objective reviews of the submitted manuscripts. I wish to thank personally Drs. John Briggs, Jack Cully, Gene Towne, Geoff Henebry and Clarence Turner for their work on the Editorial Committee, Eileen Schoefield for her excellent technical editing services, and Klara Fajzi for her hours of administrative assistance in coordinating the editorial process and putting this work together.

David C. Hartnett
Manhattan, Kansas

Diversity Among and Within Populations of *Agastache foeniculum.*

Roger G. Fuentes-Granados and Mark P. Widrlechner
North Central Regional Plant Introduction Station, Agronomy Department, Iowa State University, Ames, IA 50011.

Abstract. An electrophoretic analysis of isozymes was conducted on 11 populations of *Agastache foeniculum* maintained in the U.S. National Plant Germplasm System. Eleven enzyme staining systems, controlled by 19 putative loci, were assayed to estimate parameters of genetic diversity and to determine systematic relationships among populations of this prairie species. Polymorphism was detected in seven putative loci: *Cat1*, *Got1*, *Got2*, *Pgm2*, *Phi2*, *Tpi1*, and *Tpi2*. Percentage of polymorphic loci and average number of alleles per locus for the species were 36.8 and 1.6, respectively. Total heterozygosity was 0.08. Partitioning of genetic variability was 0.63 and 0.37 within and among populations, respectively. Interpopulational values for Nei's genetic identity coefficients ranged from 0.878 to 1.000. Partitioning of total genetic variability (63% within populations) and values of inbreeding coefficients (F) close to zero suggest that *A. foeniculum* is a cross-pollinated species. Geographical distribution and possibly human manipulation of the species may play important roles in the genetic differentiation of these populations.

Key words: Lamiaceae, polymorphic loci, heterozygosity, isozymes, genetic variability.

Introduction

Anise hyssop, [*Agastache foeniculum* (Pursh) Kuntze], is a perennial member of Lamiaceae native to Wisconsin, Minnesota, Iowa, North and South Dakota, Wyoming, Colorado, and Canada from western Ontario to Alberta (Lint and Epling, 1945), where it grows in woodlands, ditches, and prairies (Great Plains Flora Association, 1986), This species is a candidate for large-scale, domestic cultivation as a source of nectar for honey bees (Widrlechner, 1992; Ayers and Widrlechner, 1994) and as an aromatic plant with wide variation in the composition and content of its essential oils. Some of these oils, such as methylchavicol and linalool, are important to the flavoring and perfume industries (Charles *et al.*, 1991; Mazza and Kiehn, 1992; Nykänen *et al.*, 1989; Wilson *et al.*, 1992). An increasing number of recent reports indicates that horticulturists in other countries are also interested in cultivating this species (Galambosi and Galambosi-Szebeni, 1992; Mazza and Kiehn, 1992; Menghini *et al.*, 1992).

Because of increasing interest in developing *A. foeniculum* into a new crop, knowledge of patterns of intraspecific genetic variability and of its population biology is important. Vogelmann and Gastony (1987) conducted a biosystematic analysis of *Agastache* section *Agastache* and reported estimates of parameters of genetic diversity. They provided descriptions of genetic structure and putative mating systems for all species of section *Agastache* except for *A. foeniculum*. We analyzed isoenzymatic diversity in *A. foeniculum* to estimate parameters for genetic diversity and mating system. Specific objectives were to determine (1) the degree of genetic diversity and how genetic diversity is partitioned within and among populations; (2) the degree to which populations of *A. foeniculum* conform to Hardy-Weinberg equilibrium; (3) the likely mating system of the species; and (4) the systematic relationships among populations of *A. foeniculum* conserved by the USDA/ARS North Central Regional Plant Introduction Station (NCRPIS).

Materials and Methods

Plant Material

Eleven accessions of *A. foeniculum*, two accessions of Korean mint [*A. rugosa* (Fisher & Meyer) Kuntze], and one accession of catnip giant hyssop [*A. nepetoides* (L.) Kuntze] were analyzed (Table 1). Plants were grown from seeds that had received a moist chilling treatment at 4°C for a week to improve germination. Seeds were germinated in a germination chamber with temperatures alternating between 20°C and 30°C and a 16-hour photoperiod. Two-week-old seedlings were transplanted from the germination chamber into the greenhouse. For all populations except for PI-561054, which had only 31 seedlings, 40 seedlings were analyzed. Selected, sterile, interspecific hybrids (*A. rugosa* X *A. foeniculum*) also were analyzed (Fuentes-Granados, 1993).

Sample Preparation

Leaf tissue was removed from the youngest leaves, which had at least 1 cm^2 in leaf area, of each seedling and was brought to the laboratory in a cooler with crushed ice. Twenty milligrams of leaf material were ground with 100 µl of a modification of the extraction buffer reported by Hashemi *et al.* (1991): 0.1M Tris-HCl (pH=8), 0.02M dithiothreitol, 0.2 % (vol/vol) 2-mercaptoethanol, and 20% (weight/vol) polyvinylpyrrolidone. The samples were ground in an Eppendorf tube immersed in an ice water bath for 1 min with an electric grinder, microcentrifuged at 5°C for 90 sec, and stored in a freezer at -62° C for 24 h.

R.G. Fuentes-Granados and M.P. Widrlechner are affiliated with the North Central Regional Plant Introduction Station, Iowa State University, Department of Agronomy, where Mr. Fuentes-Granados is employed by Iowa State University and Dr. Widrlechner by the U.S. Department of Agriculture-Agricultural Research Service.

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Table 1. Origin of the 14 accessions of *Agastache*.

Species	Accession #[1]	Origin
A. foeniculum	A-10206	Cultivated: Puławy, Poland
A. foeniculum	PI-561054	Cultivated: Morden, Manitoba
A. foeniculum	PI-561055	Cultivated: Washtenaw Co., MI
A. foeniculum	PI-561056	Cultivated: Story Co., IA
A. foeniculum	PI-561057	Wild: Barnes Co., ND
A. foeniculum	PI-561058	Wild: Cass Co., MN
A. foeniculum	PI-561059	Wild: Hennepin Co., MN
A. foeniculum	PI-561060	Wild: Morden, Manitoba
A. foeniculum	PI-561061	Wild: Las Animas Co., CO
A. foeniculum	PI-561062	Wild: Spruce Woods Park, Manitoba
A. foeniculum	PI-561063	Wild: High Lake, Whiteshell Park, Manitoba
A. nepetoides	PI-561064	Wild: Iowa
A. rugosa	A-8411	Cultivated: Quebec
A. rugosa	A-10207	Cultivated: Puławy, Poland

[1]The A-number is a temporary accession number assigned by the NCRPIS. The PI-number is a permanent accession number assigned by the US National Plant Germplasm System. All these accessions are available from the NCRPIS.

Enzyme Electrophoresis

Two gel-buffer systems were used for the electrophoresis of enzyme systems. System C of Stuber *et al.* (1988) resolved isozymes of alcohol dehydrogenase (ADH, EC 1.1.1.1); catalase (CAT, EC 1.11.1.6); glutamate dehydrogenase (GDH, EC 1.4.1.2); glutamate-oxaloacetate transaminase (GOT, EC 2.6.1.1); menadione reductase (MNR, EC 1.6.99.2); and triose phosphate isomerase (TPI, EC 5.3.11). System D or histidine-citric acid (Stuber *et al.*, 1988) resolved the isozymes of isocitrate dehydrogenase (IDH, EC 1.1.1.41); malate dehydrogenase (MDH, EC 1.1.1.37); phosphoglucomutase (PGM, EC 2.7.5.1); phosphogluconate dehydrogenase (PGD, EC 1.1.1.44); phosphohexose isomerase (PHI, EC 5.3.1.9); and shikimic acid dehydrogenase (SKD, EC 1.11.1.25). Starch gels were prepared as described by Stuber *et al.* (1988). Frozen ground-leaf samples were allowed to thaw, and Whatman #1 paper wicks, 1.5mm X 12mm, were used to adsorb proteins from the supernatant. Lithium borate gels were electrophoresed for 6 h at a constant power of 12 watts, and histidine-citric acid gels were electrophoresed for 6.5 h at 16 watts of constant power. Stain recipes and procedures were taken from Wendel and Weeden (1989) for MNR and TPI and from Stuber *et al.* (1988) for ADH, CAT, GOT, IDH, GDH, MDH, PGM, PGD, PHI, and SKD.

Isozyme Scoring

The genetic bases of enzyme banding patterns were inferred from observed populational variation and from reported isozyme number and subunit structure for enzymes as reviewed by Vogelmann (1983). Interspecific hybrids between *A. rugosa* and *A. foeniculum*, reported by Senechal (1990), elucidated the constancy of loci among species. When more than one putative locus encoded isozymic variants of the enzyme system analyzed, the number 1 was given to the locus coding the most anodal

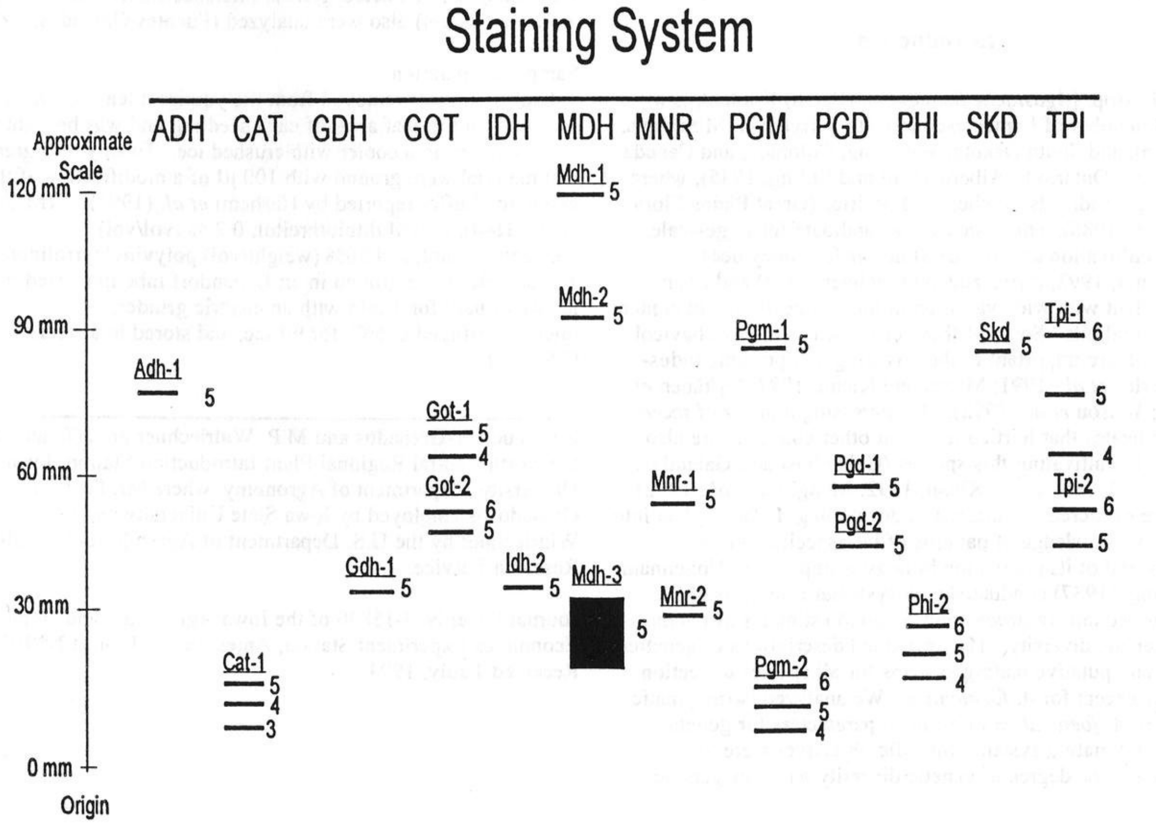

FIG. 1. Schematic drawing of the observed loci and alleles for each staining system evaluated in *A foeniculum.*

isozyme, 2 to the next, etc. The alleles of putative loci that encoded various allozymes were identified and scored numerically from the gels *per se*. A schematic drawing of the observed putative loci and/or alleles for each staining system is presented in Figure 1. In addition, each gel slice was photographed for permanent documentation.

Analysis of Genetic Diversity

Estimates of genetic diversity, including allelic frequency, mean number of alleles per locus (*A*), percentage of polymorphic loci (*P*), mean heterozygosity (H), and total panmictic heterozygosity (H_T) were calculated with BIOSYS-1, developed by D. Swofford (Center for Biodiversity, Illinois Natural History Survey, 607 E. Peabody Dr., Champaign, Illinois 61820). Nei's (1978) and Rogers's (1972) genetic similarity and distance coefficients were calculated with BIOSYS-1 to evaluate patterns of interpopulational genetic variation. Wright's (1978) fixation index (*F*) was used to analyze the genotypic structure at polymorphic loci.

Table 2. Summary of the number of putative loci, number of alleles per locus, allelic frequency, and inferred quaternary structure of the isozymes detected in *A. foeniculum*.

Enzyme system	Number of loci	Number of alleles[1]	Allelic frequency in *A. foeniculum*	Quaternary structure
ADH	2	Adh1: 2	Adh1-5: 1.00	Dimer
		Adh2: 1	[2]	Unknown
CAT	1	Cat1: 3	Cat1-3: 0.09	Unknown
			Cat1-4: 0.01	
			Cat1-5: 0.90	
GDH	1	Gdh1: 1	Gdh1-5: 1.00	Unknown
GOT	2	Got1: 2	Got1-4: 0.03	Dimer
			Got1-5: 0.97	
		Got2: 4	Got2-5: 0.91	Dimer
			Got2-6: 0.09	
IDH	2	Idh1: 1	[2]	Unknown
		Idh2: 2	Idh2-5: 1.00	Dimer
MDH	3	Mdh1: 2	Mdh1-5: 1.00	Dimer
		Mdh2: 2	Mdh2-5: 1.00	Dimer
		Mdh3: 2	Mdh3-5: 1.00	Unknown
MNR	2	Mnr1: 1	Mnr1-5: 1.00	Tetramer
		Mnr2: 2	Mnr2-5: 1.00	Tetramer
PGM	2	Pgm1: 2	Pgm1-5: 1.00	Monomer
		Pgm2: 3	Pgm2-4: 0.06	Monomer
			Pgm2-5: 0.92	
			Pgm2-6: 0.02	
PGD	2	Pgd1: 2	Pgd1-5: 1.00	Unknown
		Pgd2: 1	Pgd2-5: 1.00	Unknown
PHI	2	Phi1: 1	[2]	Unknown
		Phi2: 3	Phi2-4: 0.06	Dimer
			Phi2-5: 0.88	
			Phi2-6: 0.06	
TPI	2	Tpi1: 3	Tpi1-4: 0.10	Dimer
			Tpi1-5: 0.61	
			Tpi1-6: 0.29	
		Tpi2: 3	Tpi2-5: 0.85	Dimer
			Tpi2-6: 0.15	
SKD	1	Skd1: 2	Skd1-5: 1.00	Monomer

[1] Includes alleles present in *A. nepetoides* and *A. rugosa*.

[2] Apparently invariant, but not scored because of poor resolution.

Results and Discussion

Table 2 lists the number of putative loci, number of alleles per locus, allelic frequency, and inferred quaternary structure of the isozymes detected in *A. foeniculum*. Certain variants were not found in *A. foeniculum*. *Got2-4*, *Mdh3-4*, *Pgm1-4*, and *Pgd1-4* were restricted to *A. nepetoides*, whereas *Adh1-4*, *Idh2-6*, *Mdh1-4*, *Mdh2-4*, *Mnr2-6*, *Tpi2-4*, and *Skdh1-6* were restricted to populations of *A. rugosa*. Levels of enzyme heterozygosity are shown in Table 3. Only seven of 19 loci evaluated were heterozygous. *Tpi1* had the highest percentage of heterozygosity (0.53) among all loci.

Table 3. Genetic heterozygosity at 19 loci for 11 populations of *A. foeniculum*.

	Population[1]											
Locus[2]	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Total Heter.[3]
Cat	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.17
Got1	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06
Got2	0.00	0.00	0.00	0.36	0.36	0.16	0.32	0.00	0.32	0.38	0.00	0.16
Pgm2	0.47	0.12	0.00	0.32	0.05	0.35	0.00	0.00	0.00	0.00	0.12	0.15
Phi2	0.49	0.47	0.39	0.00	0.14	0.00	0.00	0.00	0.10	0.10	0.00	0.23
Tpi1	0.06	0.50	0.61	0.29	0.24	0.10	0.49	0.48	0.48	0.50	0.46	0.53
Tpi2	0.45	0.00	0.07	0.00	0.22	0.49	0.03	0.00	0.00	0.49	0.00	0.26
Popul. Total	0.08	0.08	0.06	0.03	0.05	0.06	0.04	0.03	0.04	0.08	0.03	

[1] Key to populations: I= PI-561054, II= PI-561055, III= PI-561056, IV= PI-561057, V= PI-561058, VI= PI-561059, VII= PI-561060, VIII= PI-561061, IX= PI-561062, X= PI-561063, XI= A-10207

[2] Monomorphic loci: Adh, Gdh, Idh, Mdh1, Mdh2, Mdh3, Mnr1, Mnr2, Pgm1, Pgd1, Pgd2, and Skd.

[3] Total heterozygosity for *A. foeniculum* ($_T$) = 0.08
Avg. heterozygosity within populations ($_s$) = 0.05
Within-population genetic variability ($_s$/ $_T$) = 0.63
Among-population genetic variability (1 - $_s$/ $_T$) = 0.37

Patterns of Genetic Variability

Table 4 summarizes the mean number of alleles per locus and percentage of polymorphic loci for populations of *Agastache*. Populations A-8411 and A-10207 of *A. rugosa*, together with population PI-561064 of *A. nepetoides*, were isozymatically invariant (A=1.00) and (P=0.00). Despite the lack of variability reported within those species, variability at the *Mdh3* putative locus was observed in one population of *A. rugosa*, A-10207. Because of the complexity of the MDH system, though, that variation could not be scored and was omitted from the analysis. Otherwise, our results for *A. rugosa* agreed with Vogelmann's (1983) report that this species was isozymatically invariant. For *A. nepetoides*, Vogelmann's value was 0.008, slightly greater than that found in this study (0.00). However, the present study analyzed only one population of *A. nepetoides*, whereas Vogelmann (1983) obtained his estimate from 11 populations, seven of which lacked any heterozygosity. Thus, his data are more representative of this species' actual genetic variability than are our data.

Among 11 populations of *A. foeniculum*, the mean number of alleles per locus (Table 4) ranged from 1.1 to 1.3 in population PI-561058, which also had the greatest percentage of polymorphic loci (26.3%). Values of total heterozygosity for individual populations of *A. foeniculum* ranged from 0.03 to 0.08 (Table 3).

Vogelmann (1983) made no inferences about the total heterozygosity of *A. foeniculum*, because he examined only a small sample of plants. Nevertheless, the total heterozygosity for *A. foeniculum* reported here (0.08) agreed with Vogelmann's (1983) statement that levels of heterozygosity within section *Agastache* increase from eastern to western species. *Agastache foeniculum* occurs in the central region of North America in a range that overlaps the ranges of both the eastern and western species. For eastern species, total heterozygosity values reported by Vogelmann (1983) were: *A. nepetoides* (0.008) and figwortleaf giant hyssop (*A. scrophulariifolia*, 0.062). For western species, he reported: nettleleaf giant hyssop (*A. urticifolia*, 0.085), littleleaf giant hyssop (*A. parvifolia*, 0.107), western giant hyssop (*A. occidentalis*, 0.122), and Cusick's giant hyssop (*A. cusickii*, 0.166). A similar east-to-west cline of genetic heterozygosity also has been reported among North American sedges of *Carex* section *Vesicarie* (Ford *et al*., 1991).

The total genetic variability of *A. foeniculum* was apportioned 0.63 and 0.37 within and among populations, respectively (Table 3). Because most of the isozymic variability of the species is distributed within populations, and the frequency of the rarest allele in individual populations is greater than or equal to 0.05, breeding and selection strategies used in population improvement should include 50 to 100 individuals per population for a high probability of capturing most of the genetic variability (Marshall and Brown, 1981). The maintenance and regeneration of those populations in *ex situ* management programs should also reflect this partitioning of genetic variability to maintain populational diversity over the long term.

Among populations of *A. foeniculum*, there was substantial congruence occurred between Nei's (1978) and Rogers's (1972) coefficients of genetic distances and identities. The values for Nei's genetic identity coefficients ranged from 0.878 to 1.000. Similar extreme values of genetic identity using Rogers's coefficient have been reported (Fuentes-Granados, 1993). These values are in the upper 60% of the range of those reported for other species of *Agastache* section *Agastache* (Vogelmann, 1983).

Table 4. Parameters of genetic variability for populations of *Agastache*. (Standard errors in parentheses)

Population species	Mean sample size per locus	Number of loci	Alleles per locus	Percentage of polymorphic loci[1]
A-10206 *A. foeniculum*	40	19	1.1 (0.1)	10.5
PI-561054 *A. foeniculum*	31	19	1.2 (0.1)	21.1
PI-561055 *A. foeniculum*	40	19	1.2 (0.1)	15.8
PI-561056 *A. foeniculum*	40	19	1.2 (0.1)	15.8
PI-561057 *A. foeniculum*	40	19	1.1 (0.1)	10.5
PI-561058 *A. foeniculum*	40	19	1.3 (0.1)	26.3
PI-561059 *A. foeniculum*	40	19	1.2 (0.1)	21.1
PI-561060 *A. foeniculum*	40	19	1.2 (0.1)	15.8
PI-561061 *A. foeniculum*	40	19	1.1 (0.1)	10.5
PI-561062 *A. foeniculum*	40	19	1.1 (0.1)	10.5
PI-561063 *A. foeniculum*	40	19	1.2 (0.1)	21.1
PI-561064 *A. nepetoides*	40	19	1.0 (0.0)	0.0
A-8411 *A. rugosa*	40 (0.0)	19	1.0	0.0
A-10207 *A. rugosa*	40	19	1.0 (0.0)	0.0
A. foeniculum[2]	431	19	1.6 (0.2)	36.8
A. nepetoides[2]	40	19	1.0 (0.0)	0.0
A. rugosa[2]	80	19	1.0 (0.0)	0.0

1 = A locus is considered polymorphic if more than one allele was detected in a sample of 80 (p 0.0125).
2 = total for the species

Cluster analyses (Fig. 2), as well as a simple arithmetic mean of Nei's (1978) and Rogers's (1972) distance coefficients, reveal that PI-561054 and PI-561061 are the most genetically divergent populations. PI-561054 is the only cultivated population among the four populations from Manitoba. Selection may have played a role in this population's divergence, or perhaps it originated from a nonlocal population, unlike most others in this study. PI-561061, on the other hand, is from Las Animas County, CO, and geographic isolation and adaptation to different ecogeographical conditions may have played a role in that population's genetic divergence.

```
  .13       .10       .07       .03       .00
--+----+----+----+----+----+----+----+----+

         ********************************** PI-561054
         *
         *                   ************** PI-561055
         *               *****
         *               *   ************** PI-561056
         *               *
         *            ********************* PI-561057
         *            *   *
         *            *   *    ************ PI-561058
         *            *   *    *
         *            *   *    *         ** PI-561060
         *            *   *    *     *****
         *  ***********   *    *******   ** PI-561062
         *  *         *   ******     *
         *  *         *        *     ******  A-10206
         *  *         *        *
         ****         *        ************ PI-561063
            *         *
            *         ********************* PI-561059
            *
            ******************************* PI-561061

--+----+----+----+----+----+----+----+----+
  .13       .10       .07       .03       .00
             Genetic distance


 Population or cluster          Clustering
   numbers joined                  level           Cycle
--------------------------------------------------------
 PI-561060  PI-561062             .00197               1
 PI-561060   A-10206              .01612               2
 PI-561058  PI-561060             .03424               3
 PI-561058  PI-561063             .03692               4
 PI-561055  PI-561056             .04477               5
 PI-561057  PI-561058             .05171               6
 PI-561055  PI-561057             .05553               7
 PI-561055  PI-561059             .06638               8
 PI-561055  PI-561061             .10007               9
 PI-561054  PI-561055             .10974              10
--------------------------------------------------------
```

FIG. 2. Cluster analysis and clustering levels of populations of *A. foeniculum*

Table 5. Inbreeding coefficient (F) and X^2 values testing Hardy-Weinberg equilibrium at intrapopulational variable loci and for populations *per se* of *A. foeniculum*.

Sample Population	Enzyme	Inbreeding size	coefficient (F)	X^2	d.f.	P
PI-561054	Pgm2	31	-0.088	0.24	1	0.625
	Phi1	31	0.205	1.30	1	0.253
	Tpi1	31	-0.033	0.03	1	0.853
	Tpi2	31	0.208	1.34	1	0.247
			F-mean 0.073			
PI-561055	Got1	40	0.088	0.31	1	0.576
	Phi1	40	0.123	0.61	1	0.436
	Tpi1	40	0.350	4.89	1	0.027
			F-mean 0.187	10.01^1	6	.1<p<.2
PI-561056	Phi1	40	0.031	0.04	1	0.842
	Tpi1	40	0.091	3.83	3	0.281
	Tpi2	40	-0.039	0.06	1	0.805
			F-mean 0.028			
PI-561057	Pgm2	40	-0.094	0.35	1	0.553
	Tpi1	40	0.134	0.72	1	0.396
			F-mean 0.040			
PI-561058	Got2	40	0.241	2.32	1	0.128
	Pgm2	40	-0.026	0.03	1	0.871
	Phi1	40	-0.081	0.26	1	0.608
	Tpi1	40	0.073	0.85	3	0.837
	Tpi2	40	-0.143	0.82	1	0.366
			F-mean 0.013			
PI-561059	Got2	40	0.217	1.89	1	0.169
	Pgm2	40	0.140	0.78	1	0.377
	Tpi1	40	-0.053	0.11	1	0.739
	Tpi2	40	0.079	0.25	1	0.616
			F-mean 0.096			
PI-561060	Got2	40	0.531	11.29	1	0.001
	Tpi1	40	-0.393	6.17	1	0.013
	Tpi2	40	-0.013	0.01	1	0.936
			F-mean 0.042			
PI-561061	Cat1	40	1.000	40.00	1	0.000
	Tpi1	40	0.063	0.16	1	0.693
			F-mean 0.063^2	0.16	1	0.693
PI-561062	Got2	40	-0.094	0.35	1	0.353
	Tpi1	40	-0.422	7.12	1	0.008
			F-mean-0.258	11.74	4	.01<p<.02
PI-561063	Got2	40	0.067	0.18	1	0.673
	Phi1	40	1.000	40.00	1	0.000
	Tpi1	40	0.045	0.08	1	0.778
	Tpi2	40	0.284	3.22	1	0.073
			F-mean 0.132^2	6.53	6	.1<p<.5
A-10206	Pgm2	40	-0.067	0.18	1	0.673
	Tpi1	40	-0.136	0.74	1	0.390
			F-mean-0.102	2.68	4	.5<p<.9

1 = X^2 values for populations obtained using the procedure "Combining Probabilities from Tests of Significance" (Sokal and Rohlf, 1981).

2 = calculated excluding enzyme systems with F = 1.000

Table 5 summarizes the inbreeding coefficients (*F*) and chi-square values testing Hardy-Weinberg expectations for polymorphic loci within populations of *A. foeniculum*. Mean values of the inbreeding coefficients for populations evaluated in this study were generally close to zero. Except for populations PI-561061 and PI-561063, the mean values were obtained from all polymorphic loci. No heterozygotes were found in one polymorphic enzyme system in each of those populations, and those systems were excluded when the mean was calculated. Three possible factors for lack of heterozygotes for *Cat* in PI-561061 and for *Phi2* in PI-561063 include artifacts of sample size, selection against heterozygotes, and heterozygotes that cannot be observed because of dominance. Alternatively, it is possible that the allele denoted herein as *Cat1-4* is artifactual and may reflect the phenotype of a *Cat1-3/5* heterozygote. *F*-values for the other polymorphic loci in populations PI-561061 and PI-561063 were near zero (Table 5).

Negative values of *F* obtained for two populations indicate that they have the structure of a cross-pollinated species with some degree of heterozygote advantage. All other populations had small, positive *F*-values. These positive *F*-values indicate that slightly more, though not significantly more, selfing occurs than would be expected from the Hardy-Weinberg model.

Results of the present study revealed that *A. foeniculum* is genetically variable and has a mating system that tends toward allogamy. Eleven enzyme systems were resolved successfully, and all 19 loci detected, whether polymorphic or not, were included in the analysis to avoid bias that might result from preferential inclusion of only highly polymorphic loci (Hamrick *et al*., 1979). Seven of the 19 loci evaluated, *Cat, Got1, Got2, Pgm2, Phi2, Tpi1*, and *Tpi2*, were polymorphic within *A. foeniculum*. Those loci constituted 36.8% of all loci evaluated.

F-values close to zero, with over half the genetic diversity distributed within populations, suggest that *A. foeniculum* has the genetic structure of a cross-pollinated species. However, in a comprehensive review of numerous published studies, Hamrick and Godt (1991) reported mean percentages of polymorphic loci of 41.8% and 50.1% for self- and cross-pollinated species, respectively. The percentage of polymorphic loci of *A. foeniculum* (36.8%) in our study is considerably lower than that of typical cross-pollinated species. The average number of alleles per locus (1.6) and the total heterozygosity (0.08) of *A. foeniculum* were also lower than the values for those estimates reported by Hamrick and Godt (1991) for cross-pollinated species. We plan to examine these atypically low levels of enzymatic diversity by acquiring additional collections from throughout the species' native range.

Most (63%) of the genetic diversity found in *A. foeniculum* occurred within populations, which, together with the intrapopulational variability for oil content and composition (Wilson *et al.* 1992), suggest the feasibility of selection for nectar production or for specific chemotypes within populations. This study showed that both this species's provenance and cultivation may have contributed to genetic differentiation of its populations. Population PI-561061 was genetically divergent from the other populations and originates from the southwestern part of the species' geographical range, where specific allelic variants may have evolved. On the other hand, cultivated population PI-561054 was genetically divergent from the other three populations from Manitoba. Either selection for different genotypes under cultivation or a different area of origin could explain that population's genetic divergence.

Our next step in studying *Agastache foeniculum* is to verify our tentative interpretations of the genetic bases of isozyme banding patterns with existing and additional accessions from throughout the native range of this species. The essential oils of *A. foeniculum* also will be analyzed to identify distinct chemotypes, their inheritance patterns, and possible genetic and biochemical pathways for their qualitative differences.

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Literature Cited

Ayers, G.S., and Widrlechner, M.P. 1994. The genus *Agastache* as bee forage: a historical perspective. American Bee Journal 134:341-348.

Charles, D.J., Simon, J.E., and Widrlechner, M.P. 1991. Characterization of essential oils of *Agastache* species. Journal of Agricultural and Food Chemistry 39:1946-1949.

Ford, B.A., and Ball, P.W. 1991. Allozyme diversity and genetic relationships among North American members of the short-beaked taxa of *Carex* sect. *Vesicariae* (Cyperaceae). Systematic Botany 16:116-131.

Fuentes-Granados, R.G. 1993. Genetic diversity and reaction to *Verticillium* among populations of *Agastache*. M.S. Thesis, Iowa State University, Ames.

Galambosi, B., and Galambosi-Szebeni, Z. 1992. Studies on the cultivation methods of *Agastache foeniculum* (Pursh) Kuntze in Finland. Acta Agronomica Hungarica 41:107-115.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence. 1392 pp.

Hamrick, J.L. and Godt, M.J.W. 1991. Allozyme diversity in plant species. *In*: A.H.D. Brown, M.T. Clegg, A.L. Kahler, and B.S. Weir (eds.) Plant Population Genetics, Breeding, and Genetic Resources. Sinauer Associates Inc., Sunderland, MA, pp 43-63.

Hamrick, J.L., Linhart, Y.B., and Mitton, J.B. 1979. Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. Annual Review of Ecology and Systematics 10:173-200.

Hashemi, A., Estilai, A., and Edhaie, B. 1991. Inheritance of aconitase, shikimate dehydrogenase, and phosphoglucose isomerase in guayule. Journal of the American Society for Horticultural Science 116:737-739.

Lint, H., and Epling, C. 1945. A revision of *Agastache*. The American Midland Naturalist 33:207-230.

Marshall, D.R., and Brown, A.H.D. 1981. Wheat genetic resources. *In*: L.T.Evans and W.J Peacock (eds.) Wheat Science - Today and Tomorrow. Cambridge University Press, Cambridge, pp 21-40.

Mazza, G., and Kiehn, F.A. 1992. Essential oils of *Agastache foeniculum*, a potential source of methylchavicol. Journal of Essential Oil Research 4:295-299.

Menghini, A., Capuccella, M., Pagiotti, R., and Spigarelli, M. 1992. Pigment content and methylchavicol production in *Agastache foeniculum* (Pursh) Kuntze cultured *invitro.* Journal of Essential Oil Research 4:483-486.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583-590.

Nykänen, I., Holm, Y., and Hiltunen, R. 1989. Composition of the oils of *Agastache foeniculum*. Planta Medica 55: 314-315.

Rogers, J. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics VII. University of Texas Publication 7213.

Senechal, N.P. 1990. Evaluation of native perennial Lamiaceae as sources of nectar for honey bees. M.S. Thesis, Iowa State University, Ames.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry (2nd ed.). Freeman and Company, New York. 859 pp.

Stuber, C.W., Wendel, J.F., Goodman, M.M., and Smith, J.S.C. 1988. Techniques and scoring procedures for starch gel electrophoresis of enzymes from maize (*Zea mays* L.). Technical Bulletin 286, North Carolina State University, Raleigh.

Vogelmann, J.E. 1983. A biosystematic study of *Agastache* section *Agastache* (Labiatae). Ph.D. Dissertation, Indiana University, Bloomington.

Vogelmann, J.E., and Gastony, G.J. 1987. Electrophoretic enzyme analysis of North American and eastern Asian populations of *Agastache* sect. *Agastache* (Labiatae). American Journal of Botany 74:385-393.

Wendel, J.F., and Weeden, N.F. 1989. Visualization and interpretation of plant isozymes. *In* D.E. Soltis and P.S. Soltis (eds.) Isozymes in Plant Biology, Dioscorides Press, Portland, OR. pp 5-45.

Widrlechner, M.P. 1992. A field evaluation of native mint family plants as honey bee forage in Iowa. *In* D.D. Smith & C.A. Jacobs (eds.) Proceedings of the Twelfth North American Prairie Conference. University of Northern Iowa, Cedar Falls, pp 39-42.

Wilson, L.A., Senechal, N.P., and Widrlechner, M.P. 1992. Headspace analysis of the volatile oils of *Agastache*. Journal of Agricultural and Food Chemistry 40:1362-1366.

Wright, S. 1978. Variability within and among Natural Populations. The University of Chicago Press, Chicago 580 pp.

Dynamics of Big Bluestem (*Andropogon gerardii*) in Ungrazed Kansas Tallgrass Prairie

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Abstract. Canopy cover was recorded annually from 1983 to 1993 in 200 permanent plots located in long-term, unburned and annually burned, upland and lowland, ungrazed, tallgrass prairie. Based on canopy cover values, *Andropogon gerardii* was the dominant species in 73% of the plots and shared dominance with other species in 16% of the plots. *Poa pratensis* was the principal subdominant species in unburned prairie, and *Andropogon scoparius* in burned prairie. Yearly transition probabilities of dominant vegetation types showed that *A. gerardii*-dominated plots were 78-86% likely to remain dominated by *A. gerardii* in the following year. Transition probabilities showed that changes from one vegetation type to another were not independent, indicating nonrandom changes. Additionally, the dominant species in a plot during one year depend largely upon the dominant species in the previous year. Thus, as the most abundant core species, *A. gerardii* plays a major role in determining the abundance of the other species. Fluctuations in the abundance of *A. gerardii* allow only short-term dominance by other species.

Key words: *Andropogon gerardii*, fire, Markov models, tallgrass prairie, transition probabilities

Introduction

Big bluestem (*Andropogon gerardii*) is the dominant plant of prairies in the Flint Hills of Kansas . It is the most abundant of the core, or matrix, species (Collins and Glenn 1991). Although other species may be common and even abundant in certain areas, *A. gerardii* is ubiquitous. Indeed, Kchler (1974) referred to this type of tallgrass prairie as bluestem prairie.

Despite the high general abundance of *A. gerardii,* its abundance varies yearly with variation in precipitation and in response to fire and grazing (Abrams *et al.* 1986, Gibson and Hulbert 1987). Many studies have considered these community, or beta-diversity scale, responses. A few studies have considered how *A. gerardii* or other core species vary at a smaller, patch scale. For example, Glenn and Collins (1990), noted that, at 1 - 10 m^2, the less common species defined patches that varied unpredictably in time and space. At these scales, the core species occurred within all patch types.

In this report, the dynamics of 10 m^2 patches are followed over a 10-year period in annually burned and long-term unburned, upland and lowland prairie to assess the persistence of *A. gerardii*-dominated patches compared with the persistence of patches dominated by other grasses and forbs.

Methods

Study Site

Field data were collected between 1983 and 1993 on the 3,487 ha Konza Prairie Research Natural Area (KPRNA) in Riley and Geary Counties in the Flint Hills of northeast Kansas. KPRNA is a tallgrass prairie dominated by *A. gerardii*, little bluestem (*Andropogon scoparius*), Indian grass (*Sorghastrum nutans*), and switch grass (*Panicum virgatum*) (Reichman 1987). The climate of the site is temperate midcontinental with annual mean temperature of 13°C and a range from -3°C in January to 27°C in July (Van Cleve and Martin 1991). Annual precipitation is 835 mm. Soils are chernozems within the Mollisol order and are represented primarily by the Florence series (clayey-skeletal, montmorillonitic, mesic Udic Argiustolls) in upland areas and by the Tully series (fine, mixed, mesic Pachic Argiustolls) in lowland areas (Jantz *et al.* 1975).

A management plan for the site initiated in the 1970's places watersheds into one of several regimes of burning and/or large herbivore grazing (*Bison bison* or cattle). Burning regimes range from watersheds burned annually in the spring (late April) to long-term unburned watersheds burned once every 20 years (Marzolf 1988). Data in the present study are restricted to ungrazed watersheds.

Field Methods

Canopy cover of all species was estimated visually using a modified Daubenmire cover abundance scale (Abrams and Hulbert 1987) in 20, 10 m^2 circular plots permanently located along four 50 m transects in upland and lowland areas of watersheds. Both upland and lowland areas of two annually burned watersheds (coded 1C and 1D) and three long-term unburned watersheds (coded N4D, N20B, 20B) on KPRNA were surveyed (Table 1). Data were collected from 1983 through 1993 in the annually burned watersheds, from 1983 through 1987 on N4D, and from 1983 through 1990 on N20B and 20B.

Table 1. Fire history of watersheds used in present study.

Burning frequency	Watershed	Start of current burning regime	Consecutive years of data used in this report
Annually burned	1C	1972	1983-1987
	1D	1978	1983-1993
		Last burn	
Unburned	N4D	1971*	1983-1987
	N20B	1980†	1983-1990
	20B	1973^{+},†	1983-1990

*Southern portion burned during escaped prescribed burn in 1973. Entered 4-year burn regime in 1987 with first burn in 1988.

$^{+}$ Small portion burned in wildfire in 1975

† Completely burned in 1991 wildfire

Data analysis

The species with the highest canopy cover in a plot was used to characterize that plot. In the event of equal canopy cover values, all codominants were used. Each plot thus was characterized by dominant or by codominant species. Initial data analysis determined the frequency of dominance/codominance of species per burning treatment and topographic position, i.e., the percentage of times that a species was a dominant or codominant over all plots in the analysis or treatment. Data from consecutive years were considered in one analysis to ensure an adequate sample size. Plots were classified subsequently into one of seven vegetation types or transition states; i.e., BB, *A. gerardii* dominated; BG, *A. gerardii* and other grasses as codominants; BF, *A. gerardii* and forbs/shrubs as codominants; G, grass dominated (not *A. gerardii*); F, forb or shrub dominated; GF, grass (not *A. gerardii*) and forb codominated; or BGF, *A. gerardii* and other grasses and forb as codominants. A matrix of transition probabilities (p_{ij}) representing the probability that a plot would be classified as one of the seven vegetation types in 1 year (p_i) and the same or a different vegetation type in the next year (p_j) was calculated for unburned uplands, burned uplands, unburned lowlands, and burned lowlands according to Usher (1992). Anderson and Goodman's (1957) test statistic (-2(ln)) for determining the independence of transition probabilities within a matrix was calculated according to Usher (1992). This statistic tests the null hypothesis that successive transitions are statistically independent (i.e., random). Values of the statistic larger than the appropriate ^{2} value with $(m-1)^2$ degrees of freedom, where m = the number of transition states in the system, allows a rejection of the null hypothesis of statistical independence. Postmultiplication of transition matrices by the average percentage composition of unburned and burned, lowland and upland, prairie vegetation types (p_2) was undertaken to determine the composition and time to reach a stable vegetation composition (i.e., the dominant eigenvector, p). The BF and BGF vegetation types were excluded from matrix calculations for burned lowlands, because the transition probability for both vegetation types remaining the same in a subsequent year was 1.0 and was based on a single plot from one 2-year transition. Inclusion of these transitions in preliminary trials revealed spurious results.

Results

Over the 10-year study period, *Andropogon gerardii* was the dominant species 73% of the time in the 200 permanent plots (Table 2). Sixteen other species were also dominant at some time, with Kentucky bluegrass (*Poa pratensis*) being the most frequent dominant, although its frequency of dominance was only 2.3%. Fifteen other species were dominant in less than 1% of the plots. An additional 11 species were codominants either with *A. gerardii* or another species. Of these, *A. scoparius* was the most common codominant with a frequency of 7.3%. *Sorghastrum nutans, Poa pratensis, Panicum virgatum,* and tall dropseed (*Sporobolus asper*) were other codominants that had a frequency > 1%.

Several differences occurred in the dominant and codominant species of annually burned and unburned prairie (Table 2). *A. scoparius* and *Sorghastrum nutans* were dominants and codominants in both annually burned and unburned prairie, although their frequencies of dominance exceeded 1% only in annually burned prairie. *A. scoparius* was a dominant > 5% and codominant > 15% in lowland annually burned prairie. *Poa pratensis* was the second most frequent dominant species overall (> 5%) after *A. gerardii* in upland and lowland, unburned prairie. Other species that were dominant or codominant in unburned prairie, but not in annually burned prairie, included smooth brome (*Bromus inermis*), Canada goldenrod (*Solidago canadensis*), prairie goldenrod (*S. missouriensis*), buckbrush (*Symphoricarpus orbiculatus*), Louisiana sagewort (*Artemisia ludoviciana*), New Jersey tea (*Ceanothus herbaceous*), aromatic aster (*Aster oblongifolius*), and *Eupatorium altissimum*. Of these, some (e.g., *S. canadensis*) occurred only in lowland prairie, whereas other species (e.g., *S. missouriensis*) occurred only in upland prairie. Dominants and codominants that occurred only in annually burned, upland prairie included Pitcher's sage (*Salvia azurea*), blue grama (*Bouteloua gracilis*), and 11 other species (Table 2).

The vegetation most frequently was composed of (> 70%) types dominated only by *A. gerardii*, regardless of the topography or burning treatment (Figure 1). The BG and G vegetation types had a frequency of 7-18% with BG being the most frequent, especially in annually burned plots. Vegetation types F, BF, GF, and BGF were poorly represented, especially in annually burned lowlands where forbs were a dominant component only in BGF < 1%. Forbs were most frequent as dominant plants in unburned lowlands.

Except for unburned uplands that showed marginal significance (-2(ln) = 48.19, $P < 0.1$), the Anderson and Goodman (1959) test statistic indicated that the transitions among the seven vegetation types were not random (burned uplands, -2(ln) = 83.04, $P < 0.005$; unburned lowlands, -2(ln) = 79.04, $P < 0.005$; burned lowlands, -2(ln) = 27.25, $P < 0.05$).

Transition probabilities between vegetation types showed that plots dominated or codominated by *A. gerardii* in one year were very likely (probabilities > 0.40) to be dominated by *A. gerardii* in the next year (Fig 2). An exception to this was on burned lowlands, where *A. gerardii* and forbs remained codominant in successive years. Plots dominated only by *A. gerardii* were highly likely (probabilities > 0.78) to remain dominated by *A. gerardii* in the next year. These high probabilities occurred irrespective of topography or burning. Transitions between the other vegetation types showed a greater relationship to topography or burning. For example, forb-dominated plots had 0.57 and 0.25 probabilities of remaining forb-dominated on unburned lowlands and uplands, respectively. They always became BF plots on burned uplands (probability = 1.0) and did not occur on burned lowlands. Probability values were larger among the seven vegetation types on unburned prairie, reflecting a lesser dominance of *A. gerardii* without annual burns.

Table 2. Frequency (%) of dominance and codominance of plots by species in unburned and annually burned upland and lowland prairie plots over a 10-year period.

Species	Unburned				Burned					
	Upland		Lowland		Upland		Lowland			
	Dom*	Co dom	Dom	Co dom	Dom	Co dom	Dom	Co dom	Av. codom	Av. Dom
Andropogon gerardii	74.40	16.25	76.50	8.75	70.75	21.75	70.50	0.18	0.16	73.04
Poa pratensis	5.60	10.75	3.50	6.25	- ‡	-	-	-	4.22	2.29
Panicum virgatum	-	-	1.50	1.25	-	1.00	2.25	5.25	1.80	0.93
Sorghastrum nutans	0.24	1.25	0.75	1.75	4.97	11.00	0.25	0.60	4.97	0.87
Solidago canadensis	-	-	2.25	1.00	-	-	-	-	0.56	0.81
Symphoricarpus orbiculatus	-	-	2.00	1.50	-	-	-	-	0.87	0.50
Sporobolus asper	-	0.75	1.25	3.25	-	0.25	-	0.50	1.18	0.31
Ambrosia psilostachya	0.98	1.00	0.25	1.25	-	0.50	-	-	0.68	0.31
Bromus inermis	0.98	0.50	-	-	-	-	-	-	0.12	0.25
Andropogon scoparius	0.73	1.50	-	1.25	3.25	11.5	5.25	15.25	7.33	0.21
Artemisia ludoviciana	-	1.00	0.50	0.75	-	-	-	-	0.43	0.12
Solidago missouriensis	0.50	1.00	-	-	-	-	-	-	0.25	0.12
Salvia azurea	-	-	-	-	0.25	4.00	-	-	0.99	0.06
Bouteloua gracilis	-	-	-	-	0.25	2.50	-	-	0.62	0.06
Coeanothus herbaceous	0.24	1.25	-	-	-	-	-	-	0.31	0.06
Aster oblongifolius	0.24	1.25	-	-	-	-	-	-	0.31	0.06
Carex spp.	-	-	-	-	-	0.25	-	-	0.06	0.06
Bouteloua curtipendula	-	0.25	-	-	-	1.25	-	-	0.43	-
Bouteloua hirsuta	-	-	-	-	-	1.00	-	-	0.25	-
Dichanthelium oligosanthes	-	-	-	-	-	0.25	-	-	0.19	-
Schrankia nutalli	-	-	-	-	-	0.50	-	-	0.12	-
Asclepias viridis	-	-	-	-	-	-	-	0.50	0.12	-
Carex brevior	-	-	-	-	-	-	-	0.50	0.12	-
Amorpha canescens	-	-	-	-	-	0.25	-	-	0.06	-
Eragrostis spectabolis	-	-	-	-	-	0.25	-	-	0.06	-
Erigeron strigosus	-	-	-	-	-	0.25	-	-	0.06	-
Eupatorium altissimum	-	-	-	0.25	-	-	-	-	0.06	-
Sporobolus heterolepis	-	-	-	-	-	0.25	-	-	0.06	-

* Dom =percentage of times (dominance frequency) that a species had the maximum canopy cover in a plot, Codom = percentage of times (codominance frequency) that a species shared the maximum canopy cover with other species in a plot. Av. codom. = average codominace freqency value of a species over all treatments, Av. dom. = average dominace freqency value of a species over all treatments.

‡ - = zero dominance or codominance frequency, i.e., species was never a dominant or codominant species.

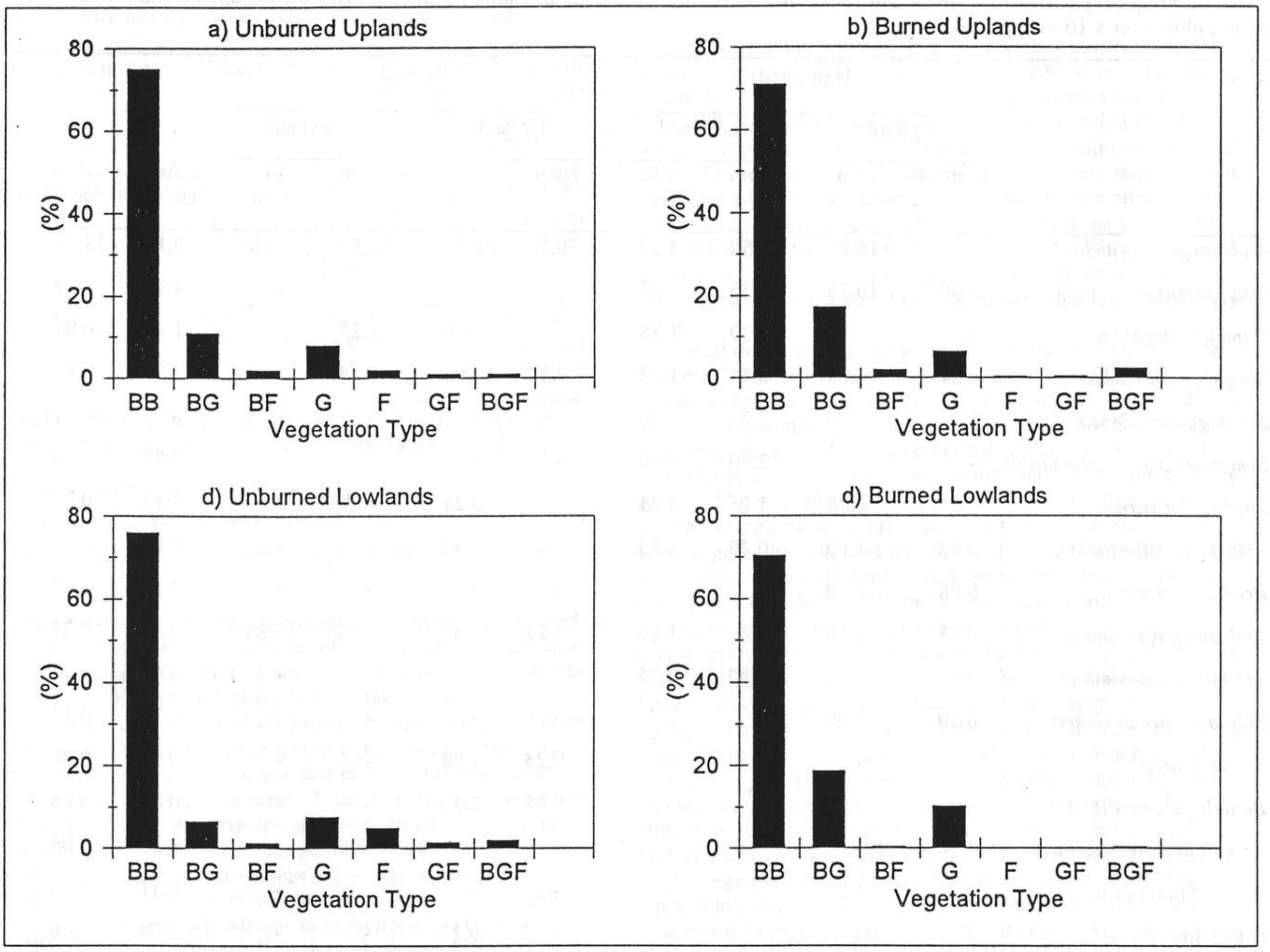

FIG. 1. Percentage of plots in seven vegetation types [(BB, *A. gerardii* dominated; BG, *A. gerardii* and other grasses codominants; BF, *A. gerardii* and forbs/shrubs as codominants; G, grass dominated (not *A. gerardii*); F, forb or shrub dominated; GF, grass (not *A. gerardii*) and forb codominated; or BGF, *A. gerardii*, other grasses and forb codominants)] on a) unburned upland, b) annually burned upland, c) unburned lowland, and d) annually burned lowland tallgrass prairie.

Unburned lowlands were perhaps the most stable between years, with three vegetation types (BB, G, and F) having probabilities of remaining the same the next year > 0.50 (Fig 2c). In addition, BG plots had a probability of 0.24 of remaining the same in the next year. Nevertheless, many other transitions between vegetation types had a probability > 0.01, indicating frequent minor changes.

On burned lowlands, forb-dominated and GF vegetation types were absent, and the transition matrix was different from those of other burned-unburned upland/lowland combinations. BB and BF were temporally stable (Fig. 2d), although the latter vegetation type was rare (Fig. 1). BGF plots were also rare and were temporally unstable, having a probability of 1.0 of changing to G plots in the next year.

Postmultiplication of the transition matrices by average percentage composition for vegetation types in unburned and burned and upland and lowland prairie showed that predicted stable compositions (dominant matrix eigenvectors, p) were similar to the average compositions (Table 3). Although represented by only three of the seven vegetation types, burned lowlands were within 2% of the predicted stable composition, and, hence, the number of years to reach stability was short, < 2 years. In contrast, the average composition of unburned lowlands was 0.28-13.06% different, depending on vegetation type, from the predicted, stable composition. Predicted stability in these sites was attained only at 15 years. Unburned and burned uplands were intermediate in compositional difference between the average and predicted stable composition and time to reach stability.

Discussion

This study has shown that, in ungrazed Kansas tallgrass prairie, the core species, *Andropogon gerardii*, dominates temporally persistent patches (10 m^2) despite differences in burning regime or topography. Annual transitions show that *A. gerardii* has a > 70% probability of being the dominant species in a plot and a > 78% probability of remaining the dominant species in the subsequent year. Patch types dominated by other species were spatially and temporally transient. This overwhelming dominance by *A. gerardii* may explain partly Bartha *et al.*'s (1995) finding that spatial and temporal variations of tallgrass prairie are constrained at the level of functional groups (e.g., grass-dominated patches).

Why is *A. gerardii* such a dominant species in this part of the tallgrass prairie? Dominance to this extent suggests an aggressive, highly competitive species. *A. gerardii* is a tall, robust, C_4, perennial grass common to mesic prairies through the Great Plains (Risser *et al.* 1981). It is genetically polymorphic (Keeler 1990) and rapidly spreads into grazed pastures following the cessation of grazing (Glenn-Lewin 1980). It has high drought resistance and achieves high photosynthetic rates under the high temperature and irradiation conditions typical of the growing season in the tallgrass prairie (Knapp 1985, 1993). Also, it is highly mycorrhizal-dependent and is an aggressive competitor in the presence of natural levels of soil mycorrhizae (Hartnett *et al.* 1993, Hetrick *et al.* 1994). Along with other mature prairie dominants, *A. gerardii* has been implicated in allelopathic effects on other species through its inhibition of soil nitrification (Smith and Rice 1983).

Given the aggressive nature of *A. gerardii*, what allows other species to occasionally usurp *A. gerardii* and become dominants or codominants in this grassland? In annually burned grassland, *A. scoparius* and *Sorghastrum nutans* were the most important species that also became dominant or codominant. Like *A. gerardii*, these are also both mesic prairie, C_4, perennial grasses. They are also both highly mycorrhizal-dependent and show a rapid growth response following spring fires. As core species in this tallgrass prairie, they also determine the matrix structure of the grassland. *A. scoparius* is generally more abundant than *S. nutans* in the more xeric areas of grasslands. In contrast, *Poa pratensis*, a C_3 perennial grass, was the most frequent dominant after *A. gerardii* in unburned grassland. *P. pratensis* is adapted for early season growth and achieves maximum biomass and flowers before the warm-season grasses. However, it recovers poorly from a spring burn. Hence, it is abundant in unburned

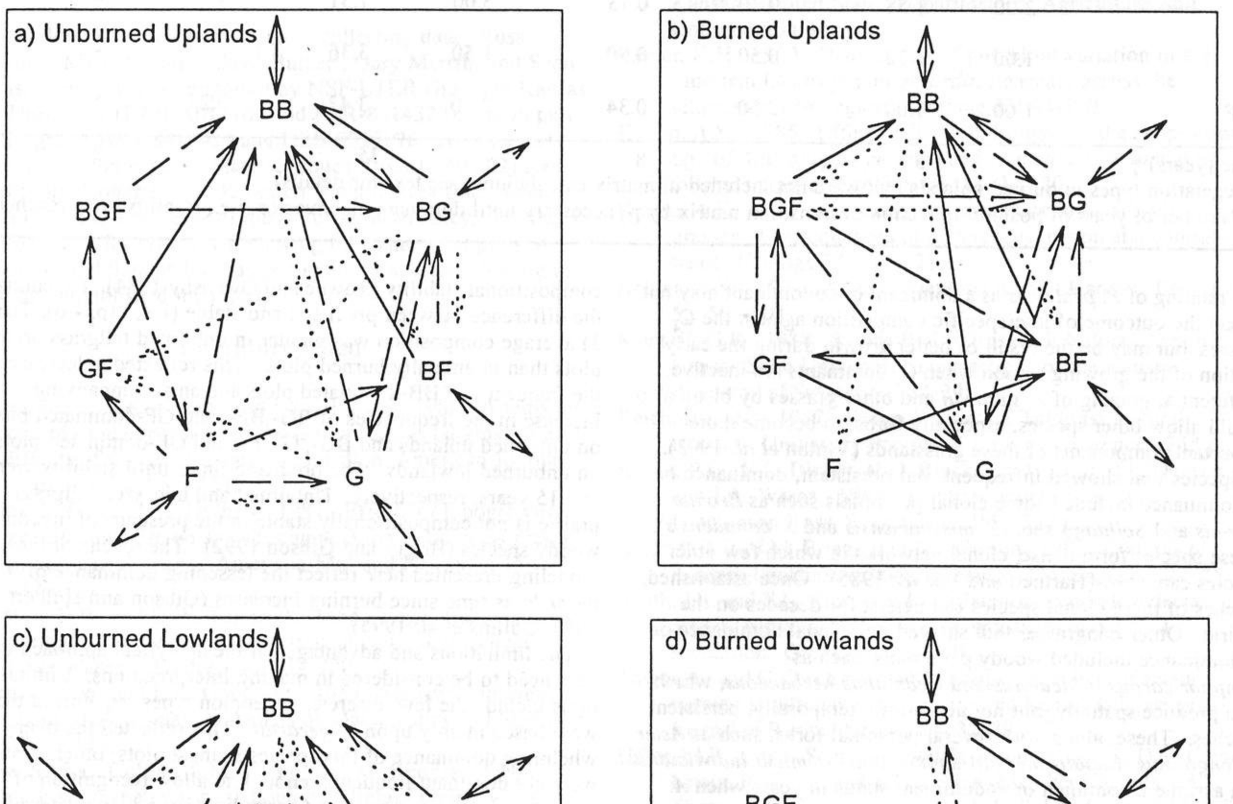

FIG. 2. Diagramatic representation of yearly transition probabilities between seven vegetation types on unburned upland, b) burned upland, c) unburned lowland, and d) burned lowland tallgrass prairie. Solid lines indicate p_{ij} 0.5, dashed lines 0.10 p_{ij} < 0.50, and dotted lines indicate 0.01 p_{ij} < 0.10. Double-headed arrows represent probability of a plot remaining in the same vegetation type in the next year. Line lengths have no meaning.prairie (Gibson and Hulbert 1987).

Table 3. Average percentage composition (p_2) and predicted, stable percentage composition (eigenvector, p) of unburned and annually burned, upland and lowland, ungrazed, tallgrass prairie from postmultiplication of transition matrices (Fig 2).

Vegetation type	Uplands				Lowlands			
	Unburned		Annually Burned		Unburned		Annually Burned	
	p_2	p	p_2	p	p_2	p	p_2	p
BB	75.00	70.84	71.00	73.13	76.00	62.94	70.5	70.6
BG	11.00	11.32	17.30	19.91	6.50	8.01	18.75	17.71
BF	2.00	2.23	2.00	2.58	1.25	1.53	0.25	*
G	8.00	1.13	6.50	6.61	7.75	13.38	10.25	11.71
F	2.00	1.58	0.30	0.73	5.00	7.31	-	-
GF	1.00	1.72	0.50	0.90	1.50	3.36	-	-
BGF	1.00	1.00	2.50	0.34	2.00	3.43	0.25	*
Time (years) ‡		5		8		15		2

* Vegetation types in burned uplands that were not included in matrix calculations (see text for details).

‡ Number of years of postmultiplication of transition matrix by p_2 necessary until dominant eigenvector (i.e., stability) was reached.

The ranking of *P. pratensis* as a dominant or codominant may not reflect the outcome of interspecific competition against the C_4 grasses, but may be the result of better growth during the early portion of the growing season when C_4 dominants are inactive. Preferential grazing of *A. gerardii* and other grasses by bison also would allow other species, especially forbs, to become more important components of these grasslands (Vinton *et al.* 1993).

Species that showed infrequent, but persistent, dominance or codominance included some clonal perennials such as *Bromus inermis* and *Solidago* spp. (*S. missouriensis* and *S. canadensis*). These species form dense, clonal networks in which few other species can grow (Hartnett and Bazazz 1985). Once established, patches of these clonal species can persist for decades on the prairie. Other nongrasses that showed occasional dominance or codominance included woody perennials, such as *Symphoricarpus orbiculatus* and *Ceanothus herbaceous*, which also produce spatially, but not necessarily temporally, persistent patches. These, along with several perennial forbs, such as *Aster oblongifolius, Eupatorium altissimum* and *Artemisia ludoviciana*, can assume a dominant or codominant status in years when *A. gerardii* has low canopy cover.

The transition probabilities indicated the replacement probabilities for patch types on a yearly basis. In addition to allowing insight into controlling mechanisms for these *A. gerardii*-dominated communities as outlined above, transition probabilities can be used to provide predictions of future community composition (Van Hecke *et al.* 1984). The present study suggested that burned lowlands were extremely close to a stable vegetation composition (Table 3). This is not surprising, given the long history of annual burning on the two watersheds (15 and 21 years) and the low diversity of burned lowlands (Gibson and Hulbert 1987). The average composition of annually burned uplands was also similar to the predicted stable composition (< 3% difference between p_2 and p, Table 3), although time to stability was 8 years compared with 2 years predicted for burned lowlands. Through the development of a soil nitrogen limitation (Seastedt *et al.* 1991) and other factors favoring *A. gerardii*, long-term annual burning of ungrazed tallgrass prairie promotes compositional stability (Towne and Owensby 1984). By contrast, the difference between predicted and stable (i.e., | (p_2 - p); Table 3) average composition was greater in unburned tallgrass prairie plots than in annually burned plots. This reflected a decrease in the frequency of BB-dominated plots and an accompanying increase in the frequencies of BG-,BF-, and GF-dominated plots on unburned uplands and BG-, G-, F-, and GF-dominated plots on unburned lowlands. The predicted times until stability were 5 and 15 years, respectively. Unburned and ungrazed tallgrass prairie is not compositionally stable in the presence of invading woody species (Briggs and Gibson 1992). The results of the modeling presented here reflect the lessening dominance of *A. gerardii* as time since burning increases (Gibson and Hulbert 1987, Collins et al. 1995).

The limitations and advantages of the analytical approach used here need to be considered in making interpretations. Limitations include the few, discrete, vegetation types recognized that were based mainly upon *A. gerardii*. This reflected the overwhelming dominance of this species in most plots; other species were not dominant frequently enough to allow recognition of separate vegetation types. A further limitation is the deterministic nature of calculating the product of postmultiplying the transition matrices. This well-recognized limitation of Markov modeling (Usher 1992) argues for caution in interpretation.

Advantages of this approach include the ability to predict future changes in vegetation composition and the development pattern towards the predicted stable endpoint. Although that endpoint is unlikely to be reached in reality because of extrinsic factors not contained within the model, it provides a potential scenario against which field-based patterns can be compared. For example, the high level of similarity between composition of burned plots and the predicted composition suggests that long-term, annually burned watersheds have reached a high level of compositional stability. Any significant future changes in the composition of these watersheds would indicate the imposition of altered or new disturbance regimes, e.g., drought (Albertson and Tomanek 1965).

The analysis presented here is also scale dependent. Sample plots were 10 m^2, and interpretations must be made at this scale. Previous studies at the whole-watershed level (Gibson and Hulbert 1987, Collins and Glenn 1991) have shown that *A. gerardii* is ubiquitous and dominant under all topographic and management regimes. At equivalent or smaller scales, other species are often dominant, especially on disturbed areas (Gibson 1989). Glenn and Collins (1990) showed that patch structure and composition at small scales was related to dispersal processes affecting the satellite species. Bartha *et al.* (1995) found that *A. gerardii* was the most frequently occurring species (40-50%) at a scale of 25 cm^2. Overall, this study has shown that *A. gerardii* plays a major role in determining the abundance of the other species. Fluctuations in the abundance of *A. gerardii* allow only short-term dominance by other species, except following the establishment of persistent, clonal species.

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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.

Abrams, M.D. and L.C. Hulbert. 1987. Effects of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. American Midland Naturalist 117: 442-445.

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

Anderson, T.W. and L.A. Goodman. 1957. Statistical inference about Markov chains. Annals of Mathematics and Statistics 28: 89-110.

Bartha, S., S.L. Collins, S.M. Glenn, and M. Kertész. 1995. Fine-scale spatial organization of tallgrass prairie vegetation along a topographic gradient. Folia Geobotanica Phytotaxonomica, Praha (In press).

Briggs, J.M. and D.J. Gibson. 1992. Effect of fire on tree spatial patterns in a tallgrass prairie landscape. Bulletin of the Torrey Botanical Club 119: 300-307.

Collins, S.L. and S.M. Glenn. 1991. Importance of spatial and temporal dynamics in species regional abundance and distribution. Ecology 72: 654-664.

Collins, S.L., S.M. Glenn, and D.J.Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: Decoupling cause and effect. Ecology 76: 486-492.

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.

Glenn, S.M. and S.L. Collins. 1990. Patch structure in tallgrass prairies: Dynamics of satellite species. Oikos 57: 229-236.

Glenn-Lewin, D.C. 1980. The individualistic nature of plant community development. Vegetatio 43: 141-146.

Hartnett, D.C. and F.A. Bazazz. 1985. The intergration of neighbourhood effects by clonal genets in *Solidago canadensis*. Journal of Ecology 73: 415-427.

Hartnett, D.C., B.A.D. Hetrick, G.W.T. Wilson, and D.J. Gibson. 1993. Mycorrhizal influence on intra- and interspecific neighbor interactions among co-occurring prairie grasses. Journal of Ecology 81: 787-795.

Hetrick, B.A.D., D.C. Hartnett, G.W.T. Wilson, and D.J. Gibson. 1994. Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie grasses. Canadian Journal of Botany 72:168-176.

Jantz, D.R., R.F. Harner, H.T. Howland, and D.A. Gier. 1975. Soil survey of Riley County and part of Geary County, Kansas. United States Department of Agriculture Soil Conservation Service.

Keeler, K.H. 1990. Distribution of polyploid variation in big bluestem (*Andropogon gerardii*, Poaceae) across the tallgrass prairie region. Genome 33: 95-100.

Knapp, A.K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. Ecology 66: 1309-1320.

Knapp, A.K. 1993. Gas exchange dynamics in C_3 and C_4 grasses: Consequences of differences in stomatal conductance. Ecology 74: 113-123.

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

Marzolf, G.R. 1988. Konza Prairie Research Natural Area of Kansas State University. Transactions of the Kansas Academy of Science 91: 24-29.

Reichman, O.J. 1987. Konza Prairie: A Tallgrass Natural History. University Presses of Kansas, Lawrence. 248 pp.

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, Stroudsberg, PA. 557 pp.

Seastedt, T.R., J.M. Briggs, and D.J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. Oecologia 87: 72-79.

Smith, J.L. and E.L. Rice. 1983. Differences in nitrate reductase activity between species of different stages of old field succession. Oecologia 57: 43-48.

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.

Usher, M.B. 1992. Statistical models of succession. In D.C. Glenn-Lewin, R.K. Peet and T.T. Veblen (eds.) Plant Succession: Theory & Prediction. Chapman & Hall, London, pp 215-248.

Van Cleve, K. and S. Martin. 1991. Long-Term Ecological Research in the United States: A Network of Research Sites · 1991. 6th edition, revised. Long-Term Ecological Research Network Office, University of Washington, Seattle. 178 pp.

Van Hecke, P., T.J. Behaeghe, and I. Impens. 1984. A Markovian approach to the dynamics of fertilized permanent grasslands. Acta Œcologica Œcologia Applicata 5:113-126.

Vinton, M.A., D.C. Hartnett, E.J. Finck, and J.M. Briggs. 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. American Midland Naturalist 129:10-18.

Environmental and Physiological Factors Influencing the Distribution of Oaks Near the Edge of Their Range

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Abstract. Several North American oaks reach the western limit of their distribution in gallery forests dissecting grassland ecosystems. Tree establishment and success in these systems may be limited by frequent drought, fire, grazing, and competitive interactions with grasses. On the Konza Prairie Research Natural Area, two oak species with distinct leaf morphologies and water relations, bur oak (*Quercus macrocarpa*) and chinquapin oak (*Q. muehlenbergii*), dominate different areas of gallery forests. At distributional extremes for other oak species, co-occurring oaks show similar differences in leaf morphology, water relations, and small-scale distribution. In this paper, we review the physiological responses of native Kansas oaks to parameters such as light level and temperature to clarify the ecophysiological mechanisms underlying tree distribution patterns near the edge of their range.

Key words: distribution, gallery forest, light, photosynthesis, *Quercus*, tallgrass prairie, temperature, water relations

Introduction

A wide range of environmental factors can limit species distribution. Examination of the physiological performance of plants at distributional extremes can clarify the mechanisms by which species maintain themselves in such locations, as well as identify common plant responses to selective variables in similar systems (Billings, 1973). Examination at distributional limits can also simplify study, since physiological performance can be matched to a few, easily identifiable factors (Hadley and Smith, 1983; Smith, 1985; DeLucia, 1987; DeLucia and Smith, 1987; Graves and Taylor, 1988; Day et al., 1989; Groom et al., 1991; Williams and Black, 1993). Thus, ecophysiological research has been dominated by work in systems that are considered extreme and dominated by abiotic forces, with clear species gradients. In this paper we explore the ecophysiological basis for tree distribution in the tallgrass prairie, where two eastern deciduous forest oaks near their western limit in distribution (Fowell, 1965). We argue that elucidating species-specific responses of these oaks to light and temperature, both of which interact with water relations, considered the primary determinant of oak distribution in this area (Abrams, 1986, 1990, and 1992), will clarify the physiological mechanisms determining the western limit of eastern North American oak distribution.

Light, temperature and water relations directly and complexly interact at the leaf level (Fig. 1). Leaf temperature is determined by the energy balance of the leaf, which is determined partially by the amount of direct beam solar radiation impinging on the leaf surface, as well as by ambient air temperature. Direct beam radiation contains the wavelengths of light that are of photosynthetic importance (photosynthetic photon flux density, PPFD; wavelength from 400 to 700 nm). Leaf temperature, in turn, strongly affects plant water status, since the amount of water vapor within the leaf that will pass through the stomata and into the atmosphere is highly sensitive to temperature (Campbell, 1977; Nobel, 1983; Jones, 1992). Leaf temperatures may be influenced by altering stomatal opening, which changes the degree of evaporative cooling, or by altering leaf angle and leaf shape, which alters interception of solar radiation and the convective exchange properties of the leaf (Campbell, 1977; Nobel, 1983; Heckathorn and DeLucia, 1991). However, direct beam irradiation and large infrared radiative inputs from surrounding vegetation and the ground can elevate leaf temperature well above air temperature (Nobel, 1983), which may increase water loss. Plants vary in their ability to function at very low tissue water potentials; nonetheless, water limitation almost always decreases plant growth and may alter competitive relationships (Kaiser et al., 1981; Kaiser and Heber, 1981; Kuppers, 1984; Epron and Dreyer, 1990 and 1992; Simoes and Baruch, 1991; Barton, 1993). It is apparent from their interactions that water relations should not be uncoupled from plant physiological responses to the primary variables (light and temperature) that determine water status. Therefore, species that separate along a moisture gradient could have unique responses to the environmental variables driving water status. Comparison of these physiological responses between species could lead to a more mechanistic understanding of species distribution.

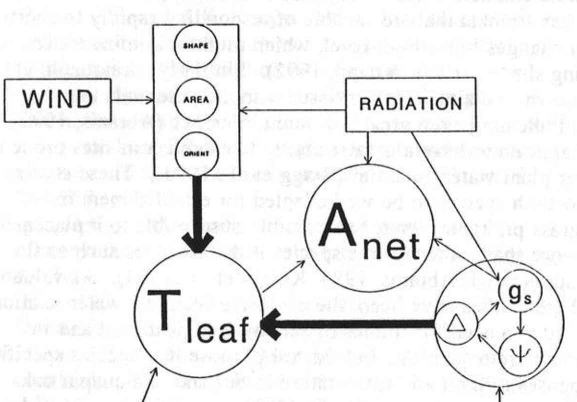

FIG. 1. Interactions of temperature, light, and water relations at the leaf level. Box (A) contains leaf physical characteristics that influence convective exchange properties. Box (B) illustrates leaf characteristics (g_s = stomatal conductance to water vapor, D = concentration gradient of water vapor between leaf and atmosphere, W = leaf water potential) that influence leaf evaporative exchange properties.

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Oaks in the Flint Hills of Kansas

In the Flint Hills of NE Kansas, bur oak (*Quercus macrocarpa*) and chinquapin oak (*Q. muehlenbergii*) dominate gallery forests lining stream courses that dissect the tallgrass prairie. In this region, mean annual rainfall is considered sufficient to allow for eventual forest coverage, but frequent drought and fire, as well as grazing, limit the expansion of tree species into the surrounding grasslands (Weaver, 1954; Axelrod, 1985; Abrams, 1985, 1990). Since European settlement and subsequent fire suppression, forest expansion has increased by nearly 40% (Abrams, 1988 and 1992; Knight et al., 1994). In addition to frequent drought and fire, woody species establishing in tallgrass prairie systems must often endure growing season conditions of extreme temperatures and high photosynthetic photon flux densities (PPFD) (Knapp, 1985), as well as competition for water from surrounding grasses (Bragg et al., 1993). Bur oak is generally more successful in lowland portions of gallery forest drainages, where overall productivity and canopy closure are greater, whereas chinquapin oak tends to establish in more often in open, upland locations (Abrams, 1986; Bragg et al., 1993), often associated with reduced phosphorus availability (Killingbeck, 1984, 1988). These differences in small-scale distribution along a putative moisture gradient are accompanied by distinct differences in leaf morphology, with bur oak having large, deeply lobed leaves, and chinquapin oak having smaller, shallowly scalloped leaf margins (Fowell, 1965). A similar pattern of distribution occurs in other oak species in the Ouichita Mountains of Oklahoma (Dooley and Collins, 1984).

Past research dealing with oak physiological ecology in this area has focussed on aspects of plant response coupled to water relations (Abrams, 1986; Abrams and Knapp, 1986; Knapp, 1992; Bragg et al., 1993). Bur oak is known to adjust tissue osmotic characteristics in response to drought (Abrams, 1990) and has stomata that are capable of responding rapidly to short-term changes in sunlight level, which might minimize water loss during shade periods (Knapp, 1992). Similarly, chinquapin oak is known to maintain lower tissue osmotic potentials than bur oak, indicating even greater drought tolerance (Abrams, 1990), and appears to have a greater ability to establish in sites prone to lower plant water potential (Bragg et al., 1993). These studies show both species to be well adapted for establishment in tallgrass prairie systems, but possibly susceptible to replacement by more shade tolerant tree species if disturbances such as fire are suppressed (Abrams, 1985; Knight et al., 1994). As valuable as these studies have been, the exclusive focus on water relations has led to a need for studies of ecophysiological light and temperature responses. Indeed, we propose that species specific responses to light and temperature in bur and chinquapin oaks could strongly influence the establishment, maintenance, and local distribution patterns of oaks in tallgrass prairie systems.

In our research, we hypothesized that bur oak should be better able to photosynthetically adjust apparent quantum requirement (Q_r; mol O_2 per mol light) in low light, as many tree species do (McMillen and McClendon, 1983; Kozlowski et al., 1991), because distribution patterns indicate that bur oak establishes in areas of higher productivity with greater canopy closure (Abrams, 1986; Bragg et al., 1993). Because all North American tree species use the C_3 photosynthetic pathway, how efficiently a species captures and utilizes light is more important ecologically than differences in photosynthetic pathway (Bjorkman, 1981; Kozlowski et al., 1991). By adjusting Q_r to be more efficient at low PPFD and reaching photosynthetic light saturation at lower light levels, some species can maximize integrated canopy carbon gain (Bjorkman, 1981; McMillen and McClendon, 1983; Kozlowski et al., 1991). We found no differences within or between bur and chinquapin oak in Q_r. We did find that bur oak had greater plasticity in leaf morphology in response to light environment (via changing specific leaf mass, leaf area, and leaf shape) than chinquapin oak, as well as higher overall photosynthetic capacity (Hamerlynck and Knapp, 1994). These morphological responses might maximize whole canopy photosynthesis by keeping inner canopy light levels above the photosynthetic light compensation point (Horn, 1971; McClendon and McMillen, 1982; Kozlowski et al., 1991) or optimize convective heat exchange efficiencies of leaves exposed to full sun (Campbell, 1977). We also expected chinquapin oak, which establishes in drier, more exposed locations, to have a higher maximum photosynthetic temperature tolerance (T_{max}; T_2 in Schreiber and Berry, 1977; Smillie and Nott, 1979) than bur oak. We found that chinquapin oak consistently had higher T_{max} (46° - 50° C) than bur oak (43° - 48° C) throughout the growing season, even in locations where both trees grew together (Hamerlynck and Knapp, 1994). This suggests that physiological temperature tolerance in these oaks is controlled more by genetic than environmental factors (Pearcy et al., 1977; Seemann et al., 1984; Williams et al., 1986). Similar measurements of plant high temperature tolerance have helped explain patterns in phenology and species coexistence in other systems (Monson and Williams, 1982; Monson et al., 1983; Williams et al., 1986). Under field conditions, bur oak tended to have leaf temperatures closer to air temperature, while chinquapin oak, especially smaller individuals, often had leaf temperatures elevated 6° to 10° C above ambient air temperatures (Hamerlynck and Knapp, 1994). These findings indicate that temperature and light do seem to be important direct factors, independent of water relations, in the distribution of oaks in tallgrass prairie gallery forests (Hamerlynck and Knapp, 1994) and might have implications in the distribution of other oak species.

In North America, oak diversity is highest in the southeastern portion of the continent, with the edges of oak distribution represented by only one or two species (Aizen and Patterson, 1990). Recent research in oak ecophysiology has examined differences in nitrogen allocation and whole canopy photosynthesis (Hollinger, 1992; Reich et al., 1991); shade tolerance responses and succession (McClendon and McMillen, 1982; Callaway, 1992); photosynthetic performance and limitations in response to drought (Bahari et al., 1985; Abrams et al., 1990 and 1994; Epron and Dreyer, 1990 and 1993; Ni and Pallardy, 1992; Kubiske and Abrams, 1993; Pallardy and Rhoads, 1993); and the relationship between light environment and photosynthetic and anatomical characteristics in relation to species distribution (Kloeppel et al., 1993; Walters et al., 1993; Ashton and Berlyn, 1994). In all these studies, each oak species differed in leaf morphology, with one oak having large, deeply lobed leaves, and the other having small, shallowly lobed leaves. Therefore, examining leaf traits in other oak systems at other edges of oak distribution, and noting if the suite of traits noted here in the gallery forests of Kansas - leaf morphology correlated to differences in photosynthetic performance, temperature tolerance, and leaf temperatures - may further elucidate the physiological mechanisms controlling the distribution of oaks at the edge of their range.

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Literature Cited

Abrams, M.D. 1985. Fire history of oak gallery forests in a northeast Kansas tallgrass prairie. *American Midland Naturalist* 114: 188-191.

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

Abrams, M.D. 1988. Effects of prescribed fire on woody vegetation in a gallery forest understory in northeastern Kansas. *Transactions of the Kansas Academy of Science* 91: 63-70.

Abrams, M.D. 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiology* 7: 227-238.

Abrams, M.D. 1992. Fire and the development of oak forests. *BioScience* 42: 346-353.

Abrams, M.D. and A.K. Knapp. 1986. Seasonal water relations of three gallery forest hardwood species in northeast Kansas. *Forest Science* 34: 1030-1046.

Abrams, M.D., J.C. Schultz and K.W. Kleiner. 1990. Ecophysiological responses in mesic versus xeric hardwood species to an early-season drought in central Pennsylvania. *Forest Science* 36: 970-981.

Abrams, M.D., M.E. Kubiske and S.A. Mostoller. 1994. Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. *Ecology* 75: 123-133.

Aizen, M.A. and W.A. Patterson III. 1990. Acorn size and geographical range in the North American oaks (*Quercus* L.). *Journal of Biogeography* 17: 327-332.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. *The Botanical Review* 51: 163-201. Ashton, P.M.S. and G.P. Berlyn. 1994. A comparison of leaf physiology and anatomy of *Quercus* (section *Erythrobalanus*-Fagaceae) species in different light environments. *American Journal of Botany* 81: 589-597.

Bahari, Z.A., S.G. Pallardy and W.C. Parker. 1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak-hickory forests in central Missouri. *Forest Science* 31: 557-569.

Barton, A.M. 1993. Factors controlling plant distributions: drought, competition and fire in montane pines in Arizona. *Ecological Monographs* 63: 367-397.

Billings, W.D. 1973. Arctic and alpine vegetations: similarities, differences and susceptibility to disturbance. *BioScience* 23: 697-704.

Bjorkman, O. 1981. Responses to different quantum flux densities. In: Physiological Plant Ecology I: Responses to the Physical Environment, O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler (eds.). Springer-Verlag, Berlin, Heidelberg and New York, pp 57-107.

Bragg, W.K., A.K. Knapp and J.M. Briggs. 1993. Comparative water relations of seedlings and adult *Quercus* species during gallery forest expansion in tallgrass prairie. *Forest Ecology and Management* 56: 29-41.

Callaway, R.M. 1992. Morphological and physiological responses of three California oak species to shade. *International Journal of Plant Sciences* 153: 434-441.

Campbell, G.S. 1977. An Introduction to Environmental Biophysics. Springer-Verlag, Berlin, Heidelberg and New York. 159 pp.

Day, T.A., E.H. DeLucia and W.K. Smith. 1989. Influence of cold soil and snowcover on photosynthesis and leaf conductance in two Rocky Mountain conifers. *Oecologia* 80: 546-552. DeLucia, E.H. 1987. The effect of freezing nights on photosynthesis, stomatal conductance, and internal CO_2 concentrations in seedlings of Engelmann spruce (*Picea engelmannii* Perry). *Plant Cell and Environment* 10: 333-338.

DeLucia, E.H. and W.K. Smith. 1987. Air and soil temperature limitations on photosynthesis in Engelmann spruce during summer. *Canadian Journal of Forest Research* 17: 527-533.

Dooley, K.L. and S.C. Collins. 1984. Ordination and classification of western oak forests in Oklahoma. *American Journal of Botany* 71: 1221-1227.

Epron, D. and E. Dreyer. 1990. Stomatal and non-stomatal limitation of photosynthesis by leaf water deficits in three oak species: a comparison of gas exchange and chlorophyll a fluorescence data. *Annales des Sciences Forestieres* 47: 435-450.

Epron, D. and E. Dreyer. 1992. Effects of severe dehydration on leaf photosynthesis in *Quercus petraea* (Matt.) Liebl.: photosystem II efficiency, photochemical and nonphotochemical fluorescence quenching and electrolyte leakage. *Tree Physiology* 10: 273-284.

Epron, D. and E. Dreyer. 1993. Long-term effects of drought on photosynthesis of adult oak tress [*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.] in a natural stand. *New Phytologist* 125: 381-389.

Fowell, H.A. 1965. Silvics of Forest Tress of the United States. Forest Service Handbook #271, U.S.D.A., Washington, DC, 762 pp.

Graves, J.D. and K. Taylor. 1988. A comparative study of *Geum rivale* L. and *G. urbanum* L. to determine those factors controlling their altitudinal distribution. *New Phytologist* 108: 297-304. Groom, Q.J., N.R. Baker and S.P. Long. 1991. Photoinhibition of holly (*Ilex aquifolium*) in the field during the winter. *Physiologia Plantarum* 83: 585-590.

Hadley, J.L. and W.K. Smith. 1983. Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, U.S.A. *Arctic and Alpine Research* 15: 127-135.

Hamerlynck, E.P. and A.K. Knapp. 1994. Leaf level responses to light and temperature in two co-occurring *Quercus* (Fagaceae) species: implications for tree distribution patterns. *Forest Ecology and Management* in press.

Heckathorn, S.A. and E.H. DeLucia. 1991. Effect of leaf rolling on gas exchange and leaf temperature of *Andropogon gerardii* and *Spartina pectinata*. *Botanical Gazette* 152: 263-268.

Hollinger, D.Y. 1992. Leaf and simulated whole-canopy photosynthesis in two co-occurring tree species. *Ecology* 73: 1-14.

Horn, H.S. 1971. The Adaptive Geometry of Trees. Princeton University Press, Princeton, 144 pp.

Jones, H.G. 1992. Plants and Microclimate, 2nd Edition. Cambridge University Press, Cambridge UK, 428 pp.

Kaiser, W.M. and U. Heber. 1981. Photosynthesis under osmotic stress. Effect of high solute concentrations on the permeability properties of the chloroplast envelope and on activity of stroma enzymes. *Planta* 153: 423-429.

Kaiser, W.M., G. Kaiser, S. Schoner and S. Neimanis. 1981. Photosynthesis under osmotic stress. Differential recovery of photosynthetic activities of stroma enzymes, intact chloroplasts, protoplasts, and leaf slices after exposure to high solute concentrations. *Planta* 153: 430-435.

Killingbeck, K.T. 1984. Nitrogen and phosphorus resorption dynamics of five tree species in a Kansas gallery forest. *American Midland Naturalist* 111: 155-164.

Killingbeck, K.T. 1988. Microhabitat distribution of two *Quercus* (Fagaceae) species in relation to soil differences within a Kansas gallery forest. *Southwest Naturalist* 33: 244-247.

Kloeppel, B.D., M.D. Abrams and M.E. Kubiske. 1993. Seasonal ecophysiology of four successional Pennsylvania barrens species in open versus understory environments. *Canadian Journal of Forest Research* 23: 181-189.

Knapp, A.K. 1985. Early season production and microclimate associated with topography in a C_4 grassland. *Oecologia Plantarum* 6: 337-346.

Knapp, A.K. 1992. Leaf gas exchange in *Quercus macrocarpa* (Fagaceae): rapid stomatal responses to variability in sunlight in a tree growth form. *American Journal of Botany* 79: 599-604.

Knight, C.L., J.M. Briggs and M.D. Nellis. 1994. Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas, U.S.A. *Landscape Ecology* 9: 117-125.

Kozlowski, T.T., P.J. Kramer and S.G. Pallardy. 1991. The Physiological Ecology of Woody Plants. Academic Press, San Diego, New York, London, and Sydney. 657 pp.

Kubiske, M.E. and M.D. Abrams. 1993. Stomatal and nonstomatal limitations of photosynthesis in 19 temperate tree species on contrasting sites during wet and dry years. *Plant Cell and Environment* 16: 1123-1129.

Kuppers, M. 1984. Carbon relations and competition between woody species in a Central European hedgerow. II. Stomatal responses, water use, and hydraulic conductivity in the root/leaf pathway. *Oecologia* 64: 344-354.

McClendon, J.H. and G.G. McMillen. 1982. The control of leaf morphology and the tolerance of shade by woody plants. *Botanical Gazette* 143: 79-83.

McMillen, G.G. and J.H. McClendon. 1983. Dependence of photosynthetic rates on leaf density thickness in deciduous woody plants grown in sun and shade. *Plant Physiology* 72: 674-678.

Monson, R.K. and G.J. Williams III. 1982. A correlation between photosynthetic temperature adaptation and seasonal phenology patterns in the shortgrass prairie. *Oecologia* 54: 58-62.

Monson, R.K., R.O. Littlejohn Jr., G.J. Williams III. 1983. Photosynthetic adaptation to temperature in four species from the Colorado shortgrass steppe: a physiological model for coexistence. *Oecologia* 58: 43-51.

Ni, B. and S.G. Pallardy. 1992. Stomatal and nonstomatal limitations to net photosynthesis in seedlings of woody angiosperms. *Plant Physiology* 99: 1502-1508.

Nobel, P.S. 1983. Biophysical and Plant Physiology and Ecology. W.H. Freeman and Co., San Francisco. 608 pp.

Pallardy, S.G. and J.L. Rhoads. 1993. Morphological adaptations to drought in seedlings of deciduous angiosperms. *Canadian Journal of Forest Research* 23: 1766-1774.

Pearcy, R.W., J.A. Berry and D.C. Fork. 1977. Effects of growth temperature on the thermal stability of the photosynthetic apparatus of *Atriplex lentiformis* (Torr.) Wats. *Plant Physiology* 59: 873-878.

Reich, P.B., M.B. Walters and D.S. Ellsworth. 1991. Leaf age and season influence the relationship between leaf nitrogen, leaf mass per area and photosynthesis in maple and oak tress. *Plant Cell and Environment* 14:251-259.

Schreiber, U. and J.A. Berry. 1977. Heat induced changes of chlorophyll fluorescence in intact leaves correlated with damage of the photosynthetic apparatus. *Planta* 136: 233-238.

Seeman, J.R., J.A. Berry and W.J.S. Downton. 1984. Photosynthetic response and adaptation to high temperature in desert plants. *Plant Physiology* 75: 364-368.

Simoes, M. and Z. Baruch. 1991. Responses to simulated herbivory and water stress in two tropical C_4 grasses. *Oecologia* 88: 173-180.

Smillie, R.M and R. Nott. 1979. Heat injury of alpine, temperate and tropical plants. *Australian Journal of Plant Physiology* 6: 135-141.

Smith, W.K. 1985. Environmental limitations on leaf conductance in central Rocky Mountain conifers. ; Establishment and Tending of Subalpine Forest: Research and Management. Proceedings of the 3rd IUFRO workshop P 1.07-00, H. Turner and W. Tranquillini, eds.

Walters, M.B., E.L. Kruger and P.B. Reich. 1993. Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic considerations. *Oecologia* 96: 219-231.

Weaver, J.E. 1954. North American Prairie. Johnsen Publishing Co., Lincoln NE. 348 pp.

Williams, D.G. and R.A. Black. 1993. Phenotypic variation in contrasting temperature environments: growth and photosynthesis in *Pennisetum setaceum* from different altitudes on Hawaii. *Functional Ecology* 7: 623-633.

Williams III, G.J., R.K. Monson and J.K. Detling. 1986. Growth temperature effects on chlorophyll fluorescence yield in 15 gramminoid species. *American Midland Naturalist* 116: 197-201.

Gas Exchange and Reproduction of *Spiranthes vernalis* (Orchidaceae) in a Kansas Tallgrass Prairie

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Abstract. Spring ladies-tresses (*Spiranthes vernalis*) is a spring emergent, summer flowering, geophyte occurring over much of the eastern half of the United States. In northeastern Kansas, it is a rare and subordinate member of upland and lowland, tallgrass prairie, plant communities. At Konza Prairie Research Natural Area in northeastern Kansas, *S. vernalis* is infrequent and found primarily in annually burned or annually mowed sites. In these locations, it emerges into a high light environment and must adjust to ever-decreasing amounts of incident light as the dominant grass canopy forms and closes. Plants growing in prairie with typical canopy cover had a peak CO_2 uptake rate (net photosynthesis) of 22 ìmol m^{-2} s^{-1} in mid-June. When canopy shading was removed in mid-June as a test of this orchid's response to natural canopy removal by grazing, plants showed a significant reduction in CO_2 uptake (8.5 ìmol m^{-2} s^{-1}) within 1 h of canopy removal, but complete recovery of CO_2 uptake to pretreatment levels within 10 d. In late July through August, plants produced scapes supporting 40 ± 5 flowers, which yielded 6 ± 2 mature fruits.

Key words: orchid, photoinhibition, phenology, tallgrass prairie.

Introduction

Studies of vegetation dynamics and plant responses to stress in tallgrass prairie systems typically have concentrated on the effects of fire and grazing on the growth, physiology, and population dynamics of the dominant grasses and forbs (Collins and Barber, 1985; Knapp and Hulbert, 1986; Gibson and Hulbert, 1987; Knapp et al., 1993). Although this effort is important in understanding large scale processes in tallgrass prairie, subdominants such as *Spiranthes vernalis*, which are infrequent or rare, may make a greater contribution to total prairie biodiversity (Freeman and Hulbert, 1985).

Spiranthes vernalis occurs in a wide range of habitats from Atlantic coastal barrier islands to the western margins of tallgrass prairie (Correll, 1950; Duncan and Duncan, 1987; McCaffrey and Dueser, 1990; Kaul, 1986). In the tallgrass prairie of northeastern Kansas, *S. vernalis* grows on uplands beneath a grass canopy (Freeman and Hulbert, 1985). In this environment, plants may be exposed to full sun during the growing season, if the overstory is removed by grazers such as American bison (*Bison bison*) or domestic cattle. Sudden changes from low to high light may lead to photoinhibition and potential damage to photosynthetic pigments (Krause, 1988). Although photoinhibition of photosynthesis and subsequent recovery responses of plants exposed to high light are well documented, most studies of involve agriculturally important species and are conducted under laboratory conditions (Krause, 1988; Liu et al., 1993; Aro et al., 1994). Conversely recovery from photoinhibition in short-statured geophytes such as *S. vernalis* in response to sudden canopy removal is not well documented. Because *S. vernalis* is one of very few species that remain photosynthetically active over much of the growing season, it may be an ideal species for testing responses of short- statured plants to sudden increases in ambient light levels.

The purpose of this study was to 1) quantify seasonal dynamics of CO_2 uptake and stomatal conductance in *S. vernalis*, 2) quantify responses of *S. vernalis* to sudden exposure to full sunlight at mid-season by the removal of canopy shade, and 3) document reproductive characteristics of *S. vernalis* in the tallgrass prairie ecosystem.

Methods

Research was conducted at the Konza Prairie Research Natural Area (KPRNA) near Manhattan, Kansas (39°08'N, 96°35'W). KPRNA undergoes periodic prescribed spring (April) burning, where watershed-sized units (3 to 220 hectares) are burned at 1- to 20-year intervals. Because *Spiranthes vernalis* is much smaller than neighboring grasses and forbs, it is easily located only when in flower. Therefore, study sites on KPRNA were selected after an intensive search for plants beginning in mid-July and continuing until late August of 1992. Of the total 18 *S. vernalis* found, (1) seven plants were located on a shallowly sloped upland site in an annually burned watershed, (2) five were in a lowland area of an annually fall-mowed fire guard between an unburned watershed and a watershed that is annually burned for 3 consecutive years and then left unburned for 3 consecutive years (denoted as 3U3B), (3) two plants were found in separate annually burned *Spartina pectinata* wetlands, (4) three were located on a hilltop in a 10-year burned watershed, and (5) a single plant was located in an upland community in a biennially burned watershed (Figure 1). Plants in the annually burned watershed were scattered over an area of ca. 50 m^2 and may be progeny from a number of parental sources whereas the plants of the mowed fire guard were in a single 0.5 m^2 clump and may represent progeny from a single parent plant. *Spiranthes* may spend as much as 10 years as belowground, corm-like structures. Therefore, the present distribution of plants may be a function of environmental conditions 10 years ago (Wells, 1981). The small upland clump (n=3) also may represent an isolated dispersal. The total sample size is small, but *S. vernalis* is rare on KPRNA (Freeman and Hulbert, 1985).

To quantify the seasonal course of CO_2 uptake (A) and stomatal conductance (g_{wv}), midday A and g_{wv} were measured using a Li-Cor LI 6200 portable gas exchange system (LICOR, Inc., Lincoln, NE). Measurements were made on two mature leaves located in the middle of the leaf cluster at the base of plants. Values for A and g_{WV} for each plant were means of these two measurements. In early May, leaves were exposed to full sunlight (>1500 ìmol m^{-2}

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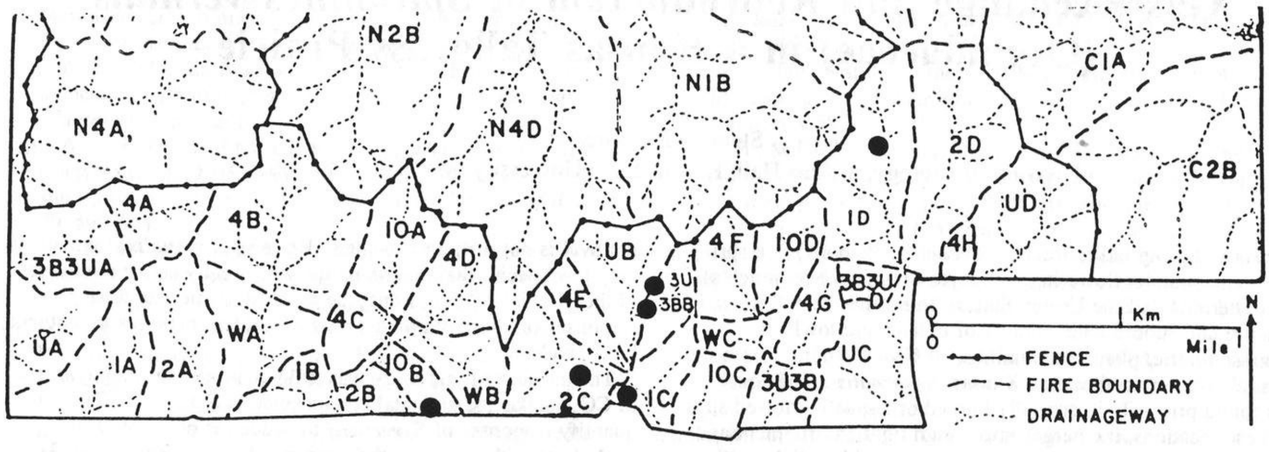

FIG. 1. Map of the southern third of Konza Prairie Research Natural Area indicating the positions (·) of *Spiranthes vernalis* plants or patches described in the text. Two points appear in 3U3BB because one patch of orchids growing in upland is distinct from a single plant growing in a *Spartina pectinata* wetland.

s^{-1}, photosynthetic photon flux density (PPFD) 0.4 - 0.7 ìm), but ambient light on *S. vernalis* had been reduced to less than 50 % of full sunlight by late May to early June and to 25 % of full sunlight by late June (Fig. 2). In both 1992 and 1993, air temperatures were between 34 and 36°C and RH between 30 and 45% during field measurements.

To estimate the response of *S. vernalis* to canopy removal, vegetation within an area of 0.25 m^2 surrounding four plants in the annually burned watershed was clipped to a height of 1 cm in mid and late June. Photosynthetic CO_2 uptake was measured in exposed *S. vernalis* within 1 hour of canopy removal with the Li-Cor 6200. Simultaneous measurements were made on unmanipulated plants in the same annually burned watershed, the two wetlands, and the 10-year unburned upland (n=10). Because inclement weather over northeastern Kansas in the summer of 1993 (with rainfall 25 cm above a 30-year mean; KPRNA weather data, unpubl.), these plants could not be remeasured until 10 days had elapsed following the clipping treatment.

In August and September of 1992 and 1993, I measured heights of mature scapes, flower numbers per scape, initiated fruits, and subsequent mature fruits per scape. Fruits counted as initiated were those that had slightly swollen and remained attached to scapes after flowers had withered. These were visibly different from ovaries, which had fallen away from scapes with withered flowers, and from mature fruits, which were greatly swollen. In order to minimize the effects of elevation and treatment, only the plants of the annually burned watershed were counted. Because sample sizes were small and there were essentially no replicates of any sites where *S. vernalis* grew, this study is best described as mensurative (Hurlbert, 1984) and is meant only as a descriptive study of *S. vernalis* ecology in tallgrass prairie. Where statistical analysis was appropriate, such as with the comparison of plants with canopy removal and without canopy removal, a paired t-test procedure was used at an á=0.05 significance level (Zar, 1984).

Results and Discussion

The seasonal course of net CO_2 uptake (A) (Fig. 2) was typical of an understory geophyte (Yoshie and Yoshida, 1987). The peak A (22.6 ± 1.4 ìmol CO_2 m^{-2} s^{-1} (mean ± 1 se); n=15 plants), which occurred in mid-June, was similar to peak rates of C_3 prairie forbs such as *Baptisia leucophaea* (S. Johnson, unpubl. data). This maximum A was similar to peak A in the tropical, open canopy orchid *Arundinia graminifolia* (15.5 ìmol m^{-2} s^{-1}; S. Johnson, unpubl. data). In addition, this rate is higher than peak rates for understory tropical orchids such as *Paphiopedilum armeniacum* (Johnson, 1992; 1993). Seasonal patterns in stomatal conductance (g_{wv}) closely followed A and ranged from 330 ± 53 mmol m^{-2} s^{-1} in mid-May to 581 ± 38 in late June and to 200 ± 16 mmol m^{-2} s^{-1} in late August.

Following canopy removal in mid-June, A in exposed plants decreased from 22.6 to 8.5 ± 0.8 ìmol CO_2 m^{-2} s^{-1} in 1 h (n=4, Figure 2). Ten days later, A in the exposed orchids had increased to 18.2 ± 1.6 ìmol CO_2 m^{-2} s^{-1}, whereas A in shaded plants was 17.4 ± 2.6 ìmol CO_2 m^{-2} s^{-1} (n=10, Figure 2). Following peak periods of CO_2 uptake, A in plants of both exposed and shaded treatments steadily declined through the rest of the season. The lower CO_2 uptake by exposed plants may have been due to protective mechanisms associated with PSII during photoinhibition (Krause, 1988, Aro et al., 1994, Lovelock et al, 1994). However, other mechanisms such as stomatal closure may have been involved. Stomatal conductance was significantly ($p<0.05$) reduced in exposed plants 1 h after clipping in mid-June (136 ± 25 mmol m^{-2} s^{-1} in exposed plants vs 433 ± 73 mmol m^{-2} s^{-1} in shaded plants, $p<0.001$) indicating stomatal closure in treatment vs. control plants.

Table 1. Numbers of flowers per scape, initiated fruits, and matured fruits of *Spiranthes vernalis* on KPRNA in 1992 and 1993*.

Year	No. of flowers	No. of initiated fruits	No. of matured fruits
1992	43.8 ± 3.3	36.1 ± 5.1	4.4 ± 1.9
1993	34.5 ± 5.2	28.6 ± 6.2	8.7 ± 2.3

* Flower numbers were counted in early August, initiated fruits in late August to early September, and matured fruits in mid-October of both years of the study. Values represent means ± 1 SE (n=7).

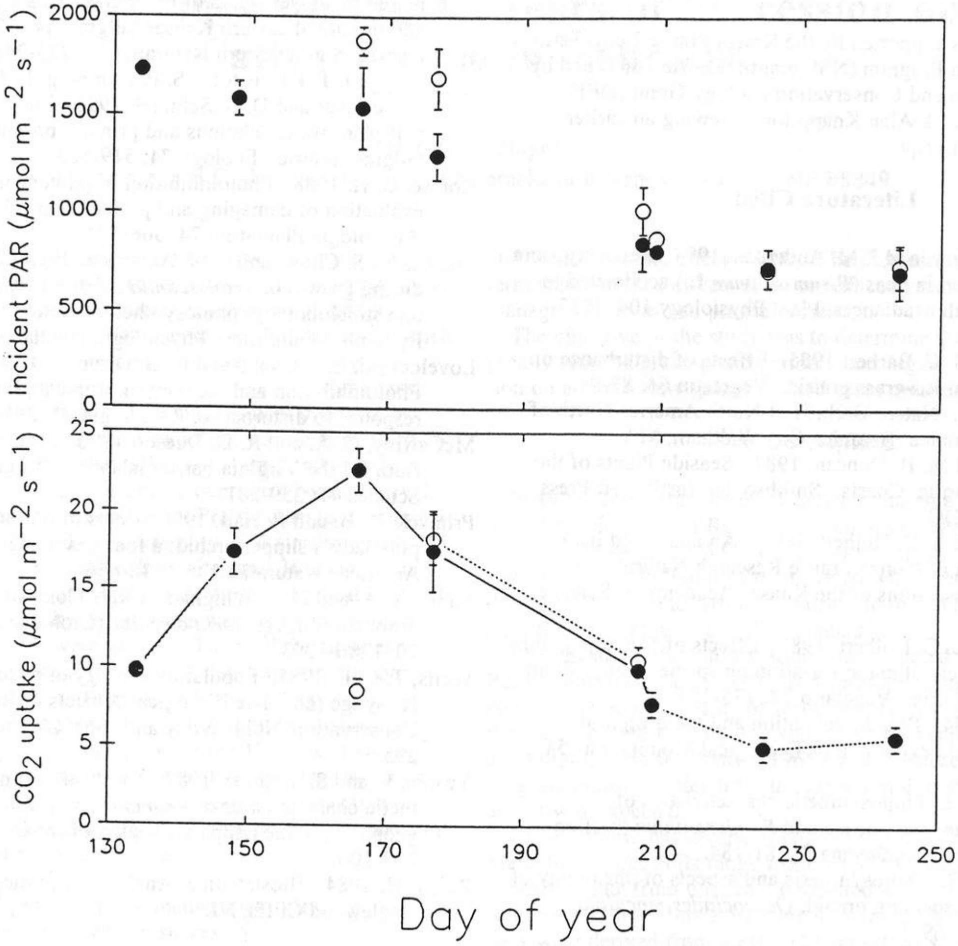

FIG. 2. Incident PAR (top) and CO_2 uptake (ìmol m^{-2} s^{-1}) for *Spiranthes vernalis* that remained shaded (·) or had shading removed on June 15 and 25 (DOY=166 and 176, °) during the 1993 growing season. Each value is the mean of measurements of three separate leaves on 10 shaded plants and on four exposed plants. Vertical bars indicate one standard error of the mean.

Flower production was higher and fruit production lower in 1992 than in 1993, although the differences between years were not significant (Table 1). The ratio of the number of fruits successfully matured to the initial number of flowers was consistent over the 2 years of the study and may be the maximum number that *S. vernalis* can support successfully (Snow and Whigham, 1989; Primack and Hall, 1990). Although flowering was consisent in plants of the annually burned watershed in 1992 and 1993, large variations in flowering occurred between years in plants at the other locations (Table 2).

Although *S. vernalis* occupies a subordinate position in tallgrass prairie, it is ecologically interesting, because it occurs in a wider range of habitats than do the dominant grasses and most other subdominant forbs. The seasonal course of photosynthetic CO_2 uptake of *S. vernalis* was similar to that associated with many forest understory geophytes. The response to simulated grazing of competitors was a reduction in A immediately following exposure to full sun. Depending on the time needed for recovery of A following exposure, such exposure might affect seasonal CO_2 gain. However, the recovery of *S. vernalis* was fairly rapid and not associated with any visible tissue damage or loss. This may indicate that *S. vernalis* in the tallgrass system is adapted to respond to sudden and lengthy transformations from low to high light that may result when the canopy is grazed away by large vertebrates.

Table 2. Comparison of numbers of *Spiranthes vernalis* which generated flowering scapes in 1992 and 1993.

Location	Number of plants which flowered 1992	 1993
Annually burned watershed (n=7)*	7	7
Biennially burned watershed (n=1)	1	0
3U3B fireguard (n=5)	3	5
S. pectinata wetland (n=2)	2	2
10-year burned watershed (n=3)	3	0

* n=number of plants at each location.

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Literature Cited

Aro, E., S. McCaffery, and J. M. Anderson. 1994. Recovery from photoinhibition in peas (*Pisum sativum* L.) acclimated to varying growth irradiances. Plant Physiology 104: 1033-1041.

Collins, S. L. and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64: 87-94.

Correll, D. S. 1950. Native Orchids of North America North of Mexico. Chronica Botanica Co., Waltham, MA.

Duncan, W. H. and M. B. Duncan. 1987. Seaside Plants of the Gulf and Atlantic Coasts. Smithsonian Institution Press, Washington, DC.

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.

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.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Johnson, S. R. 1992. Photosynthetic characteristics of *Paphiopedilum malipoense* and *P. micranthum* (section Parvisepalum). Lindleyana 7: 181-184.

Johnson, S. R. 1993. Photosynthesis and aspects of phenology of the rapidly dispersing orchid, *Oeceoclades maculata*. Lindleyana 8: 69-72.

Kaul, R. 1986. Orchidaceae. *In*. Flora of the Great Plains (Great Plains Flora Assoc.), Univ. Press of Kansas, Lawrence, pp. 1268-1284.

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. Southwestern Naturalist 31: 235-241.

_________., J. T. Fahenstock, S. P. Hamburg, L. B. Statland, T. R. Seastedt and D. S. Schimel. 1993. Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. Ecology 74: 549-560.

Krause, G. H. 1988. Photoinhibition of photosynthesis. An evaluation of damaging and protective mechanisms. Physiologia Plantarum 74: 566-574.

Liu, L., W. S. Chow, and J. M. Anderson. 1993. Light quality during growth of *Tradescantia albiflora* regulates photosystem stoichiometry, photosynthetic function and susceptibility to photoinhibition. Physiologia Plantarum 89: 854-860.

Lovelock, C. E., M. Jebb and C. B. Osmond. 1994. Photoinhibition and recovery in tropical plant species: response to disturbance. Oecologia 97: 297-307.

McCaffrey, C. A. and R. D. Dueser. 1990. Preliminary vascular flora for the Virginia barrier islands. Virginia Journal of Science 41: 259-281.

Primack, R. B. and P. Hall. 1990. Costs of reproduction in the pink lady's slipper orchid: a four year experimental study. American Naturalist 136: 638-656.

Snow, A. A. and D. F. Whigham. 1989. Costs of flower and fruit production in *Tipularia discolor* (Orchidaceae). Ecology 70: 1286-1293.

Wells, T. C. E. 1981. Population ecology of terrestrial orchids. In H. Synge (ed.) The Biological Aspects of Rare Plant Conservation. John Wiley and sons, Chichester, pp 281-295.

Yoshie, F. and S. Yoshida. 1987. Seasonal changes in photosynthetic characteristics of *Anemone raddeana*, a spring-active geophyte, in the temperate region of Japan. Oecologia 72: 202-206.

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ.

Vegetative Changes During 17 Years of Succession on Willa Cather Prairie in Nebraska

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Abstract. Willa Cather Prairie was a moderately grazed, southern Nebraska pasture when purchased by The Nature Conservancy in 1975 and is typical of mixed prairie preserves purchased by conservation organizations. Management of these prairies, which show effects of continuous grazing by cattle, usually involves removing the grazing and introducing burning. Few long-term data exist on the effect of these two management practices in mixed prairie preserves. Quadrat sampling was done in 1975-76 and in 1992 to determine what effect nine burns and greatly reduced grazing had on Cather Prairie over the 17-year interval. All three range sites located on Cather Prairie changed: composition between 1975-76 and 1992 was only 39% similar in silty upland , 48% similar in shallow limy sites and 36% similar in silty overflow. Shallow limy sites were almost identical by 1992, with 92% similarity. Silty upland sites were only 48% similar, and silty overflow sites were 46% similar in 1992. Species composition of the shallow limy site by 1992 appeared to be nearly identical with that of typical tallgrass prairie. Species showing increased abundance were: big bluestem, sedges, and tall dropseed. Species declining during the 17 years of succession were: sideoats grama, blue grama, buffalograss, and annual bromes. Kentucky bluegrass was not affected by burning and resting. Another cool-season exotic, smooth brome, increased in spite of the fire and reduced grazing.

Key words: mixed prairie, prairie management, fire, rest, Kentucky bluegrass, big bluestem, succession

Introduction

Prairie preserves located in the mixed prairie region usually are grazed pastures at the time of preservation by conservation organizations. These prairies show marked effects from the confined and usually continuous grazing by cattle. Under conservation organization ownership, management strategy typically changes to no or very low intensity grazing or haying and usually involves periodic spring burning to reduce cool-season exotics. The conservation organization frequently attempts to burn about half of the area annually, with mixed success, because of weather conditions in spring, attitudes of local fire chiefs, and availability of burning equipment and personnel. (Personal experience working with The Nature Conservancy, The National Audubon Society, Platte River Habitat Maintenance Trust, Prairie/Plains Resources Institute, and others in Nebraska during the past 25 years.)

Most attempts to evaluate change in mixed prairie preserves from the management changes have involved 1 or 2 years of sampling following a spring burn. These reports usually have documented good control of Kentucky bluegrass and other vascular plant exotics (examples from mixed prairie: Nagel 1980, Engle and Bultsma 1984, Schacht and Stubbendieck 1985, and Whisenant and Uresk 1989.) The literature shows no long-term studies of the effects of no or reduced grazing plus fire management in mixed prairie preserves.

The objective of the study was to determine the effect of greatly reduced grazing and periodic burning on species composition on a moderately grazed, mixed grass prairie.

Site Description

In 1975, The Nature Conservancy purchased a 240 ha tract of mixed prairie south of Red Cloud Nebraska. This grazed pasture became known at the Willa Cather Memorial Prairie (hereafter, Cather Prairie), in honor of the novelist who lived in Red Cloud during her youth and wrote of prairie life in Nebraska in novels such as "My Antonia" and "O Pioneers".

Ecological baseline information was collected in 1975-76. Resampling was done in 1992 to determine changes in species composition after 17 years of secondary succession. Cather Prairie is located near the transition line between mixed prairie and tallgrass prairie (Weaver 1965), and so succession towards tallgrass prairie species from the grazed mid to shortgrass prairie aspect was expected.

Cather Prairie has diverse topography and soils (Nicholson and Marcotte 1979). Soils range from deep lowland soils with a high deposition rate from upstream cultivated areas to very shallow soils derived from limestone parent material. Most of the prairie soils were derived from loess. The limestone soils and chalk breaks provided unique associations in Nebraska's flora. The baseline study in 1975-76 found 236 vascular plant species on Cather Prairie. Eight additional species have been added to the list over the 17 years.

Three range sites were found on Cather Prairie (Paden and Ragon 1974). These were: silty (upland, 63% of area), shallow limy (hillsides, 25%) and silty overflow (lowland, 12% of area). Additional information about climate, soils, etc. of Cather Prairie can be found in Nicholson and Marcotte (1979).

Cather Prairie is being managed to restore it to approximately its pre-European settlement condition. The prairie is used for education, research and aesthetic purposes. Management practices have included periodic burning and resting from grazing (during the 17 years, it was lightly grazed for 4 years, 2 of these in early spring to reduce cool season invader species). Parts of the prairie were burned in 9 of the 17 years between 1975 and 1992 (on the average, all of the prairie was burned once every 3 years during the period of 1980 to 1989, when most large burns were conducted.)

Noxious weeds are controlled by digging or hand spraying. Only in one year since 1975 has any broadcast spraying of herbicide been done, that in 1978 for musk thistle (*Carduus nutans*).

Methods

In 1975, 59, and in 1976, 71 square-meter quadrats (N = 130) were sampled from June to August. These quadrats were taken at 19 permanently established sites. Three quadrats were located randomly at each of these sites, at each sampling date. The percentage of total biomass contributed by each species in each quadrat was estimated by three people, and averages were recorded. Plants then were clipped at ground level and separated into forbs, shrubs, and graminoids, air dried and weighed. Percentage contributed toward composition then was determined by multiplying ocular estimates X total biomass for each life form of plant.

In 1992, the percentage of total biomass contributed by each species was estimated by Daubenmire procedures in 24-1/10 m^2 quadrats (Mueller-Dombois and Ellenberg 1974) at the same 19 locations (total N = 450). Estimates were made by two or three people, and averages were used. These samples were taken in June.

Coefficients of similarity (Morisita 1959 quantitative method) were calculated for each range site within a sample (i.e., between sites) and between sampling times (viz. 1975-76 and 1992). "t" tests were performed on each species between the two dates of sampling.

Results and Discussion

Because of the different size of quadrats and number of quadrats taken in the 2 years, direct comparisons about species diversity were difficult. Species composition changes over the 17 years will be the main focus of this paper.

Table 1 gives species composition data on 69 taxa for both dates by range site and total for the prairie. One hundred and two species of plants were found in quadrats in 1975-76 when 130 m^2 of area was sampled. In 1992, although considerably less area of quadrats was sampled (43 m^2), 90 species of plants were found.

Composition changes by range site and probable cause of change

Warm Season Mid-Height to Tall Graminoids.

Big bluestem (*Andropogon gerardii*): This warm-season grass increased more than any species, from 7% in 1976 to 23% in 1992. This increase occurred on all three range sites, but was especially prevalent on the shallow limy sites (Table 1). Big bluestem has been shown to respond favorably to both fire treatment and reduced grazing (Blankespoor 1987; Stubbendieck et al. 1977).

Little bluestem (*Andropogon scoparius*): Little bluestem declined about 5% overall (Table 1). The greatest decline was shown on the silty upland site, where it was probably replaced by big bluestem and smooth brome (*Bromus inermis*).

Sideoats grama (*Bouteloua curtipendula*): Inexplicably, this species almost disappeared, decreasing from 12% in 1976 to 1% in 1992. A significant decline occurred at all range sites (Table 1). Weaver (1965) called sideoats grama an "interstitial" species, making up very little composition in climax prairie, but making up as much as 60% in overgrazed rangelands.

Tall dropseed (*Sporobolus asper*): This midgrass was the third most important grass in 1992 (fourth in 1976). Although the overall percentage stayed about the same, changes were dramatic on individual range sites. It disappeared from the overflow site, was reduced by half on the shallow limy site and doubled on the silty upland site (Table 1).

Warm Season Short grasses

This group declined almost to extirpation on Cather Prairie. Blue grama (*Bouteloua gracilis*) declined from 5% to a trace, and buffalograss (*Buchloe dactyloides*) from 6% to a trace. These two species were especially abundant on the silty upland sites, which were grazed heavily prior to The Nature Conservancy taking ownership.

These short grasses were at a competitive disadvantage to tall and mid-height warm-season grasses as well as smooth brome, which increased on the site.

Cool-Season Graminoids

Cool-season graminoids, in theory at least, are selected against by spring burning, such as that practiced on Cather Prairie during the last 17 years. Most species responded negatively to the new conditions on Cather Prairie (viz. periodic spring burning and reduced and very light grazing pressure).

Western wheatgrass (*Agropyron smithii*): This species was fairly important on silty upland and silty overflow sites in 1976. By 1992, it made up less than 1% at all three sites (Table 1). Whisenant and Uresk (1989) also found it to decrease with fire in mixed prairie, but Gartner et al. (1986) reported that it increased in productivity with spring burning.

Sedges (*Carex* spp.): These did not respond as predicted. They increased moderately at all sites except the silty overflow. They increased especially on the silty upland site.

Annual bromes (*Bromus japonicus* and *B. tectorum*): These two species made up 4.5% in 1976, and were found mostly on sites disturbed by grazing cattle. By 1992, hardly a plant was found, because all the disturbed sites had been revegetated by perennials.

Kentucky bluegrass (*Poa pratensis*): This species, which was widespread throughout the prairie at purchase, was the primary reason for the spring burning management program. In 1976 it was the most important species on the silty upland site (Table 1). Seventeen years of reduced grazing and seven spring burns later, Kentucky bluegrass had the same overall abundance. It declined about 2% on shallow limy and lowland sites, but was exactly the same on the silty upland sites. Previous research (Nagel 1980; Schacht and Stubbendieck 1985) had shown spring burns to reduce this species dramatically in south-central Nebraska. However, those two studies followed the fate of bluegrass for only 2 years, and apparently the burning effect does not last much longer than that. Cather prairie had been burned last in 1989, 3 years before the sampling.

Smooth brome (*Bromus inermis*): This introduced species made up only 2% of the vegetation in 1976, mostly along the east side where it invaded from a highway right-of-way seeding. In the intervening 17 years, it spread throughout the prairie, although it was still most prevalent on the east side. The silty overflow sites were especially invaded by this species, making up 32% of the vegetation there. Blankespoor (1987) found that fire was not an effective control for smooth brome in South Dakota. As with Kentucky bluegrass, smooth brome on Cather Prairie did not produce enough litter to carry a hot fire capable of killing the plants. It tended to form monocultures on Cather Prairie, with virtually no other species in these stands.

Table 1. Percent species composition of vascular plants on Willa Cather Prairie. From quadrat data collected in 1975-76 and 1992 and presented for three range sites. An asterisk following a mean for 1992 indicates that "t"-test analysis showed a significant change from 1975-76 mean, significant at P<.05 (** indicates significance= P<.01).

		ALL SITES		**LOWLAND**		**LIMY UPLAND**		**SILTY UPLAND**	
SPECIES	**COMMON NAME**	**1976**	**1992**	**1976**	**1992**	**1976**	**1992**	**1976**	**1992**
GRAMINOIDS									
Agropyron smithii	Western wheatgrass	5.16	0.65	10.55	0.0	0.62	0.19	5.32	0.97**
Andropogon gerardi	Big bluestem	6.95	22.71	16.67	26.32	12.04	42.88**	2.82	15.08**
A. scoparius	Little bluestem	8.65	3.35	0.6	0.5	9.33	7.68	10.43	2.62*
Bouteloua curtipendula	Sideoats grama	11.54	1.12	10.62	0.07*	16.22	2.55**	10.2	0.9**
B. gracilis	Blue grama	4.54	0.12	0.2	0.0	5.75	0.24**	5.21	0.12**
B. hirsuta	Hairy grama	0.06	0.01	0.0	0.0	0.26	0.0	0.0	0.02
Bromus inermis	Smooth brome	1.94	7.87	9.92	32.48**	1.19	0.0	0.2	4.34**
B. japonicus & tectorum	Japanese brome	4.47	0.03	5.33	0.0	2.71	0.0	4.84	0.04**
Buchloe dactyloides	Buffalo-grass	6.46	0.31	1.42	0.0	3.61	0.0	8.66	0.49**
Carex spp.	Sedges	3.92	5.9	4.96	3.5	1.24	2.33	4.52	7.69*
Elymus virginicus	Virginia wild rye	0.02	0.06	0.0	0.0	0.07	0.0	0.0	0.09
Eragrostis trichodes	Sand lovegrass	0.02	0.0	0.04	0.0	0.05	0.0	0.0	0.0
Hordeum pusillum	Little barley	0.1	0.01	0.0	0.0	0.1	0.0	0.13	0.01
Koeleria pyramidata	Junegrass	0.4	0.33	0.0	0.0	1.11	0.12*	0.27	0.48
Muhlenbergia asperifolia	Scratch grass	0.03	0.0	0.0	0.0	0.14	0.0	0.0	0.0
Panicum oligosanthes	Small panicgrass	2.23	1.85	2.78	0.47	1.52	2.77	2.33	1.88
P. capillare	Witchgrass	0.02	0.0	0.0	0.0	0.07	0.0	0.01	0.0
P. virgatum	Switchgrass	0.27	0.08	0.11	0.0	0.56	0.11	0.21	0.09
P. wilcoxianum	Wilcox panicum	0.07	0.01	0.0	0.0	0.0	0.0	0.11	0.02
Poa pratensis	Kentucky bluegrass	14.16	13.28	12.57	10.09	7.14	4.91	16.9	16.86
Sorghastrum avenaceum	Indiangrass	0.81	1.54	0.0	0.0	0.0	4.87	1.28	0.82
Sporobolus asper	Rough dropseed	7.83	9.91	15.09	0.0	4.31	1.93*	7.19	15.04
S. cryptandrus	Sand dropseed	0.51	0.17	0.14	0.0	0.28	0.0	0.67	0.27
Total Graminoids		**80.2**	**69.3**	**91.0**	**73.4**	**68.3**	**70.6**	**81.3**	**67.8**

Table 1 continued.

		ALL SITES		LOWLAND		LIMY UPLAND		SILTY UPLAND	
SPECIES	COMMON NAME	1976	1992	1976	1992	1976	1992	1976	1992
FORBS AND SHRUBS									
Ambrosia psilostachya	Western ragweed	1.73	3.64	2.35	6.88*	0.86	1.19	1.87	3.64
Amorpha canescens	Lead plant	0.02	0.13	0.0	0.0	0.09	0.51	0.0	0.04
Antennaria neglecta	Field pussytoes	0.11	0.17	0.0	0.0	0.1	0.73	0.14	0.02
Artemisia ludoviciana	White sage	1.12	2.7	1.24	5.03*	1.32	0.29	1.03	2.92
Asclepias spp.	Milkweed	0.07	0.16	0.02	0.08	0.0	0.41	0.12	0.05
Aster ericoides	White aster	0.44	1.8	0.07	0.83*	1.64	0.54	0.13	1.67*
A. oblongifolius	Aromatic aster	0.06	0.08	0.0	0.0	0.18	0.4	0.03	0.0
Astragalus spp.	Milk vetch	0.08	0.02	0.0	0.0	0.39	0.07	0.0	0.0
Callirhoe involucrata	Purple poppy mallow	0.08	0.61	0.22	2.61*	0.18	0.38	0.01	0.19
Cirsium spp.	Thistle	0.03	0.09	0.0	0.0	0.0	0.15	0.05	0.07
Echinacea angustifolia	Purple coneflower	0.11	0.04	0.0	0.0	0.54	0.17	0.0	0.0
Erigeron strigosus	Daisy fleabane	0.09	0.04	0.03	0.0	0.34	0.06	0.02	0.04
Euphorbia spp.	Euphorbia	0.08	0.3	0.0	0.53	0.01	0.66	0.03	0.11
Kuhnia eupatoriodes	False boneset	0.1	0.2	0.0	0.0	0.21	0.03	0.09	0.3
Lactuca serriola	Prickly lettuce	0.07	0.13	0.01	0.36	0.0	0.18	0.11	0.05
Liatris punctata	Blazing star	1.03	0.84	0.0	0.0	2.43	0.56	0.82	1.14
Lotus purshianus	Prairie trefoil	0.05	0.65	0.02	0.35	0.0	0.13	0.07	0.9
Lygodesmia juncea	Skeletonweed	0.13	0.03	0.0	0.0	0.0	0.06	0.2	0.04
Medicago lupulina	Black medick	0.3	0.94	1.74	0.32	0.1	1.39	0.01	0.95
Calylophus serrulatus	Yellow evening primrose	0.1	0.0	0.0	0.0	0.02	0.0	0.14	0.0
Onosmodium molle occidentale	False gromwell	0.13	0.0	0.05	0.0	0.6	0.0	0.0	0.0
Oxalis stricta	Yellow wood sorrel	0.02	0.16	0.02	0.0	0.6	0.0	0.02	0.21
Oxytropis lambertii	Purple locoweed	0.18	0.02	0.09	0.19	0.79	0.11	0.0	0.0
Petalostemon spp.	Prairie clover	0.32	0.11	0.0	0.0	0.0	0.54	0.0	0.0
Physalis spp.	Ground cherry	0.01	0.43	0.08	0.26	0.0	0.53	0.0	0.43
Plantago spp.	Plantain	0.02	0.3	0.02	0.0	0.03	0.5	0.02	0.31
Polygala alba	White milkwort	0.02	0.02	0.01	0.0	0.07	0.07	0.0	0.0
Psoralea spp.	Scurf-pea	4.93	5.58	0.0	0.0	2.60	6.99*	6.86	6.52

Table 1 continued.

		ALL SITES		**LOWLAND**		**LIMY UPLAND**		**SILTY UPLAND**	
SPECIES	**COMMON NAME**	**1976**	**1992**	**1976**	**1992**	**1976**	**1992**	**1976**	**1992**
Ratibida columnifera	Prairie coneflower	0.16	0.04	0.0	0.0	0.08	0.06	0.23	0.04
Rosa arkansana	Prairie wild rose	0.0	0.29	0.0	0.0	0.0	0.0	0.0	0.46
Solidago canadensis	Canada goldenrod	0.0	0.36	0.0	0.06	0.0	0.0	0.0	0.55
S. missouriensis	Prairie goldenrod	1.82	0.72	0.41	0.0	3.64	2.1	1.58	0.44
S. mollis	Soft goldenrod	1.94	2.49	0.0	0.05	6.36	3.45	0.96	2.77
S. rigida	Rigid goldenrod	1.06	0.28	0.0	0.08	4.62	1.19	0.14	0.03
Spharalcea coccinea	Red false mallow	0.02	0.16	0.02	0.0	0.0	0.0	0.02	0.25
Symphoricarpos occidentalis	Western snowberry	0.27	3.42	0.0	1.41	0.01	0.0	0.43	5.06
Taraxacum officinale	Dandelion	0.04	0.0	0.15	0.0	0.0	0.0	0.03	0.0
Teucrium candense	American germander	0.0	0.84	0.0	5.19	0.0	0.0	0.0	0.0
Thelesperma megapotamicum	Greenthread	0.08	0.03	0.0	0.0	0.36	0.14	0.0	0.0
Toxicodendron radicans	Poison ivy	0.0	0.36	0.0	0.0	0.0	0.21	0.0	0.5
Tragopogon dubius	Goatsbeard	0.86	0.05	0.22	0.0	0.18	0.0	1.24	0.08
Verbascum thapsus	Common mullein	0.06	0.0	0.38	0.0	0.0	0.0	0.0	0.0
Verbena stricta	Hoary vervain	0.27	0.51	0.83	0.0	0.37	1.07	0.1	0.46
Vernonia baldwini	Western ironweed	0.22	0.33	0.35	0.65	0.1	0.66	0.23	0.14
Vicia americana	American vetch	0.05	0.0	0.0	0.0	0.0	0.0	0.08	0.0
Viola pratincola	Meadow violet	0.0	0.04	0.0	0.0	0.0	0.0	0.0	0.06
Total Forbs & Shrubs		**18.3**	**29.1**	**8.3**	**24.9**	**26.2**	**25.5**	**16.8**	**30.4**

Forbs and shrubs

A few new species of forbs appeared over the 17 years of succession. Most important of these new arrivals were Canada goldenrod and American germander (*Teucrium canadensis*,Table 1), both found mostly in lowlands.

Little change was found in the forb/shrub component except for overall abundance. Species increasing substantially were: western ragweed (*Ambrosia psilostachya*), field pusseytoes (*Antennaria neglecta*), white sage (*Artemisia ludoviciana*), white aster (*Aster ericoides*), and western snowberry (*Symphoricarpos occidentalis*) Forbs/shrubs showing substantial declines were Missouri goldenrod (*Solidago missouriensis*), rigid goldenrod (*S. rigida*), and goatsbeard (*Tragopogon dubius* Scop.)

Most species of forbs and shrubs either contributed little to composition or stayed about the same over the 17-year period. Scurf peas (mostly few-flowered, *Psoralea tenuiflora*) made up about 5% in both samples. Goldenrods made up about 4% in both samples.

Community Comparisons

The percentage of graminoids declined about 10%, from 80% in 1976 to 69% in 1992 (Table 1). Forbs and shrubs increased by 11%, from 18% in 1976 to 29% in 1992.

The percent similarity among all samples taken in 1976 compared with 1992 was 48% The silty upland sites were 50% similar in 1975-76 and 48% similar in 1992. A comparison of 1975-76 with 1992 composition on the silty upland site showed that the coefficient of similarity was only 39%, indicating great change during the 17 years of succession. The lowland sites (silty overflow), not surprisingly, with the invasion by smooth brome showed the greatest change and had only 36% similarity between sample dates. Shallow limy sites (hillsides) were in the best condition in 1976 and had 67% similarity among sample sites on that range site. Variability among these sites was lost by 1992, when they were 92% similar. Considerable succession took place between sampling dates, with similarity being only 48%. This change was primarily due to the increase in big bluestem. These shallow limy sites on Cather Prairie appear to have nearly identical species composition with that of tallgrass prairie (e.g., compare with similar sites on Konza Prairie, Gibson 1989).

Conclusions

Removing grazing from a mixed grass prairie in 13 of 17 years and burning all of the prairie at least twice during this period caused dramatic changes in some species, yet left other species unaffected. Overall, the species composition changed by 52% during the period. Variability among samples on the same range site remained large except on the limy upland site, where composition was almost identical from location to location. Forbs and shrubs increased by 11% overall, whereas graminoids decreased by the same amount.

Big bluestem benefited the most, whereas side-oats grama and short grasses were reduced the most. Kentucky bluegrass was unchanged, and smooth brome increased during the 17-year period. These two species are extremely persistent in mixed grass prairies.

After 17 years of succession with light grazing and periodic burning, the hillsides appeared to have species composition almost identical to that of tallgrass prairie. The uplands and lowlands, which had been more severely overgrazed at time of purchase, had a much larger composition of exotic species after 17 years of succession. On these two sites, classical succession, such as predicted by Weaver and Clements (1938), was not clearly evident.

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Literature Cited

Blankespoor, G.W. 1987. The effects of prescribed burning on a tallgrass prairie remnant in eastern South Dakota. Prairie Naturalist 19: 177-188.

Engle, D.M., and P.M. Bultsma. 1984. Burning of northern mixed prairie during droughts. Journal of Range Management 37: 398-401.

Gartner, F.R., J.R. Lindsey and E.M. White. 1986. Vegetation responses to spring burning in western South Dakota. Proceedings of the Ninth North American Prairie Conference. Gary Clambey and Richard

Pemble Editors. Tri-College Center of Environmental Studies. Moorhead Minnesota. pp. 143-146.

Gibson, D.J. 1989. Hulbert's study of factors effecting botanical composition of tallgrass prairie. Proceedings of the Eleventh North American Prairie Conference. James Stubbendieck Editor. University of Nebraska. Lincoln Nebraska. pp. 115-133.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Memoirs Faculty Science Kyushu University, Series E (Biology) 3:65-80.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. Wiley & Sons, New York.

Nagel, H.G. 1980. Effect of spring burning date on mixed-prairie soil moisture, productivity and plant species composition. Proceedings of the Seventh North American Prairie Conference. Clair Kucera Editor. Southwestern Missouri State University. Springfield Missouri. pp. 259-263.

Nicholson, R. A. and M.G. Marcotte. 1979. Vegetation of the Willa Cather Memorial Prairie. Journal of Range Management 32: 104-107.

Paden, H.E. and L.G. Ragon. 1974. Soil survey of Webster County, Nebraska. USDA, SCS, Univ. Nebraska Conservation & Survey Division. 72 pp. GPO.

Schacht, W. and J. Stubbendieck. 1985. Prescribed burning in the loess hills mixed prairie of southern Nebraska. Journal Range Management 38: 47-51.

Stubbendieck, J., J.T. Nichols, and K.K. Roberts. 1977. Nebraska range and pasture grasses. Nebraska Cooperative Extension Service, Extension Circular 85-170. 75 pp.

Weaver, J.E. 1965. Native vegetation of Nebraska. Univ. Nebraska Press. Lincoln Nebraska. 185 pp.

_______ and F.E. Clements. 1938. Plant Ecology. McGraw-Hill Book Co., New York.

Whisenant, S., and D.W. Uresk. 1989. Burning upland, mixed prairie in Badlands National Park. Prairie Naturalist 21: 221-227.

Sources of Variation in Leaf Moisture Content of Eastern Red Cedar

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Abstract. Leaf moisture content (LMC) may be useful in scheduling fires to optimize control of eastern red cedar (*Juniperus virginiana*). Mortality of larger trees under low fuel loads is uncommon and usually results from crown ignition. Low moisture content may enhance crown ignition. The study's objective was to detect LMC differences over time among height classes and among individual trees. The LMC of eastern red cedars in four height classes was sampled monthly for 12 months at two sites. Blight-infected trees at Site 1 reached their lowest LMC in April or May, then LMC increased until July. At Site 2, LMC rose gradually from February to April, then increased more rapidly. Trees at Site 1 were consistently drier. Only two of 40 trees were found to be considerably drier than their cohorts at critical times. The results suggest that late April to early May fires are best for control of larger trees. Site 1 results suggest that populations with severe foliage disease are especially good candidates for burning.

Key words. eastern red cedar, *Juniperus virginiana*, leaf moisture content, prescribed burning, repeated measures, brush control

Introduction

Prescribed fire is an effective means to control small eastern red cedars (*Juniperus virginiana*). However, mortality decreases with increasing tree height (Buehring et al. 1971, Owensby et al. 1973), especially for fires with low fine-fuel loads. Although lower foliage of larger trees may be scorched, the upper foliage often escapes damage (Engle and Stritzke 1992). Under low fine-fuel loads, larger trees usually succumb only on the rare occasions when the foliage ignites.

Highly variable foliage ignition is common during prescribed fires for eastern red cedar control. Larger trees occasionally are ignited, whereas most nearby, seemingly similar trees are unaffected. Fuel moisture content is an important factor in ignition time (Wright and Bailey 1982). Further, leaf moisture content (LMC) has been correlated highly with ignition time of redberry juniper (*J. pinchotii*) (Bunting et al. 1983). In Oklahoma, the herbicide paraquat has been used desiccate eastern red cedar before broadcast fire (Engle and Claypool 1988). This has been shown to increase fire mortality of trees <2.5-m tall and partially compensate for low fine-fuel loads. Thus, scheduling fires during periods of low LMC may enhance control of larger eastern red cedar trees.

The LMC of eastern red cedar follows a seasonal pattern corresponding to precipitation and soil moisture content (Engle et al. 1987), which are highest during the late spring and early summer under a continental climate. Given the observed variability of eastern red cedar ignition, smaller LMC differences could exist both among and within trees within the pattern of seasonal variation. This study's objective was to examine the effects of tree size, individual trees, and aspect, or side of tree, on LMC. Aspect was included because insolation levels, particularly during winter, might influence LMC.

Methods and Materials

Site Descriptions

The experiment was conducted from February 1993 to January 1994 on two sites in western Lancaster County, Nebraska. Site 1 (N 40°, 50' 53.7"; W 96°, 51' 40.2") was located on an eroded Sharpsburg silty clay loam soil, a fine, montmorillonic, mesic, Typic Argiudoll formed in loess. It had 5 to 7% east-facing slopes and was a silty range site. The soil's surface permeability was 15.2 to 50.8 mm/h (Soil Survey Staff 1980). The site, a wildlife management area seeded in the mid-1960s and never burned or grazed by wildlife (J.D. Hoffman, Nebraska Game and Parks Commission, pers. comm.), was dominated by little bluestem (*Schizachyrium scoparium*), indian grass (*Sorghastrum nutans*) and goldenrods (*Solidago* spp).

Site 2 (N 40°, 45' 19.6"; W 96°, 49' 31.4") had a Burchard clay loam soil, a fine-loamy, mixed, mesic, Typic Argiudoll formed in calcareous Kansan glacial till. It had 6 to 11% east-facing slopes and was a silty range site. The soil's surface permeability was 5.1 to 15.2 mm/h. The site was in heavily grazed, low-condition native range dominated by smooth bromegrass (*Bromus inermis* subsp. *inermis*), Kentucky bluegrass (*Poa pratensis*), and annual bromes (*Bromus* spp.), with remnants of native tallgrass prairie species.

Both sites had volunteer infestations of eastern red cedar. Some gross morphological differences were apparent between tree populations at the two sites. Most notably, Site 1 trees had sparser, more open branching and foliage and an overall redder color than Site 2 trees. In addition, many dead twig tips were apparent on the trees at Site 1 but not at Site 2 in January 1993. The condition was diagnosed as Kabatina tip blight (D.A. Merrell, Department of Plant Pathology, University of Nebraska-Lincoln, pers. comm.), which is caused by the fungus *Kabatina juniperi* (Coziahr and Wysong 1987).

Infected foliage was not excluded from the samples. Although all of the trees at both sites eventually showed some symptoms of the disease, those at Site 1 were infected much more severely.

Sampling and Laboratory Procedures

Samples of about 5 to 10 g were clipped into plastic bags, sealed, and chilled until wet-weight determination. Samples were clipped from nonwoody twigs only. In practice, this meant that samples from smaller trees were taken only from the outer twig tips, whereas samples from larger trees included material from lateral twig tips from the crown interiors.

After weighing, the bags were slit open, and the foliage was allowed to air dry at room temperature for about 2 weeks. The air-dried samples were desiccated further with calcium chloride in closed containers at room temperature to a constant weight (Budavari 1989). This minimized the loss of volatile oils, which otherwise could have been confused with moisture loss. Moisture content was determined by the wet-weight method, using the formula: (wet weight - dry weight/wet weight) x 100 = % moisture.

Precipitation records for the study were obtained from the Lincoln Municipal Airport National Weather Service Station 8.4 km from Site 1 and 12.4 km from Site 2. Precipitation for May-August 1993 was 93% above the 30-year average, although precipitation during the rest of the study period was near or below average (Fig. 1).

Statistics

The experiment was a completely random design with a split-plot treatment structure (Steel and Torrie 1980). Height class of trees was the whole-plot factor (<1 m, 1-2 m, 2-3 m and >3 m). Aspect was the subplot factor (north, east, south, and west sides of the trees). Five trees were selected randomly per height class per site. In addition, the study was repeated over time, with each tree sampled at about mid-month for 12 months. The data were analyzed as a repeated measures split-plot design (SAS 1990).

After preliminary analysis sites were analyzed separately because of their different blight-infection levels and resulting behavior. The aspect term was discarded, because aspect differences in LMC were only about 1 percentage point around monthly means of 45 to 70% The second analysis produced significant time x height interactions for each site. Monthly height-class means for time periods with significant differences were separated using Fisher's least-significant-difference tests.

Control charts were drawn for site x height classes containing individual trees with extreme LMC levels. The monthly standard deviations were used to calculate three-sigma limits about the overall site x height class means, an approach most often used in industrial quality control (Wheeler and Chambers 1992). Because the three-sigma limits embraced about 99% of the observations, the method provided a quick visual gauge of an individual's departure from the mean. When extreme individuals were noted, LMC among individual trees was tested further with an analysis of covariance performed with Proc GLM after adjusting for time as a linear, quadratic, or cubic effect as necessary (SAS 1990).

Results

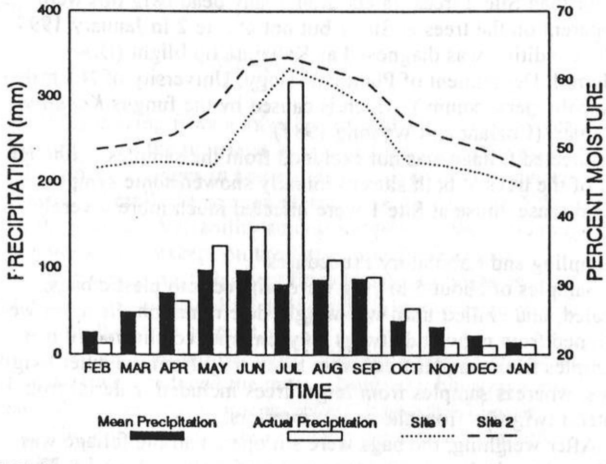

FIG. 1. Average leaf moisture content (%) by site of eastern red cedar and recorded and 30-year-average precipitation during the study period (mm).

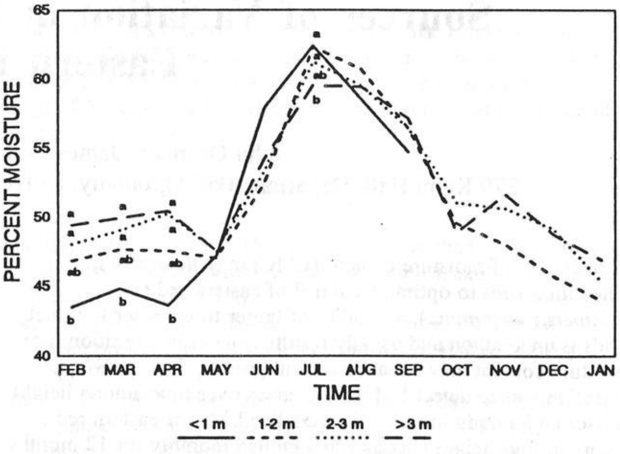

FIG. 2. Site 1 leaf moisture content means (%) of eastern red cedar by tree-height class (m) with letters for months with significant differences (P<0.05). Means within dates with the same letters are not significantly different.

The general seasonal LMC trends of the two sites were similar (Fig. 1), but not parallel. Although the difference between LMC at the two sites was not constant, that at Site 1 was always lower. At Site 1, LMC for the class of trees <1 m tall increased after the April sampling (Fig. 2), whereas LMC for the three taller classes there declined between the April and May samplings and then increased. At Site 2, LMC for the class 2-3 m tall increased after the May sampling (Fig. 3), whereas the other classes rose after the April sampling. Six of eight site x height classes reached peak LMC at the July sampling.

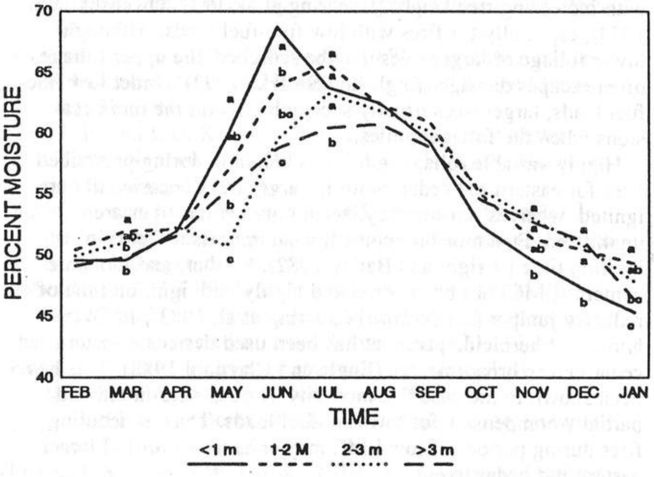

FIG. 3. Site 2 leaf moisture content means (%) of eastern red cedar by tree-height class (m) with letters for months with significant differences (P<0.05). Means within dates with the same letters are not significantly different.

For Site 1 (Fig. 2), significant differences ($P<0.05$) in LMC among height classes were detected in February, March, April, and July 1993. For Site 2 (Fig. 3), significant differences ($P<0.05$) among height classes were detected in March, May, June, July, November and December 1993, and January 1994. Site 1 trees <1 m tall in the fall were dropped from the study after the September 1993 sampling because of a lack of remaining foliage on nonwoody twigs.

The control charts and analysis of covariance revealed that only two of 40 trees had LMC consistently lower than that of their classmates. Both trees were especially heavily diseased individuals at the heavily diseased Site 1. In the first case (Fig. 4), on the control chart for trees <1 m tall, tree #2 was outside the control limits in February and April. In the second case (Fig. 5), on the control chart for trees 1-2 m tall, tree #3 was outside the control limits in April, December, and January.

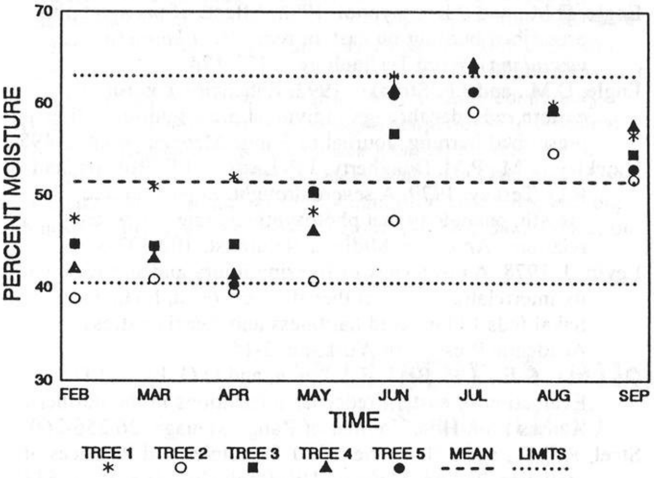

FIG. 4. Control chart showing individual tree leaf moisture content (%) of eastern red cedar by month for Site 1 trees <1 m tall, class mean averaged over time and three-sigma limits around the mean.

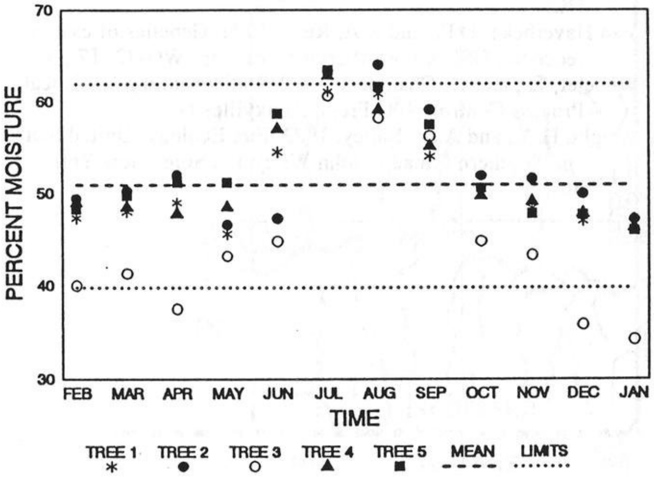

FIG. 5. Control chart showing individual tree leaf moisture content (%) of eastern red cedar by month for Site 1 trees 1-2 m tall, class mean averaged over time and three-sigma limits around the mean.

Discussion and Conclusions

The yearly pattern of LMC of eastern red cedar at both sites was similar to that in Oklahoma (Engle et al. 1987). Leaf moisture content rose during the growing season and was much lower during the cooler months. However, in the Oklahoma study, which didn't compare height classes, LMC was found to peak in June and decline during July and August. In our study, LMC peaked in July for all Site 1 height classes (Fig. 2). At Site 2, the class <1 m tall peaked in June, the class >3 m tall in August and the other two classes in July (Fig. 3). Generally later dates for peak LMC may result from Nebraska's higher latitude and later onset of the growing season. In the current study, LMC remained relatively high until September, when more rapid decreases were noted.

The Kabatina tip blight infection probably accounts for the consistently lower LMC levels at Site 1, because of the quantity of dead foliage sampled there (Fig. 1). The finding that the three taller classes of trees at Site 1 did not begin to increase LMC until after the May sampling (Fig. 2) also may be due to the blight, because diseased tissue continued to dry out until the effect was masked by new growth.

Consideration of LMC differences among height classes is more complex. Factors of tree architecture, sampling procedures, leaf type, and root depth likely interacted with the disease to influence LMC.

Tree architecture and sampling procedures are important because both new growth and diseased tissue are concentrated at the twig tips on the crown surface. Trees <1 m tall were sampled on the surface only, because they essentially had no interior, which probably produced exaggerated LMC levels. In the case of larger trees, samples included more mature and healthy foliage from lateral twig tips in the crown interiors. This likely reduced peak LMC levels and moderated LMC fluctuations through time.

Differences in leaf type also may have contributed to LMC differences among tree height classes. Eastern red cedars have three types of leaves (Van Haverbeke and Read 1976), including a "long-shoot whip" characteristic of rapid growth. However, most leaves on mature trees are scale-like and closely appress the stem. Trees up to about 5 years old, which would include most <1 m trees, have larger needle-like leaves. However, these can be present in declining numbers on larger trees. Needle-like leaves are more succulent than the scale type and have a higher LMC, at least until foliage hardens in the fall (Levitt 1978).

Finally, root depth may have contributed to LMC differences among tree height classes. Mature eastern red cedars growing in deep soils generally are deeply rooted, whereas smaller trees have roots nearer the surface (Bannan 1942, Hinckley et al. 1979). Thus, smaller trees may be more sensitive to dry or wet periods.

Interactions of these factors could explain the finding that LMC peaks generally were inversely proportional to height class. Larger trees would have had proportionally fewer succulent needle-like leaves and less new foliage in the samples, but their deeper root systems buffered them against the effects of high or low precipitation.

Considering month-to-month differences, trees <1 m tall at Site 1 were drier ($P<0.05$) than the two tallest classes during February-April (Fig. 2). Again, the high proportion of dead foliage in samples from these trees, possibly interacting with below-average precipitation affecting these shallow-rooted trees, could account for this ranking. In July, leaves from the Site 1 class of trees >3 m tall were driest ($P<0.05$) . This class would have had the lowest proportion of both new growth and needle-like leaves in the samples at that time.

At Site 2 (Fig. 3), the height classes <1 m and >3 m tall were significantly drier ($P<0.05$) than the class 1-2 m tall in March. However, these differences were only about 2 percentage points and may not be important in the context of foliage ignition. Larger differences were detected in the period May-July, with levels again generally being inversely proportional to height. The height class <1 m tall was drier ($P<0.05$) than the two tallest classes during November-January, and the class >3 m tall was drier ($P<0.05$) than the class 1-2 m tall by January. Precipitation was below average during this period, which may have affected the shallow-rooted <1 m class most. The low LMC in January of trees >3 tall may have been due to the higher proportion of mature foliage and scale-type leaves in the samples, the effect of which would be more pronounced after new foliage had hardened.

The analysis of individual trees' LMC showed that only two of 40 trees were significantly drier than their cohorts. This analysis, coupled with the results from Sites 1 and 2, suggest that foliage disease can substantially reduce LMC of eastern red cedar. This appears to be so both for populations with different levels of infection and for individuals within infected populations. These differences probably are large enough to reduce ignition time and may partially account for the relatively rare event of large tree ignition (Bunting et al. 1983).

Management Implications

Our results reinforce the existing practice of conducting prescribed fires for eastern red cedar control in late April to early May in Nebraska because at least three factors are optimized. First, the warm, dry conditions conducive to higher-intensity fires are more likely to occur then than earlier. Second, fires then are most likely to suppress undesirable introduced cool-season grasses than at earlier dates, whereas a later date risks damaging desirable warm-season grasses (Wright and Bailey 1982). Finally, the results, particularly from Site 2, showed that delaying burning beyond early May will allow LMC to rise to levels that may discourage foliage ignition.

Management objectives and the factors of weather, herbaceous plant response, tree-size distribution and LMC should be weighed for each management unit to be burned. For areas with many large trees, if cool-season grasses are not a major problem and good burning conditions are predicted, a late April fire would capitalize on the period of low LMC for eastern red cedar. If cool-season grasses are a problem, burning at a later date will enhance their suppression even though control of larger trees may suffer.

The general dryness and delayed LMC increase of larger trees at Site 1 suggest that tree populations with foliage disease are especially good candidates for control by prescribed burning. The Site 1 trees more than 1 m tall reached their spring LMC low point in mid-May, averaging 47.3% LMC compared to 54.3% for corresponding trees from Site 2. Such populations could be made a priority for prescribed burning, if the number of management units in need of treatment is too great to be burned in a given spring. Or they could be scheduled for burning later in the spring, while healthy populations are burned earlier.

Literature Cited

Bannan, M.W. 1942. Wood structure of the native Ontario species of *Juniperus*. American Journal of Botany. 29:245-252.

Budavari, S., (ed.). 1989. Calcium chloride. *In* The Merck Index, 11th ed. Merck, Rahway, NJ, p. 252.

Buehring, N., P.W. Santelmann, and H.M. Elwell. 1971. Responses of eastern red cedar to control procedures. Journal of Range Manage. 24:378-382.

Bunting, S.C., H.A. Wright, and W.H. Wallace. 1983. Seasonal variation in the ignition time of redberry juniper in west Texas. Journal of Range Manage. 36:169-171.

Coziahr, L.V., and D.S. Wysong. 1987. Juniper Blight Diseases, NebGuide G87-858. Univ. of Nebraska.

Engle, D.M. J.F. Stritzke, and P.L. Claypool. 1987. Herbage standing crop around eastern redcedar trees. Journal of Range Manage. 40:237-239.

Engle, D.M., and P.L. Claypool. 1998. Effects of paraquat plus prescribed burning on eastern redcedar ((*Juniperus virginiana*). Weed Technology. 2:172-174.

Engle, D.M., and J.F. Stritzke. 1992. Enhancing control of eastern redcedar through individual plant ignition following prescribed burning. Journal of Range Manage. 45:493-495.

Hinckley, T.M., P.M. Dougherty, J.P. Lassoie, J.E. Roberts, and R.O. Teskey. 1979. A severe drought: impact on tree growth, phenology, net photosynthetic rate and water relations. American Midland Naturalist. 102:307-316.

Levitt, J. 1978. An overview of freezing injury and survival, and its interrelationships toother stresses. *In* Li, P.H., and A. Sakai (eds.) Plant cold hardiness and freezing stress. Academic Press, New York, pp. 3-15.

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 Manage. 26:256-260.

Steel, R.G.D., and J.H. Torrie. 1980. Principles and Practices of Statistics. 2nd ed. McGraw-Hill Book Co., New York. 633 pp.

SAS Institute Inc. 1990. SAS/STAT User's Guide, Version 6, Fourth Edition, Vol. 2, Cary, NC: SAS Institute Inc.

Soil Survey Staff. 1980. Soil Survey of Lancaster County, Nebraska. USDA-SCS. U.S. Gov. Print Office, Washington, DC.

Van Haverbeke, D.F., and R.A. Read. 1976. Genetics of eastern redcedar. USDA ForestService Res. Pap. WO-32. 17 pp.

Wheeler, D., and D. Chambers. 1992. Understanding Statistical Process Control. SPC Press, Knoxville, TN.

Wright, H.A., and A.W. Bailey. 1982. Fire Ecology: United States and Southern Canada. John Wiley and Sons, New York. 501 pp.

Plant Community Analysis of Schultz Prairie, Webster County, Nebraska

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Abstract. Schultz Prairie is a 259 ha tract of native mixed-grass prairie located in the loess hills region of south-central Nebraska on the Kansas border. It is owned and managed by the Nebraska Academy of Sciences and is 8.1 km directly east of Willa Cather Memorial Prairie, a Nature Conservancy site. Each of 41 site locations were sampled during the 1993 growing season by quadrat and point-step methods. Soils and vegetation data were gathered to (1) determine plant species composition and plant community relationships and (2) provide a basis of comparison to the Willa Cather Memorial Prairie. Major range community types are little bluestem (Andropogon scoparius)-big bluestem (A. gerardii)-blue grama (Bouteloua gracilis) on shallow limy range sites, little bluestem-Kentucky bluegrass (Poa pratensis)-sideoats grama (Bouteloua curtipendula) on silty sites, and big bluestem-little bluestem-Buffalo grass (Buchloe dactyloides) on lowland silty overflow sites. The flora consists of 239 species represented by 12 trees, 8 shrubs, 59 graminoids, 154 forbs, and 6 hydrophytes. Species composition reflects the prairie s transitional location between eastern tallgrass prairie and western mixed-grass prairie. Although invasion by smooth brome (Bromus inermis) is not significant, forb densities have been affected adversely by grazing and limited herbicide applications used to control populations of musk thistle (Carduus nutans).

Key words/phrases: mixed-grass prairie; bluestem-grama prairie; biodiversity; little bluestem; *Andropogon scoparius*; grazed prairie; loess hills prairie; range types; mixed-grass/tallgrass transition

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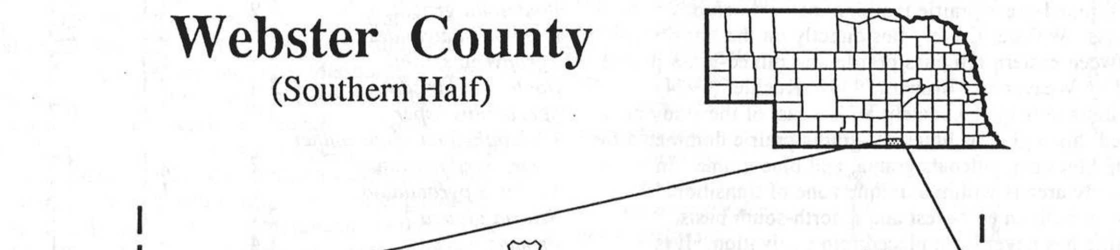

FIG. 1. The southern one-half of Webster County, Nebraska, showing the location of Schultz Prairie

Introduction

The C. Bertrand and Marian Othmer Schultz (BMS) Prairie is a 259 ha tract of mixed-grass prairie located in the loess hills region of extreme south central Nebraska (T1N, R10W, Sec. 35; 6.5 km south and 8.1 km east of Red Cloud, Webster County). It was purchased by the Schultz family and donated to the Nebraska Academy of Sciences, Inc. in 1990. BMS Prairie is bordered on the south by the Kansas state line and is 8.1 km due east of U.S. Highway 281 and the Willa Cather Memorial Prairie, a Nature Conservancy Preserve (Fig. 1).

The topography consists of gentle to steep slopes containing silty soils on a parent material of chalky limestone. The major soil associations are Kipson, Geary/Hobbs, and Holdrege, which relate directly to the range sites classified in this region (Paden and Ragon 1974). The three major range types in the Schultz Prairie are (1) shallow limy (found on Kipson silt loam associations), (2) silty (found on Holdrege and Geary silt loam associations), and (3) lowland silty overflow (found on Geary-Hobbs associations).

The study area is located in the rolling plains and breaks region of the central Great Plains (Nicholson and Hulett 1969). Remnant prairie vegetation typical of the study area was characterized by Hulett et al. (1968), Nicholson and Hulett (1969), and Nicholson and Marcotte (1979). The extent of the original loess hills mixed-grass prairie in Nebraska is described by Kaul and Rolfsmeier (1993), and historical studies by Weaver and Bruner (1948), Hopkins (1951), and Weaver and Albertson (1956) documented the loess hills vegetation of central Nebraska. However, the study area has a number of species with affinities to the southern mixed-grass prairie that dominates much of north central Kansas. Webster County lies directly on the transitional ecotone between eastern tallgrass prairie and mixed-grass prairie as proposed by Weaver and Bruner (1954). Kuchler (1974) placed this transition approximately 80 km east of the study area, but identified this region as bluestem-grama prairie dominated by big and little bluestem, sideoats grama, and blue grama. In effect, the study area is within a unique zone of transitional grasslands - on both an east-west and a north-south basis.

BMS Prairie has never been placed into cultivation. It is bordered on the north, west, and southwest by grazed prairie and by mostly cultivated lands on the east and southeast. The earliest known aerial photo of the site dates to 1 June 1937 (Conservation and Survey Division 1937) and indicates that topographical changes have been minor. The grazing history of the site has been consistent, prior to and after acquisition by the Academy of Science, with approximately 75 cow-calf pairs utilizing the entire area from 1 June to 15 November annually.

Methods

Forty-one field sites were sampled from 2 June 1993 to 9 September 1993 using both the modified step-point method (Owensby 1973) and 0.1 m2 quadrats. Of these study sites, 9 were located on shallow limy range sites, 21 on silty range sites, and 11 on lowland silty sites. One hundred step points per site were taken randomly within a 400 m2 area to obtain percent basal cover and percent species composition. Twenty-five 0.1 m2 quadrats (totaling 2.5 m2/site) were placed randomly along lines of uniform topography in order to determine forb density, frequency, and importance. Aerial cover (%) also was estimated for all species present within each 0.1 m2 quadrat.

Composite soil samples extracted from the top 25 cm (10 in) of soil were taken in triplicate at each site. These samples were analyzed at Ward Laboratories, Kearney, Nebraska, for pH, lime content, available P (ppm), available K (ppm), nitrate-nitrogen (ppm), and organic matter (%). Correlation coefficients between these quantitative factors and the most important graminoid species were calculated for each of the three major range types. Nomenclature follows the Great Plains Flora Association (1991). Voucher specimens were collected and are on file at the herbarium at the University of Nebraska at Kearney.

Results and Discussion

Mean basal cover (%) of the 25 most frequently occurring species was calculated and appears in Table 1. The dominant graminoid species, little bluestem, sideoats grama, Kentucky bluegrass, big bluestem, and blue grama, are comparable to those derived from estimated aerial cover (Table 2). Based on aerial cover estimates, little bluestem, big bluestem, sideoats grama, buffalo grass, and Kentucky bluegrass are the top five graminoids. Sideoats grama and Kentucky bluegrass rank ahead of big bluestem when mean basal cover (%) is considered alone.

Table 1. Mean basal cover (%) of the 25 most frequently occurring species for each of three major range types on Schultz Prairie, Nebraska.

Species	Average All Sites	Limy Sites	Silty Sites	Lowland Sites
Andropogon scoparius	21.8	25.5	21.3	17.0
Bouteloua curtipendula	14.4	14.4	14.7	14.4
Poa pratensis	9.5	3.1	14.4	4.8
Andropogon gerardii	9.1	14.1	4.8	13.8
Bouteloua gracilis	7.9	14.3	5.4	5.6
Buchloe dactyloides	5.6	6.4	2.9	11.1
Agropyron smithii	5.3	1.0	7.2	5.3
Bouteloua hirsuta	3.4	7.4	0.9	5.2
Sporobolus asper	3.4	5.3	0.7	3.2
Dichanthelium oligosanthes var. scribnerianum	3.2	2.5	4.3	1.3
Koeleria pyramidata	3.0	1.9	2.2	6.2
Setaria glauca	2.7	0.7	4.1	0.7
Bromus inermis	1.4	- -	2.1	1.4
Aristida purpurea var. robusta	1.1	- -	2.0	- -
Carex gravida var. gravida	1.0	0.8	1.4	0.3
Eragrostis spectabilis	1.0	0.6	1.3	0.6
Carex brevior	0.9	0.4	1.3	0.4
Sorghastrum nutans	0.8	0.8	0.4	- -
Bromus japonicus	0.6	- -	0.8	0.8
Oxalis dillenni	0.6	0.3	0.1	0.9
Verbascum thapsus	0.5	0.3	0.7	0.2
Antennaria neglecta	0.4	0.5	0.1	0.9
Hordeum pusillum	0.4	0.1	0.1	1.3
Cyperus lupulinus	0.3	- -	0.6	- -
Panicum virgatum	0.2	0.3	0.1	0.6

Table 2. Species rankings for each major range type based on relative cover (RC %) on Schultz Prairie, Nebraska.

Limy Sites	Silty Sites	Lowland Sites
Andropogon scoparius (28.5)	Andropogon scoparius (21.5)	Andropogon gerardii (17.1)
Andropogon gerardii (17.2)	Poa pratensis (12.4)	Andropogon scoparius (15.9)
Bouteloua gracilis (11.1)	Bouteloua curtipendula (11.7)	Buchloe dactyloides (11.5)
Bouteloua hirsuta (9.4)	Setaria glauca (6.1)	Bouteloua curtipendula(10.1)
Bouteloua curtipendula (9.1)	Buchloe dactyloides (5.8)	Koeleria pyramidata (9.5)
Buchloe dactyloides (5.4)	Andropogon gerardii (4.3)	Bouteloua gracilis (7.6)
Poa pratensis (3.6)	Dichanthelium oligosanthes var. scribnerianum (4.2)	Hordeum pusillum (3.8)
Koeleria pyramidata (1.9)	Agropyron smithii (4.1)	Poa pratensis (3.8)
Carex gravida var. gravida (1.5)	Sporobolus asper (3.1)	Agropyron smithii(3.5)

Because the step-point method (Owensby 1973) tends to over-emphasize graminoid species, importance values (relative density + relative frequency) for forbs were calculated for each of three range types (Table 3). The 10 most prevalent species, ranked according to average importance values, are field pussy-toes (Antennaria neglecta), spotted spurge (*Euphorbia maculata*), gray-green wood sorrel (*Oxalis dillenii*), hoary vervain (*Verbena stricta*), common mullein (*Verbascum thapsus*), purple prairie clover (*Dalea purpurea*), dandelion (*Taraxacum officinale*), western ragweed (*Ambrosia psilostachya*), white milkwort (*Polygala alba*), and Dakota vervain (*Verbena bipinnatifida*). Species composition differs markedly at the Willa Cather Memorial Prairie, located only 8.1 km west of the study site, where dominant forbs are western ragweed, Missouri goldenrod (*Solidago missouriensis*), field pussy-toes, Louisiana sagewort (*Artemesia ludoviciana*), and scurfpea (*Psoralea tenuiflora*) (Nicholson and Marcotte 1979). A regional perspective is given by Nicholson and Hulett (1969), who reported western ragweed, scurfpea, Missouri goldenrod, white milkwort, scarlet gaura (*Gaura coccinea*), and hoary vervain as dominants in the rolling hills and breaks region of northern Kansas and southwestern Nebraska. Weaver and Albertson (1956) also listed western ragweed, scurfpea, and white milkwort as abundant on mixed-grass prairies of central Nebraska. Some of the forbs that occur in BMS Prairie approach the northernmost limit of their range and extend far to the south into the southern mixed-grass prairies of Kansas and Oklahoma. Some examples include spider milkweed (*Asclepias viridus*), woolly loco (*Astragalus mollissimus*), Fendler s aster (*Aster fendleri*), silktop dalea (*Dalea aurea*), and stenosiphon (*Stenosiphon linifolius*).

Forbs were impacted, both negatively and positively, by (1) seasonal grazing and (2) an aerial application of picloram (4-amino-3,5,6-trichlora-2-pyridinecarboxylic acid) as TordonR in an attempt to control musk thistle populations on the north and west sides of the prairie. The high number of weedy invaders among these forbs indicates a degree of disturbance to the prairie, even though grazing effects are minimal. Perhaps several of these invaders are more herbicide-tolerant than are the native forbs.

BMS Prairie is dominated heavily by graminoids as indicated by quadrat cover estimates for all species (Table 2). The bluestems, grama grasses, and Kentucky bluegrass have not decreased appreciably as a result of grazing pressure. Displacement of these species by Japanese brome (Bromus japonicus) and smooth brome is relatively light when compared to other area grasslands, such as Willa Cather Prairie. Relative cover was used to provide a ranking of species for each of three major range types.

Table 3. Average importance values of the most frequently occurring forbs and woody plants in each of three major range types on Schultz Prairie, Nebraska.

Species	Limy Sites	Silty Sites	Lowland Sites
Ambrosia psilostachya	- -	16.8	0.3
Antennaria neglecta	27.4	20.9	29.4
Artemisia ludoviciana	0.7	8.2	0.3
Astragalus crassicarpus	5.4	0.9	4.6
Astragalus lotiflorus	5.4	0.6	5.5
Callirhoe involucrata	6.3	1.7	2.6
Cirsium altissimum	- -	1.4	0.3
Cirsium undulatum	1.9	- -	0.6
Cirsium vulgare	- -	- -	5.1
Conyza canadensis	- -	3.5	- -
Dalea purpurea	28.2	0.7	7.2
Echinacea angustifolia	1.0	0.2	- -
Erigeron strigosus	1.1	1.8	3.5
Euphorbia maculata	15.4	14.6	28.6
Euphorbia marginata	- -	3.8	5.9
Hedeoma hispidum	2.5	0.6	1.5
Lactuca serriola	2.1	0.5	0.7
Liatris punctata	0.6	3.0	6.9
Linum rigidum	1.1	3.0	8.2
Lithospermum incisum	- -	0.7	2.0
Medicago lupulina	9.7	- -	- -
Oxalis dillenii	15.8	37.4	20.5
Oxytropis lambertii	2.0	- -	5.9
Physalis longifolia	- -	4.0	2.4
Polygala alba	4.8	3.5	7.9
Senecio plattensis	4.7	2.0	0.9
Strophostyles leiosperma	- -	2.3	9.2
Taraxacum officinale	9.6	9.2	7.0
Triodanus perfoliata	- -	1.7	1.0
Verbascum thapsus	14.2	17.8	4.8
Verbena bipinnatifida	7.5	0.6	4.8
Verbena stricta	6.7	15.1	18.3
Viola pratincola	9.1	- -	- -

Based on species composition, soils, and topography, three major range types were recognized on BMS Prairie.

Range Community Types

Limy range sites. Shallow limy range sites are found on calcareous uplands where slopes average 7-31%. The soils are mainly Kipson silt loam (KsD), which comprise 21% of BMS Prairie. Shallow limy soils have low available water capacity because underlying bedrock limits effective water movement and root penetration. A degree of drought tolerance is necessary for plants that must adapt to these steep, dry slopes with rapid runoff. The major plant association is little bluestem-big bluestem-blue grama mixed with moderate amounts of hairy grama (*Bouteloua hirsuta*), sideoats grama, and buffalo grass (Table 2). Prominent forbs are purple prairie clover, field pussy-toes, gray-green wood sorrel, spotted spurge, and common mullein.

Silty range sites. Silty range sites are supported by deeper silt loam soils of the Geary and Holdrege series, which cover 45% of BMS Prairie. Most of these sites have average slopes of 3-7%. Sites are eroded more severely where slopes range from 7-10%. A little bluestem-Kentucky bluegrass-side-oats grama association is dominant, with buffalo grass, big bluestem, and blue grama present in lesser amounts. Deeper soils and moderate drainage allow for more optimal growing conditions that support a diverse combination of forbs and grasses (Table 1). For example, smooth brome and Japanese brome were found mostly on silty sites. Japanese brome is adapted better to relatively flat silty sites and is found rarely on shallow limy sites where dry conditions prevail (Nicholson and Hui 1993). Gray-green wood sorrel, field pussy-toes, common mullein, and western ragweed are common forbs.

Lowland silty overflow range sites. An association of big bluestem-little bluestem-buffalo grass, intermixed with sideoats grama, Junegrass (Koeleria pyramidata), and blue grama, occupies the short sides and narrow bottoms of upland drainage ways. These Geary soils are moderately steep (up to 31% slopes) on the canyon sides, with nearly level or gently sloping Hobbs soils on the bottomlands. The silty-alluvial Hobbs series is flooded occasionally. The slopes are well drained but are quite permeable, with moderate to high available water capacity (Paden and Ragon 1974). The most important forbs are field pussy-toes, spotted spurge, gray-green wood sorrel, and hoary vervain.

Riparian Forest Community

A fourth plant community type is riparian forest. On the southwest and west sides of BMS Prairie, savanna-like stands of woody vegetation, dominated by bur oak (*Quercus macrocarpa*), white mulberry (*Morus alba*), green ash (*Fraxinus pennsylvanica*), and silver maple (*Acer saccharinum*), occur within the bottomlands. Understory species include rough-leaved dogwood (*Cornus drummondii*), bittersweet (*Celastrus scandens*), and Missouri gooseberry (*Ribes missouriense*). This remnant of riparian forest also is present on the 1937 aerial photos. Riparian forest species are restricted to the lowlands along Lost Creek, which drains from south to north on the west side of the grassland. Lost Creek is a permanent stream that has continued to flow even during drought cycles (Lyle Henderson 1993, pers. comm.). Postsettlement lack of fire has allowed these woody plants to increase their numbers and extend their coverage. On Konza Prairie in northeast Kansas, fire repression resulted in a doubling of forest acreage in the 40-year period from 1939-1978 (Reichman 1987).

Relationships of Soil and Plant Communities

Soil chemical parameters are shown in Table 4. Available P (ppm), K (ppm), OM (%), and pH on limy sites are comparable to values for shallow limy range sites studied by Hulett and Tomanek (1969) in North Central Kansas. Soil chemistry on other remnant grassland sites in northwestern Kansas and southwestern Nebraska also was similar to that on BMS Prairie (Hulett et al. 1968). Even though Hulett et al. (1968) and Nicholson and Marcotte (1979) linked prairie species distributions in this region to topography and site moisture conditions, little variation in soil moisture (%) occurred among limy, silty, and lowland silty overflow sites. These data likely reflect the fact that the 1993 growing season was unusually wet, punctuated with frequent heavy rains. Sloping sites and uplands did not completely dry out, as would be expected during a more typical growing season.

Table 4. Soil chemistry data from three range types on Schultz Prairie, Nebraska.

Range Type	pH	OM (%)	N (ppm)	P (ppm)	K (ppm)	% Moisture
Limy						
X̄	7.63	2.58	1.88	3.44	171.33	17.11
(9 sites)						
SD	0.30	0.72	0.69	2.30	71.90	2.43
Silty						
X̄	6.51	3.56	3.77	9.10	392.47	16.85
(21 sites)						
SD	0.49	0.56	2.54	5.65	107.20	2.12
Lowland						
X̄	6.89	3.06	4.09	10.00	330.63	16.31
(11 sites)						
SD	0.60	0.75	3.78	7.18	82.71	2.35

Inspection of correlation coefficients indicates that big bluestem and little bluestem are correlated closely to several soil factors on silty sites but not on limy and lowland sites (Table 5). Brown (1985) demonstrated that C4 grasses generally use N more efficiently than C3 grasses. Sideoats grama, a C4 species, was an exception on BMS Prairie, because it was correlated significantly to pH and lime on limy sites and to N on both limy and silty sites. Warm-season grasses generally have lower critical requirements for P and K than do cool-season grasses (Samson and Omielan 1994). Potassium (K), pH, and OM were the most critical factors to Kentucky bluegrass, the most abundant cool-season grass in the study area. It is also of interest that blue grama was correlated significantly to P on all three major range sites. On lowland overflow sites, the general lack of significant correlation between soil factors and all graminoid species suggests that other edaphic factors are likely of primary importance.

Another adaptive advantage of C4 grass species is their use of mycorrhizal symbiosis for nutrient uptake. Cool-season grasses, such as Kentucky bluegrass, tall fescue (*Festuca arundinacea*), smooth brome, and junegrass often have little or no infection by mycorrhizal fungi (Dhillion and Friese 1994). Kentucky bluegrass, Japanese brome, and smooth brome compete favorably with warm-season grasses on level and sloping silty sites where soil moisture supplies are adequate.

Table 5. Correlation coefficients between six soil characteristics and estimated aerial cover (%) of the most common graminoids at each of three range community types of Schultz Prairie, Nebraska.

	LIMY SITE						SILTY SITES						LOWLAND OVERFLOW SITES					
	pH	Lime	P	K	N	OM	pH	Lime	P	K	N	OM	pH	Lime	P	K	N	OM
pH	-.-						-.-						-.-					
Lime	-.82**	-.-					-.82**	-.-					.93**	-.-				
P	-.65*	.41	-.-				-.20	.46*	-.-				-.11	-.32	-.-			
K	-.90**	.66*	.83**	-.-			-.24	.32	.20	-.-			.13	.06	.71*	-.-		
N	-.71*	.54*	.43	.69*	-.-		-.21	.27	.18	.31	-.-		-.11	-.04	.17	.58	-.-	
OM	-.70*	.39	.81**	.82**	.52	-.-	-.23	.26	.32	-.10	.22	-.-	-.83**	-.68*	-.22	-.18	.17	-.-
<u>Agropyron</u> <u>smithii</u>	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	.41	.46	.24	.52	.57	-.39
<u>Andropogon</u> <u>gerardii</u>	.47	-.53	-.22	-.38	.33	-.41	.77**	-.54**	-.54**	-.56**	.57**	-.44*	-.16	.01	-.33	.15	.54	.54
<u>Andropogon</u> <u>scoparius</u>	-.62	.17	.16	.41	.10	.00	.72**	-.49*	-.49*	-.50*	.62**	-.38	-.22	-.26	-.24	-.04	.45	.40
<u>Bouteloua</u> <u>curtipendula</u>	.76*	-.75*	.25	-.39	-.69*	.03	.06	-.12	.03	-.11	.40*	.38	-.44	-.23	-.21	-.10	.27	.55
<u>Bouteloua</u> <u>gracilis</u>	.33	-.28	.72*	.15	-.25	.29	.12	.15	.50*	-.34	-.14	.38	-.03	-.18	-.67*	.23	-.43	-.44
<u>Bouteloua</u> <u>hirsuta</u>	-.13	.28	-.14	.05	-.74*	-.41	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-
<u>Bromus</u> <u>japonicus</u>	-.-	-.-	-.-	-.-	-.-	-.-	.02	.31	.00	-.02	.29	.14	-.-	-.-	-.-	-.-	-.-	-.-
<u>Buchloe</u> <u>dactyloides</u>	.06	-.10	-.27	0.6	-.14	-.20	-.58**	.14	-.03	.51*	.24	.57**	-.11	-.26	.78*	.43	-.31	-.26
<u>Dichanthelium</u> <u>oligosanthes</u>	-.-	-.-	-.-	-.-	-.-	-.-	-.40	.32	.49*	.24	.11	.45	-.-	-.-	-.-	-.-	-.-	-.-
<u>Koeleria</u> <u>pyramidata</u>	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	.49	.44	-.21	-.19	-.44	-.63
<u>Poa</u> <u>pratensis</u>	-.79**	.41	.22	.84**	.43	.87**	-.34	.16	.36	.15	.11	.15	-.22	.03	-.50	-.07	.31	.64

Significant at (P = 0.05)*

Significant at (P = 0.01)**

Diversity of BMS Prairie

The overall significance of BMS Prairie is the conservation of biodiversity in a region intermixed with cultivated and overgrazed rangelands. A total of 239 plant species and 58 families representing 42% of Nebraska s 136 plant families are known from the entire 259 ha prairie (Rothenberger 1994). Rare species that occur here are bog rush (Juncus effusus), Fendler s aster, and cardinal flower (*Lobelia cardinalis*). Fremont s clematis (*Clematis fremontii*), reported in only three counties in Nebraska and 15 in Kansas, grows along roadsides near the prairie. As reported by Kaul and Rolfsmeier (1994), species richness is often surprisingly high in relatively small areas. Quadrat data from this study included a total of 33 species on 9 limy sites (avg. = 1.47 species/m2), 56 species on 21 silty sites (avg. = 1.07 species/m2), and 40 species on lowland silty overflow sites (avg. = 1.46 species/m2).

BMS Prairie is an excellent representative of bluestem-grama prairie on calcareous parent material. These mixed-grass prairies are not common in Nebraska, where the loess hills mixed-prairie north of the Republican River and sandhills prairie north of the Platte River are predominant. In the absence of fire, moderate grazing pressure apparently facilitates native graminoids (Dyer and Bokhari 1976, McNaughton 1979). Forb frequencies are influenced more dramatically where disturbance favors invaders at the expense of native species. Most area sites comparable to BMS Prairie are either heavily overgrazed or cultivated to support alfalfa, wheat, or corn. BMS Prairie is an important remnant of the once extensive grasslands of the Great Plains. Because of its species diversity, natural beauty, and its significance for study, BMS Prairie should be managed properly and protected for the future.

Conclusions

BMS Prairie is a grazed, mixed-grass, native prairie found in the loess hills/calcareous breaks region of south-central Nebraska. It consists of approximately 45% silty, 21% shallow limy, and 34% lowland silty range sites. A small, unique, riparian forest community borders Lost Creek mainly in the SW 1/4 Section. Overall, the dominant graminoid species are little bluestem, sideoats grama, Kentucky bluegrass, and big bluestem, with significant amounts of buffalo grass and blue grama intermixed. Dominant forbs are field pussy-toes, spotted spurge, gray-green wood sorrel, hoary vervain, common mullein, and purple prairie clover. Native forbs have been affected adversely by grazing and by picloram as Tordon R applications used to control musk thistle invasion, which represents a serious threat to the integrity of BMS Prairie. Soil factors (moisture, pH, lime, N, K, P, and OM) also play an important role in species distribution. Warm-season, C4 grasses generally have lower critical requirements for N, P, and K than do cool-season, C3 species. Invasion by smooth brome is relatively light given its widespread abundance on other prairies in this area.

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Literature Cited

Brown, R.H. 1985. Growth of C3 and C4 grasses under low N levels. Crop Science 25:954-957.

Conservation and Survey Division. 1937. Aerial photograph, Section 35, Township 1 North, Range 10 West, Webster County, Nebraska. Institute of Agriculture and Natural Resources, University of Nebraska, Lincoln.

Dhillion, S.S. and C.F. Friese. 1994. The occurrence of mycorrhizas in prairies: application to ecological restoration. In R.G. Wickett, P.D. Lewis, A. Woodliffe, and P. Pratt (eds.) Proceedings of the Thirteenth North American Prairie Conference, Spirit of the Land, Our Prairie Legacy. Windsor, Ontario, Canada, pp 103-114.

Dyer, M. I. and U.G Bokhari. 1976. Plant-animal interactions: studies of the effects of grasshopper grazing on blue grama grass. Ecology 57:762-772.

Great Plains Flora Association. 1991. Flora of the Great Plains, 2nd printing. University Press of Kansas, Lawrence. 1402 pp.

Hopkins, H.H. 1951. Ecology of the native vegetation of the loess hills in central Nebraska. Ecological Monographs 21:125-147.

Hulett, G.K., C.D. Sloan, and G.W. Tomanek. 1968. The vegetation of remnant grasslands in the loessial region of northwestern Kansas and southwestern Nebraska. Southwestern Naturalist 13:377-391.

Hulett, G.K. and G.W. Tomanek. 1969. Remnant prairies on the shallow limy range site in north central Kansas. Journal of Range Management 22:19-23.

Kaul, R.B. and S.B. Rolfsmeier. 1993. Native vegetation of Nebraska. Conservation and Survey Division; Institute of Agriculture and Natural Resources, University of Nebraska, Lincoln. (Map, 1:1,000,000)

Kaul, R.B. and S.B. Rolfsmeier. 1994. Diversity of vascular plants and intensity of plant collecting in Nebraska. Transactions of the Nebraska Academy of Sciences 21:13-20.

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

Nicholson, R.A. and G.K. Hulett. 1969. Remnant grassland vegetation in the central Great Plains of North America. Journal of Ecology 57:599-612.

Nicholson, R.A. and M.G. Marcotte. 1979. Vegetation of the Willa Cather Memorial Prairie. Journal of Range Management 32:104-108.

Nicholson, R.A. and C. Hui. 1993. Growth and survival of Japanese brome on limestone soils in western Kansas. Prairie Naturalist 25:185-195.

McNaughton, S.J. 1979. Grassland-herbivore dynamics. In A.R.E. Sinclair and M. Norton-Griffiths (eds.) Serengeti: Dynamics of an Ecosystem. The University of Chicago Press, pp. 46-81.

Owensby, C.E. 1973. Modified step-point system for botanical composition and basal cover estimates. Journal of Range Management 26:302-303.

Paden, H.E. and L.G. Ragon. 1974. Soil survey of Webster County, Nebraska. U.S.D.A. Soil Conservation Service, Washington, DC. 72 pp.

Reichman, O.J. 1987. Konza Prairie: a Tallgrass Natural History. University Press of Kansas, Lawrence. 226 pp.

Rothenberger, S.J. 1994. Floristic analysis of the C. Bertrand and Marian Othmer Schultz Prairie, A mixed-grass prairie in south-central Nebraska. Transactions of the Nebraska Academy of Sciences 21:21-30.

Samson, R.A. and J.A. Omielan. 1994. Switchgrass: a potential biomass energy crop for ethanol production. In R.G. Wickett, P.D. Lewis, A. Woodliffe, and P. Pratt (eds.) Proceedings of the Thirteenth North American Prairie Conference, Spirit of the Land, Our Prairie Legacy. Windsor, Ontario, Canada, pp 253-258.

Weaver, J.E. and F.W. Albertson. 1956. Grasslands of the Great Plains. Johnsen Publishing Company, Lincoln, NE. 395 pp.

Weaver, J.E. and W.E. Bruner. 1948. Prairies and pastures of the dissected loess plains of central Nebraska. Ecological Monographs 18:508-549.

Weaver, J.E. and W.E. Bruner. 1954. Nature and place of transition from true prairie to mixed prairie. Ecology 35:117-126.

Low Plant Diversity Found in Communities Dominated by Reed Canary Grass (*Phalaris arundinacea*)

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Abstract. Reed canary grass (*Phalaris arundinacea*) has gained a reputation as an undesirable plant because it apparently outcompetes desirable native plant species. However, literature does not exist to support or discredit this status. Therefore, presence/absence vegetation surveys were conducted in south-central Wisconsin, in competing communities of prairie cordgrass (*Spartina* pectinata, n=4) and reed canary grass (*Phalaris*, n=4), at four sites in 1992 and in competing communities of tussock sedge (*Carex stricta*, n=1) and *Phalaris* (n=2) in a meadow at the Waubesa Mound in 1993. In all sites, communities dominated by *Phalaris* contained fewer number of species. Shannon diversity indices (H') were calculated for all communities and were the lowest for the *Phalaris*-dominated communities. A t-test indicated significant differences between *Phalaris* and native (*Spartina* and *Carex*)-dominated communities at four of the five sites. This study supports previously held qualitative views of low plant diversity in *Phalaris*-dominated communities and provides quantitative data to guide management. Future management and research of *Phalaris* dominated communities should focus on control or reduction of reed canary grass to maintain or improve native plant diversity.

Key words: *Phalaris arundinacea*, *Spartina* pectinata, *Carex stricta*, Shannon diversity, plant diversity, competition

Introduction

Phalaris arundinacea is a grass of wetlands and moist soil areas (Hutchinson 1990, Scheaffer et al. 1990, Bookout et al. 1989, Lefor 1987, Reuter 1986, Nishimura et al. 1985, Apfelbaum 1984, Wilcox et al. 1984, Tessier et al. 1983, Univ. Wisc. Extension Serv. 1950, U.S. Dept. Agri. 1938). Although the species is native to North America, most botanists believe that the *Phalaris* present today is aEuropean ecotype (Swink and Wilhelm 1994, Dore and McNeill 1980). This ecotype has been identified as a pest plant species (Hutchinson 1990, Apfelbaum and Sams 1987, West 1984, Marten and Heath 1973) and is believed to outcompete native plant species (Apfelbaum and Sams 1987, Nishimura et al. 1985, Buele 1979, Fassett 1957), resulting in decreased plant species diversity and loss of preferred vegetation (Holland and Tesar 1988).

The European ecotype of *Phalaris* was introduced to the United States in the late 19th century as a forage crop and is still promoted by government agencies. Because of its high rate of vegetative reproduction, seed output, and seed viability, has escaped from agricultural lands onto adjacent compatible lands. Waterways have further increased the dispersal rate for this species and introduced it to uncultivated natural areas that seasonally flood and/or have moist soils.

Conservationists have observed a qualitative decrease in floral and faunal diversity within *Phalaris*-dominated communities and are concerned that the unchecked spread of *Phalaris* may lead to local, regional, or even global extinction of some plant species. However, qualitative observations may be deceptive and may lead to erroneous policy and management decisions. I could not locate any studies that evaluated the species diversity of *Phalaris*-dominated communities; therefore, I conducted vegetation surveys to determine the plant species diversity differences, measured by species richness (H'), between *Phalaris*-dominated communities and adjacent native communities.

Study Areas and Methods

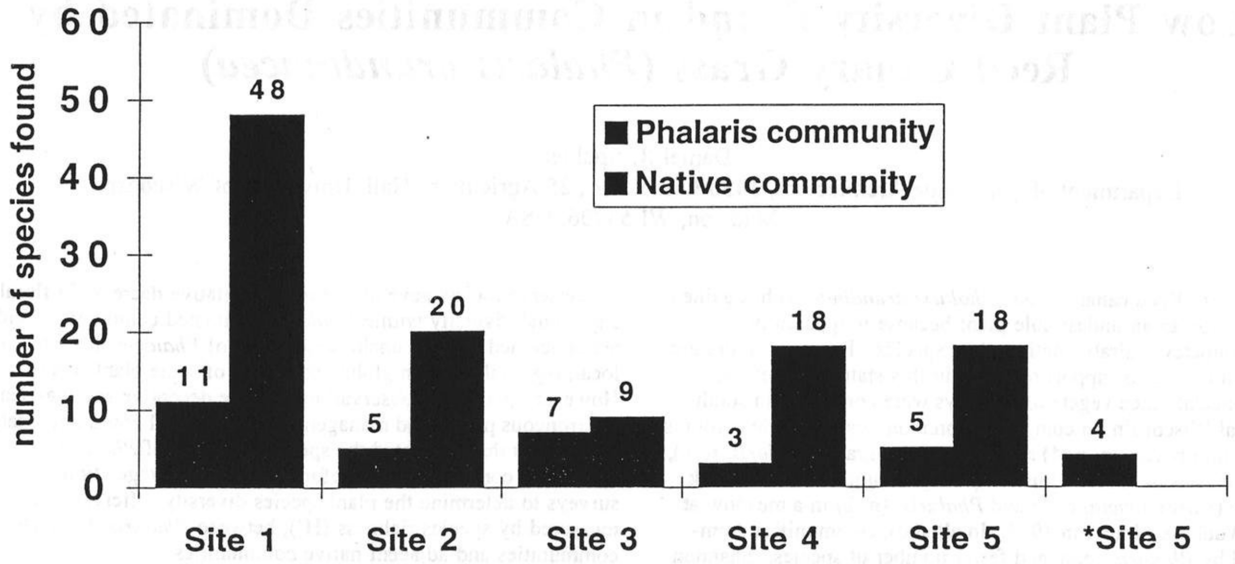
This study was conducted at five sites in south-central Wisconsin. Criteria for site selection were: 1.) *Phalaris* must appear visually dominant, 2.) the native community must be dominated visually by *Spartina* or *Carex*, and 3.) *Phalaris*-dominated and native-dominated communities must be in direct competition, as shown by *Phalaris* and *Spartina* or *Carex* co-occuring in transition zones between the dominant communities.

Locations of study sites were: Site 1.) along a bicycle trail in a former railroad right-of way, Site 2.) further west along the same bicycle trail, Site 3.) Waunakee Marsh State Wildlife Area, Site 4.) Dodge County road right-of-way, and Site 5.) north of, and adjacent to, Murphy's Creek and the Waubesa Peat Mound.

None of the sites appeared to have been burned in the past several years as evidenced by: 1) presence of young/short woody species, 2) lack of fire scarring of larger woody vegetation, and 3) accumulation of dead vegetation. Also none of the sites apparently had been cultivated in recent decades, but were currently (or had been recently) bordered by crop fields or pasture.

Approximately equal-sized areas were delineated by pace count for sampling of native and *Phalaris* communities at each site. All communities within a site were uniform in slope, topography, and aspect. Borders were at least 3 m from apparent landscape change or disturbance, i.e., drainage ditch, embankment, or fence. Recent soil disturbance from trampling, machinery, or sedimentation was not evident. Because the actual area covered during sampling at each site was small (< 1 ac), I assumed that differences in soils, hydrology, and disturbance history were slight.

Presence/absence surveys were conducted by locating transects within both communities and randomly placing 1-m2 quadrats along the transects in each of the communities. Number and length of transects varied enough among sites and among communities to allow for 40 quadrat samples. Transects were at least 2 m from the outer edge of the communities to prevent edge effects. Vegetation was identified to genus and species when possible following Gleason and Cronquist (1991).



*Two Phalaris communities and one native community were surveyed at Site 5.

FIG. 1. Number of plant species found per community, per site.

Shannon diversity (H') indices (Magurran 1988, Brower and Zar 1984) were derived for all communities in each of the sites using the number of quadrats in which a species was observed. A t-test was conducted on the H' values following Magurran (1988) and Brower and Zar (1984). The null hypothesis was: differences occur in plant species diversity (species richness) between *Phalaris*- and native-dominated communities within each site.

Results

The number of species found in each community at each site was highest in the native (*Spartina* or *Carex*) community and lowest in the *Phalaris* community (Figure 1.).

The H' values were higher for the native communities than for the *Phalaris* dominated communities at all sites (Table 1.).

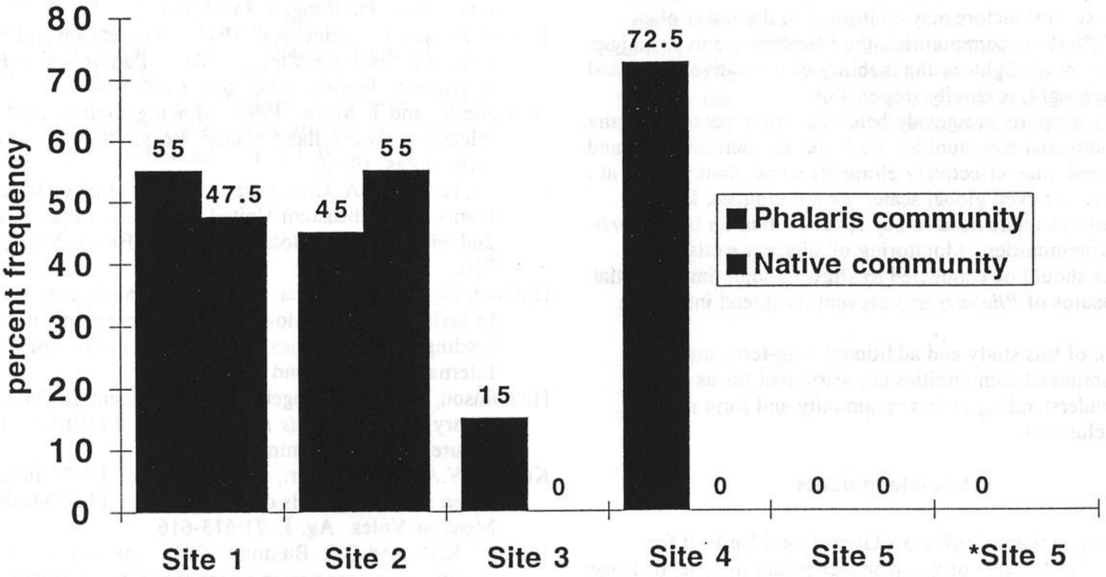
The t-test conducted on the Shannon diversity indices (Table 1.) indicated that significant differences occurred between *Phalaris*- and native-dominated communities in four (sites: 1, 2, 4, 5) of the five sites. Therfore, the null hypothesis was rejected for the four sites. Site 3 was the only site where the t-test did not find a significant difference between H' values.

Discussion

The sites were located many miles from one another and had different adjacent land-uses; therefore, it is likely that they had different past-use (disturbance) histories. In this study, the native communities consistently showed greater diversity. This may indicate that the *Phalaris* communities were outcompeting other vegetation for some limiting resource(s) and were less related to past-use history. Competition as defined by Pianka (1978): "... occurs when two or more organismic units use the same resources and when those resources are in short supply. It may also occur through direct interference such as the production of toxins."

Table 1. Shannon diversity indes (H') for communities and results of t-test comparing H' values.

Site	Dominated by	H'	P value
1 1992	Phalaris Spartina	0.68 1.38	P < 0.01
2 1992	Phalaris Spartina	0.39 1.05	P < 0.01
3 1992	Phalaris Spartina	0.64 0.71	P > 0.05
4 1992	Phalaris Spartina	0.34 0.92	P < 0.01
5 1993	Phalaris1 Carex Phalaris2	0.40 1.04 0.35	P < 0.01 P < 0.01
H' = Σpi log pi		pi = ni/N	α = 0.05



*Two Phalaris communities and one native community were surveyed at Site 5.

FIG. 2. Percent frequency of saw-toothed sunflower.

Phalaris is a C3 grass (Kephart and Buxton 1989) and begins growth early in the spring. It is able to form a dense canopy by mid- to late-spring, thus preventing solar radiation from reaching the ground or other vegetation lower in height. This lack of solar radiation will prevent soils from warming to levels required by various species to germinate and will limit photosynthesis of shorter species, resulting in decreased growth or death.

A possible reason for the lower plant diversity in *Phalaris*-dominated communities is the production of toxins by *Phalaris* (Kendal et al. 1979). In this study the *Phalaris* community displayed a fairly distinct 'edge' or 'border', possibly requiring a high density of roots per given area to produce enough toxin to invade established communities or to crowd out established species. This also may explain why saw-toothed sunflower (*Helianthus grosseserratus*), known to be allelopathic (Curtis and Cottam 1950), maintained relatively high abundance in the *Phalaris* community (Figure 2.).

Another possibility is competition for light. Although Fowler and Antonovics (1981) recorded co-occurrence of C3 and C4 grasses and forbs because of differing temporal patterns and resource partitioning of light, the species in their study did not include a plant with the ability to create a nearly complete to complete canopy as does *Phalaris*.

In Nebraska, Weaver and Rowland (1952) found reduced height, weight, soil temperature, basal area, flowering culms, and plant species diversity in areas where mulch accumulated naturally compared to areas where it was removed in the spring.

Fenner (1980) showed that leaf canopy was very effective in inhibiting germination of Bidens pilosa achenes, and Silvertown (1980) found that germination for 17 of 27 species studied was significantly lower under a leaf canopy. Kephart and Buxton (1989) found a reduced leaf area ratio in two C4 and three C3 grass species grown under reduced irradiance. Assuming other native plant species would respond similarly, a lower leaf area ratio would further inhibit a plant's ability to photosynthesize available light, thus reducing the growth rate.

Many areas dominated by *Phalaris* appear to be burned infrequently if at all, and the accumulation of *Phalaris* litter will further decrease light penetration. Burning or mowing can be effective in removing the litter and canopy of *Phalaris*; however, timing of burning or mowing may be crucial.

The UW-Madison Arboretum has been burning its Greene Prairie yearly for the past 11 years in early spring, but *Phalaris* continues to invade (V. Kline UW-Madison Arboretum pers. commun.). However, late spring or early summer burning or mowing appears to effectively reduce *Phalaris* and increase *Spartina* pectinata and other plant species (Gillespie and Murn 1992, Larson and Stearns 1989). The literature supports both temporal observations that early spring burning increases flowering of C3 grasses and late spring or early summer burning effectively eliminates C3 sexual reproduction but increases flowering of C4 grasses, and of other forbs (Curtis and Partch 1948, 1950).

Although the rhizome network of *Phalaris* has been described as very dense (Troughton 1957), the rhizome network for *Spartina* is also very dense (Weaver 1954), and anyone who has attempted to collect a specimen of *Carex* for an herbarium can tell you that its rhizome network is extremely dense as well. The effect of *Phalaris*' rhizome network alone is unlikely to be responsible for the lower H' found in those communities. However, the combined effects of litter accumulation (reduced photosynthesis and cooler soils), toxins, and the *Phalaris* rhizome network may be very important.

Conclusion

Although several factors may contribute to the lower plant diversity of *Phalaris* communities, the literature seems to suggest that competition for light, or the inability of the native plants and soil to receive light, is chiefly responsible.

This study supports previously held qualitative perceptions that *Phalaris*-dominated communities are lower in plant diversity and, left unmanaged, may effectively eliminate some plant species at a local, regional, or even global scale. Restorationists, land managers, and planners need to pay special attention to *Phalaris*-dominated communities. Monitoring of adjacent wetland communities should be conducted to allow enough time to initiate control measures of *Phalaris* and prevent its spread into these sites.

Repetition of this study and additional long-term study of *Phalaris*-dominated communities are warranted for us to gain additional understanding of this community and form more concise conclusions.

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Literature Cited

Apfelbaum, S.I. 1984. Cattail (Typha spp.) management. Natural Areas Journal 5:9-17.

Apfelbaum, S.I., and C.E. Sams. 1987. Ecology and control of reed canary grass (*Phalaris arundinacea*). Natural Areas Journal 7:69-74.

Bookout, T.A., K.E. Bednarik, and R.W. Kroll. 1989. The Great Lakes Marshes. pp. 131-156. in L.M. Smith, R.L. Pederson, and R.M. Kaminski (eds). Habitat Management for Wintering Waterfowl in North America. Texas Tech University Press, Lubbock. pp. 560.

Brower, J.E. and J.H. Zar. 1984. Field and Laboratory Methods for General Ecology. Wm. C. Brown Publishing, Dubuque, Iowa pp. 226.

Buele, J.D. 1979. Control and Management of Cattails in Southeastern Wisconsin wetlands. Technical Bulletin No. 112. Department of Natural Resources, Wisconsin pp. 39.

Curtis, J.T., and G. Cottam. 1950. Antibiotic and autotoxic effects in prairie sunflower. Bulletin Torrey Botanical Club 77:187-191.

Curtis, J.T., and M.L. Partch. 1948. Effect of fire on the competition between bluegrass and certain prairie plants. American Midland Naturalist 39:437-443.

Curtis, J.T., and M.L. Partch.. 1950. Some factors affecting flower production in Andropogon gerardi. Ecology 31:488-489.

Dore, W.G. and J. McNeill. 1980. Grasses of Ontario. Monograph 26. Agriculture Canada. pp. 566.

Fassett, N.C. 1957. A manual of aquatic plants. University of Wisconsin Press, Madison. pp. 405.

Fenner, M. 1980. The inhibition of germination of Bidens pilosa seeds by leaf canopy shade in some natural vegetation types. New Phytologist 84:95-101.

Fowler, N., and J. Antonovics. 1981. Competition and coexistence in a North Carolina grassland: Patterns in undisturbed vegetation. Journal of Ecology 69:825-841.

Gillespie, J., and T. Murn. 1992. Mowing controls reed canary, releases native wetland plants. Restoration and Management Notes 10:93.

Gleason, H.A., and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada: 2nd ed. New York Botanic. Garden. Bronx, NY. pp. 910.

Holland, C., and M.B. Tesar. 1988. Simulated grazing compared to herbicide suppression of grass competition when sod seeding forage legumes. pp. 561-562 in Proc. of theXVth International Grassland Congress.

Hutchinson, M. 1990. Vegetation management guideline: Reed canary grass (*Phalaris arundinacea*). 1.(19):1-5. Illinois Nature Preserves Commission.

Kendal, W.A., R.R. Hill, Jr., and J.S. Shenk. 1979. Inhibition by Some Allelochemicals of Intake of Individual Meals by Meadow Voles. Ag. J. 71:613-616.

Kephart, K.D., and D.R. Buxton. 1989. Adaptation and forage quality of grasses grown under shade. pp. 819-820. in Proc. XVIth International Grassland Congress.

Larson, J., and F. Stearns. 1989. Effects of mowing on a woolgrass (Scirpus cyperinus) dominated sedge meadow in southeastern Wisconsin. Note 105.2. Restoration and Management Notes 7:92.

Lefor, M.W. 1987. *Phalaris arundinacea* L. (Reed Canary Grass-Gramineae) as a hydrophyte in Essex, Connecticut, USA. Environmental Management 11:771-773.

Magurran, A.E. 1988. Ecological Diversity and Its Measurement. Princeton Univ. Press, Princeton, NJ. pp. 179.

Marten, G.C., and M.E. Heath. 1973. Reed Canary Grass. pp. 263-276. in M.E. Heath, D.S. Metcalfe, and R.F. Barnes (eds). Forages: The Science of Grassland Agriculture. Third Ed. Iowa State University Press, Ames. pp. 775.

Nishimura, N., Suyama, and N. Ohga. 1985. Affects of indicator plants as criteria for grassland development in wetland. pp. 660-662. *in* Proc. XVth International Grassland Congress.

Pianka, E.R. 1978. Interactions between populations. Ch. 6. pp. 173-200. in Evolutionary Ecology, 2nd Ed. Harper & Row, New York.

Reuter, D.D. 1986. Sedge meadows of the Upper Mid-West: A stewardship summary. Natural Areas Journal 6:27-34.

Scheaffer, C.C., G.C. Marten, D.L. Rabas, N.P. Martin, and D.W. Miller. 1990. Reed canary grass. Minnesota Agriculture Experiment Station Bulletin 595-1990. University of St. Paul. pp. 8.

Silvertown, J. 1980. Leaf-canopy-induced seed dormancy in grassland flora. New Phytologist 85:109-118.

Swink, F., and G. Wilhelm. 1994. Plants of the Chicago Region. 4th edition. The Morton Arbor. Lisle, Illinois pp. 922.

Tessier, C., A. Aubin, and D. Chenevier. 1983. Les facteurs elevation et distance dans la structure et la productivite d'une communaute riveraine de macrophytes. Can. J. Bot. 62:2260-2266.

Troughton, A. 1957. The Underground Organs of Herbage Grasses. Commonwealth Agri. Bureaux. Farnham Royal, Bucks, England. pp. 163.

United States Department of Agriculture. 1938. Reed Canary Grass. Farmer's Bulletin No. 1602. US Government Printing Office, Washington, DC. pp. 12.

University of Wisconsin-Extension Service. 1950. For Wisconsin Lowlands: Reed Canary Grass. Stencil Circular 312. College of Agriculture Madison, WI. pp. 13.

Weaver, J.E. 1954. North American Prairie. Johnsen Publ. Co. Lincoln, NE. pp. 348.

___, and N.W. Rowland. 1952. Effects of excessive natural mulch on development, yield, and structure of native grassland. Botanical Gazette. 144:1-19.

West, K.A. 1984. Major pest species listed, control measures summarized at Natural Areas Workshop. Restoration and Management Notes 2:34.

Wilcox, D.A., S.I. Apfelbaum, and R.D. Hiebert. 1984. Cattail invasion of sedge meadows following hydrologic disturbance in the Cowles Bog Wetlands Complex, Indiana Dunes Natural Lakeshore. Wetlands, 4:115-128.

Fungus Pathogens of Prairie Plants in Iowa

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Abstract. Parasitic fungi have long been recognized as significant factors in the normal growth, survival, and yield of cultivated plants. However, little attention has been given to the parasitic fungi of native prairie plants or to their impact on their host plants in a tallgrass prairie. Basic to consideration of their impact is information concerning the presence and prevalence of specific fungi on host plant species. Since the early 1980's, we have made collections throughout the growing season of fungal parasites on the aboveground parts of plants from prairie preserves and private prairies in Iowa. Over two hundred species of fungi have been documented. This report discusses the fungi found on 25 common tallgrass prairie plants from 10 prairies in northern Iowa and one in central Iowa. It includes 43 fungi not reported in Gilman and Archer's 1929 paper on the plant parasitic fungi in Iowa or in Gilman's later supplements to that paper. An additional six fungus species were not reported previously on the hosts on which we found them but were listed on other host species. With knowledge of the fungus flora, we can evaluate its impact on the host plant's competitive ability and better interpret this component of the biological and environmental factors that shape our prairies.

Key words: Prairie plant diseases, fungus diseases, rusts, smuts, leaf spots

Introduction

Often overlooked and underappreciated, the fungi are crucial members of the prairie biological community. Major activities of the fungi include:

1. The fungi recycle such mineral nutrients as nitrogen, phosphorous, and potassium which are necessary to continued life for *every* organism. The fungi decompose cellulose and other materials in plant debris and use the carbohydrates as their energy source, assimilating some of the minerals into their living protoplasm. Individual cells of the mycelium are often short-lived, and the minerals eventually are available for use by other living organisms, including prairie plants.
2. Some fungi are very significant because they establish a mycorrhizal relationship with the roots of green plants. The mycorrhizal fungus expedites the movement of phosphorus, water, and possibly other nutrients into the plant, while it receives from the plant the materials necessary for its growth and survival.
3. Fungi are the major pathogens of plants. They may interfere with seedling survival and establishment, restrict the development and competitive ability of growing plants, prevent reproduction, or even directly kill individuals.

These three vital activities have not been studied intensively for fungi associated with prairies. General studies of decomposer fungi as they break down plant materials of all kinds do give insight into what happens in the prairie (Frankland et al, 1982). Numerous studies of mycorrhizal relationships of many nonprairie plants also give insight into what may be probably happening in the prairie (Read et al, 1992). In both situations, more specific studies of the fungi involved are needed to gain a better view of how these fungi affect and are affected by the prairie plants.

The limited information on fungal diseases of midwestern prairie plants has come primarily from state treatments of fungal diseases on plants. Trelease (1884) and Davis (1903, 1926) reported on the parasitic fungi of Wisconsin. Later, Greene added to the information on fungal plant parasites in Wisconsin in a series of 33 papers published from 1940 to 1968. Gilman and Archer (1929) listed the fungi of Iowa parasitic on cultivated and native plants. Two supplemental lists of parasitic fungi were compiled by Gilman (1932, 1949). More recently, information on distribution of a leaf spot fungus, *Elsinoe panici,* on switchgrass (Gabel and Tiffany, 1987) and of kernel smut, *Sphacelotheca occidentalis*, on big bluestem (Snetselaar and Tiffany, 1992) documented these diseases in Iowa.

Farr et al (1989) developed an extensive compilation of occurrence of fungi on plants and plant products in the United States. Monographic treatments of genera or groups of fungi such as Cummin's books on rust fungi on grasses (1971) and rust fungi on legumes and composites (1978), Fischer's treatment of the smut fungi (1953), and books dealing with fungal parasites of a specific group of plants such as cereals and grasses (Sprague, 1950) have made available general distribution information on these fungus species. However, we lack information on the distribution and occurrence of particular fungi on their hosts in given geographic areas in specific habitats.

Our present prairie heritage in Iowa consists of scattered remnant prairies of various sizes. The plant parasitic fungi may well be determining factors in the survival or the successful growth and reproduction of individual host species. A base of current information about the disease-inducing fungi on specific host species on each prairie may be useful in interpreting changes over time. A part of this ongoing project is discussed in this paper.

Materials and Methods

Beginning in the early 1980's, but continuing more intensively to the present, collections of diseased plants have been made throughout the growing season from tallgrass prairies in Iowa. State prairie preserves and Nature Conservancy prairie preserves in these counties have been our major sources of information, but county prairie preserves and private prairies have been visited as time permitted. We have tried to visit each site in early June, in late July, and in late August but have not been able to complete these visits in each collection year. Different parasitic fungi may be present in any given year, because they are influenced by temperature regimes and available moisture. Some may develop at different times during the growing season. For example, aecial stages of rust fungi usually develop during the spring and early summer, and the host leaves or entire plants colonized by the rust soon die. Thus, they are not evident at later visits and would not be included in disease information from that site.

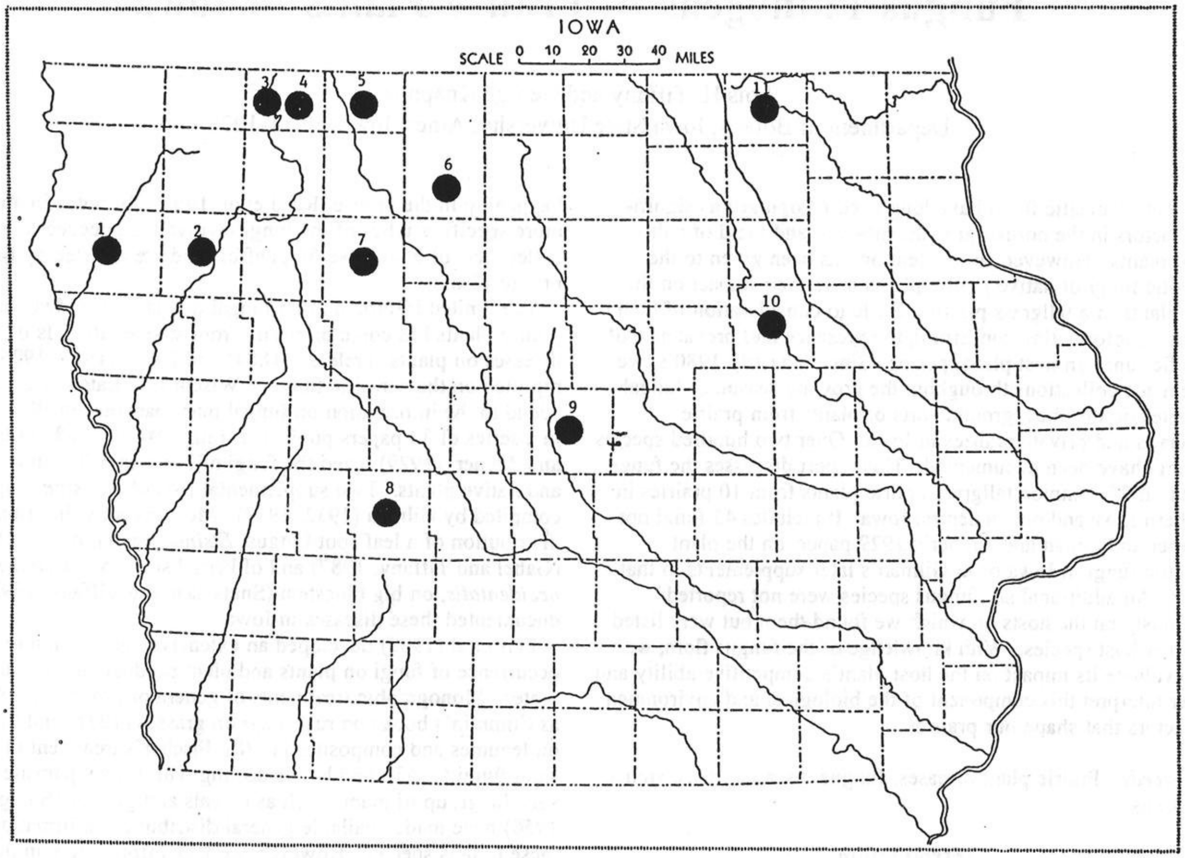

FIG. 1. Primary Iowa prairie sites included in survey of plant parasitic fungi.

Collections of diseased plant material were made in a nondestructive manner. When possible, plants were identified in the field, and only diseased parts collected, pressed, and processed. Identified fungus material in good fruiting condition on known hosts has been deposited in the mycology section of the Ada Hayden Herbarium of the Botany Department, Iowa State University (ISC) for permanent reference.

This report discusses the disease-inducing fungi found on 25 species of host plants in four groups collected on 10 native tallgrass prairies in northern Iowa and one in central Iowa (Fig. 1). These prairies are: [1]Five Ridges prairie, Plymouth County; [2]Steele prairie, Cherokee County; [3]Cayler prairie, Dickinson County; [4]Freda Haffner Kettlehole, Dickinson county; [5]Anderson prairie, Emmet County; [6]Stinson prairie, Kossuth County; [7]Kalsow prairie, Pocahontas County; [8]Sheeder prairie, Guthrie County; [9]Doolittle prairie, Story County; [10]Cedar Hills sand prairie, Black Hawk County; [11]Hayden prairie, Howard County.

Results

Our total collections thus far in this project include about 200 fungi parasitic on over 130 species of prairie plants. The four groups of plants discussed in this paper include the most common species on many Iowa tallgrass prairies. Fungal parasites are presented for four common grasses (Table 1), five legumes (Table 2), seven common composites (Table 3), and nine common prairie species from several plant families (Table 4).

The fungi reported here include 43 species not reported in Gilman and Archer's 1929 report on the plant parasitic fungi of Iowa or in Gilman's later supplements (Gilman, 1932, 1949) to that report. An additional six fungus species are not included in those reports on the hosts on which we have encountered them but were listed on other plant hosts.

The data on fungal parasites presented here based on collections from common prairie plant species on the 11 Iowa prairies are typical of the information we have from these and additional hosts in other sites. The most common, potentially quite destructive, parasitic fungi on most grass hosts (Table 1) are the rusts. Two of these hosts, big bluestem and switchgrass, each had two different rust fungi on their leaves, a not unusual situation for the grasses. At least one rust was consistently present on three of the grass hosts by the end of the growing season on all prairies. The disease situation was different with Indian grass. A parasitic rust occurs on Indian grass leaves, but it is uncommon in Iowa. The most common and destructive pathogen on Indian grass is an imperfect fungus, *Stagonospora simplicior*, a leaf spot pathogen. This same fungus also produces characteristic large elliptical lesions with surrounding chlorotic tissue on leaves of big bluestem and little bluestem throughout the season. Tar spot develops on the leaves of big bluestem and little bluestem late in the season, usually in August.

Table 1. Fungal parasites of the most common tallgrass prairie grasses (Poaceae) of selected Iowa prairies.

	Prairies										
Host & Fungus	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Andropogon gerardii (big bluestem)											
Rusts											
Puccinia andropogonis	x	x	x	x	x	x	x	x	x	x	x
Uromyces andropogonis					x						
Smuts											
Sphacelotheca occidentalis	x	x	x	x			x				
Ergot											
Claviceps purpurea								x			
Tar spot											
Phyllachora luteo-maculata	x	x	x	x		x	x	x	x	x	x
Leaf Spots											
Ascochyta agropyrina				x							
Ascochyta brachypodii	x				x						
Ascochyta sorghi	x										
Colletotrichum caudatum	x	x									
Colletotrichum graminicola						x					
Septoria andropogonis					x		x				
Stagonospora simplicior	x	x	x	x	x	x	x	x	x	x	x
Sphaerellopsis filum (On *Puccinia andropogonis* pustules)	x										
Schizachyrium scoparium (little bluestem)					a			a			
Rust											
Puccinia andropogonis	x						x	x		x	x
Tar spot											
Phyllachora luteo-maculata	x	x									x
Leaf spots											
Colletotrichum caudatum				x			x				
Colletotrichum graminicola			x					x			x
Stagonospora simplicior	x		x	x	x		x	x		x	
Sphaerellopsis filum (On *Puccinia andropogonis* pustules)								x			
Sorghastrum nutans (Indian grass)											
Leaf spots											
Colletotrichum caudatum		x		x		x	x			x	
Pseudoseptoria donacis				x							
Stagonospora simplicior	x	x	x	x			x			x	
Panicum virgatum L. (switchgrass)											
Rusts											
Puccinia emaculata		x		x		x		x		x	
Uromyces graminicola				x	x	x	x				x
Leaf spots											
Colletotrichum graminicola		x	x	x	x	x	x		x	x	x
Elsinoe panici	x	x	x	x		x	x		x	x	

a = host plant not collected

Even though the black sclerotia of ergot are common in the florets of open-pollinated grasses such as western wheat grass, rye and brome, this disease is seldom present on the tallgrass prairie grasses. It has been collected once during this project, on big bluestem at Sheeder prairie.

Although the smut fungi have been significant destructive parasites on agronomic grasses, the only smut fungus recorded on the native prairie grasses in this report is kernel smut of big bluestem, *Sphacelotheca occidentalis*. It occurs only in the native prairies of the northwestern portion of the state, although it is also present on planted prairies elsewhere in the state. Another smut of big bluestem, *Sorosporium provinciale*, is present on native prairies only in southern Iowa and destroys the entire inflorescences of diseased host plants.

Leaf spots, usually caused by species of imperfect fungi, occur on all of the prairie grasses. Some fungus species can parasitize several grass hosts, such as *Stagnospora simplicior* on leaves of Indian grass, big bluestem, and little bluestem (Table 1). Conversely, *Elsinoë panici* is a destructive leaf pathogen only on switchgrass. It does not parasitize other prairie species of *Panicum*, but can be lethal for its switchgrass host.

Table 2. Fungal parasites of common legume (Fabaceae) hosts of selected Iowa prairies.

	Prairies										
Host & Fungus	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Amorpha canescens (lead plant)									a	a	
Rust											
Uropyxis amorphae	x				x	x	x	x			x
Desmodium canadense (tick-trefoil)											
Rust											
Uromyces hedysari-paniculati		x	x		x	x	x			x	x
Powdery mildew											
Microsphaera diffusa		x	x		x					x	x
Black mildew											
Parodiella hedysari		x				x	x				
Leaf spots											
Cercospora desmodiicola		x			x	x	x	x			
Gloeosporidiella desmodii							x				
Phyllosticta desmodii					x	x					
Ramularia desmodii						x	x		x		x
Sphaerellopsis filum (on *Uromyces hedysari-paniculati* pustules)						x					
Lathyrus venosus (bushy vetchling)	a					a		a	a	a	
Rust											
Uromyces fabae		x	x	x	x		x				x
Downy mildew											
Peronospora trifoliorum											x
Leaf spot											
Cercospora lathyrina					x						
Lespedeza capitata (bush clover)	a			a	a	a			a		
Rust											
Uromyces lespedezae-procumbentis			x				x			x	x
Tar spot											
Phyllachora lespedezae										x	x
Pediomelum argophyllum (scurf pea)	a						a	a	a	a	a
Rust											
Uromyces psoralea var. *argopyllae*			x	x		x	x				
Leaf spot											
Colletotrichum psoraleae			x	x	x	x					

a = host plant not collected

Rusts, species of *Uromyces* and *Uropyxis*, are the commonest parasitic fungi on the legume hosts (Table 2). *Lathyrus venosus* often is damaged severely by the extensive development of rust by mid-summer. However, two leaf-surface inhabiting fungi are the most destructive on tick-trefoil. Powdery mildew, characterized by a grayish-white covering of fungus mycelium on the leaf surfaces, and black mildew, with a jet black, external, leaf covering, may severely inhibit the development of young leaves and stems. The resulting dwarfed plants struggle to survive.

Table 3. Fungal parasites of most common composite hosts (Asteraceae) of selected Iowa prairies.

	Prairies										
Host & Fungus	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Artemesia ludoviciana (prairie sage)											
Rust											
Puccinia similis			x	x						x	x
Leaf spot											
Nematostoma occidentalis	x	x	x	x	x	x	x	x	x	x	x
Aster simplex (panicled aster)	a		a	a						a	
Rusts											
Coleosporium asterum		x			x			x			x
Puccinia cnici-oleracea		x						x	x		x
White smut											
Entyloma compositarum						x					
Powdery mildew											
Erysiphe cichoracearum		x						x			
Leaf spots											
Ascochyta compositarum		x			x			x	x		
Cercosporella virgaureae								x			
Placosphaeria haydeni						x	x				x
Septoria atropurpurea					x	x					x
Coreopsis palmata (prairie coreopsis)	a						a		a	a	
Leaf spots											
Cercospora coreopsidis						x					x
Phyllosticta coreopsidis			x	x							
Septoria coreopsidis		x	x		x			x			x
Helianthus grosseserratus (sawtooth sunflower)	a										
Rust											
Puccinia helianthi		x	x	x	x	x	x	x	x	x	x
Downy mildew											
Plasmopara halstedii									x		x
Powdery mildew											
Erysiphe cichoracearum		x	x				x			x	
Leaf spots											
Colletotrichum helianthi								x			
Septoria helianthi						x					
Liatris aspera Michx. (rough blazing star)	a						a	a	a		
Leaf spot											
Septoria liatridis		x	x	x	x	x				x	x
Ratibida pinnata (grayhead coneflower)										a	
White smut											
Entyloma compositarum	x	x	x	x	x	x	x	x	x		x
Downy mildew											
Plasmopara halstedii								x			
Leaf spot											
Septoria infuscata								x			
Solidago canadensis (Canada goldenrod)	a							a			
Rust											
Coleosporium asterum		x	x	x		x	x			x	x
Leaf spots											
Ascochyta compositarum					x						
Cercospora stomatica			x						x		
Colletotrichum dematium		x									
Septoria virgaureae		x	x	x			x		x		x

a = host plant not collected

Rusts, caused by *Puccinia* and *Coleosporium* species, are common on the aster, sunflower, and goldenrod species presented here (Table 3). The same rusts, or other species in these genera, also are common on the other aster, sunflower, and goldenrod species of these prairies. The other composite hosts in Table 3 have a different range of common fungus parasites. White smut, a leaf spot smut causing white to yellowish spots, was present wherever grayhead coneflower was observed. It occurs throughout the season, but the round to oval white spots are not well delimited and are less obvious early in the season. *Nematostoma occidentalis*, identified in Table 3 as a leaf spot, is an ascomycete that develops black superficial ascocarps on the leaves of prairie sage. They could be interpreted easily as ascocarps of a powdery mildew, but the fungus does not develop the surface white mycelium of a powdery mildew. The black ascocarps may develop in sufficient number to impart a characteristic dark gray color to the leaves. These diseased leaves also may be less than normal size.

The miscellaneous species of common prairie plants summarized in Table 4 often are parasitized by rusts, usually by *Puccinia* species. Rose leaf rust, *Phragmidium rosae-arkansanae,* is very common on wild rose species. Indefinite chlorotic areas develop on the upper leaf surface as orange powdery pustules of urediospores and superficial clusters of black teliospores are formed on the lower leaf surface. The other common rose rust, *Phragmidium speciosum,* is evidenced by orange pustules of spores on the leaves or fruits in early summer and extensive black crusts of teliospores on the stems later in summer or early fall. Leaf spots also are common on rose.

Leaf spot fungi are the most frequently encountered parasites on the anemones, but *Puccinia anemones-virginianae,* a rust characterized by mounds of dark teliospores on the leaves, is expected by mid-summer.

The rusts on common milkweed and on bastard toadflax are evidenced in late May or June by clusters of white-rimmed, orange, spore-producing structures (aecia) on the leaves. These occur in spots on the leaves and are followed by killing of portions of the leaf or entire leaves. These rusts develop on the alternate grass hosts later in the summer, forming different spore-producing structures on the grass host. For example, *Puccinia andropogonis* produces clusters of cup-like orange structures (aecia) on bastard toadflax in early summer, then later produces pustules of orange-red spores (uredia) and eventually black spores (telia) on the leaves of big bluestem and little bluestem.

Powdery mildew, *Erysiphe cichoracearum*, often is well developed on leaves of wild bergamot, the superficial mycelium giving the leaves a gray color and a powdery appearance. The most common fungus parasite on rattlesnake master is *Cylindrosporium* leaf spot. The rectangular elongate spots may eventually coalesce, resulting in major destruction of leaf tissue as the season progresses.

Table 4. Fungal parasites of common prairie plant hosts (various families) of selected Iowa prairies.

	Prairies										
Host & Fungus	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Anemone canadensis (Canada anemone)	a							a		a	
Rust											
Puccinia anemones-virginianae					x						x
Downy mildew											
Plasmopara pygmaea		x			x	x					x
Leaf spots											
Phleospora anemones		x			x	x			x		
Ramularia didyma		x	x	x		x	x				x
Anemone cylindrica (thimble weed)		a			a				a		
Rust											
Puccinia anemones-virginianae	x					x	x			x	x
Leaf spots											
Phleospora anemones	x		x	x		x	x	x			
Phyllosticta anemonicola											x
Septoria anemones						x					
Asclepias syriaca (common milkweed)					a			a		a	
Rusts											
Puccinia chloridis	x					x					
Puccinia seymouriana		x		x					x		x
Leaf spots											
Cercospora clavata	x	x	x			x	x		x		
Cercospora venturioides				x		x					x
Colletotrichum fusarioides		x									
Comandra umbellata (bastard toadflax)											
Rust											
Puccinia andropogonis	x	x		x	x	x	x	x	x	x	x
Leaf spot											
Cercospora comandrae	x					x					
Eryngium yuccifolium (rattlesnake master)	a			a	a				a	a	
Leaf spots											
Cylindrosporium eryngii		x	x			x	x	x			x
Septoria eryngicola						x					
Monarda fistulosa (bergamot)		a			a		a				a
Rust											
Puccinia menthae			x			x		x			
Powdery mildew											
Erysiphe cichoracearum	x		x	x		x		x		x	
Leaf spot											
Ramularia brevipes						x					
Phlox pilosa (prairie phlox)	a									a	
Rust											
Uromyces acuminatus						x	x	x	x		x
Leaf spots											
Ascochyta phlogis			x								
Cercospora omphacodes		x		x	x	x	x	x	x		x
Septoria phlogis						x					
Rosa arkansana (rose)											a
Rusts											
Phragmidium rosae-arkansanae		x	x	x	x	x	x	x		x	
Phragmidium speciosum			x			x	x	x	x		
Leaf spots											
Cercospora rosicola	x	x	x	x	x	x		x	x	x	
Discosia artocreas					x	x					
Marssonina rosae							x				
Seimatosporium discosioides		x									
Zizia aurea (golden alexanders)	a				a					a	
Leaf gall											
Physoderma pluriannulatum							x		x		x
Leaf spots											
Cercospora ziziae		x	x	x		x	x	x	x		x
Septoria ziziae		x									
Stagnospora thaspii		x						x			

a = host plant not collected

Discussion

Parasitic fungi have long been recognized as significant factors in the establishment, survival, growth, and yield of cultivated plants. However, little attention has been given to fungi as factors in these critical events for native plants (Burdon, 1987). Fungi, usually those species already present in the soil, may interfere with plant establishment by causing seedling damping-off or root rots. We have not attempted to consider these fungi or other fungi associated with underground plant structures in the research project discussed in this paper.

Fungi may affect the survival of individual plants or alter their competitive ability. Leaf spots may cause immediate necrosis of leaf tissue, resulting in significant loss of photosynthetic tissue. The effects of tar spot fungi, leaf smuts, powdery mildew, and rusts may be more subtle and less immediately expressed. When the rusts produce spores in local pustules, the leaf epidermis and cuticle are broken, causing an immediate effect on transpiration rates.

Still other fungi may interfere with reproduction of the diseased plants. *Epichloe typhina* mycelium may invade the apical meristem of host grass species so that the inflorescence does not develop; which is the disease situation referred to as choke (Webster, 1980). Mycelium of *Claviceps* species, ergot, invades individual florets of grasses or sedges, replacing the ovary with a mass of fungus tissue that develops as a hard black sclerotium (Webster, 1980). Smut fungi that replace individual florets or entire inflorescences are common parasites on the grasses. These smut fungi may be perennial in their grass hosts, destroying floral tissue each year (Snetselaar and Tiffany, 1990, 1992).

As more complete information becomes available about the presence and incidence of these fungi (Tiffany et al., 1990), we can begin to evaluate their influence on competitive ability and survival of their host plants and interactions with the numerous other factors that will determine successful establishment and persistence of prairie plants. Resistance to penetration and subsequent establishment of a fungus in a host plant certainly is influenced, if not prevented, by the genetic components of the plant. Over the hundreds of years that prairie communities have been in existence with ongoing and various biological and environmental interactions, genetically susceptible individuals have consistently been at a disadvantage for survival or reaching reproductive maturity.

Plant-fungal disease interactions are constantly changing. As more virulent strains of fungal pathogens develop or as new fungi are introduced into an area, competitive abilities of the host plants may be altered. For example, kernel smut of big bluestem in Nebraska was reported by Dunleavy (1956). It was first observed in Iowa in 1978 on Cayler Prairie in the northwest part of the state (Knaphus and Tiffany, 1986). As reported in Table 1, it has now been observed in prairies throughout the northwest portion. Kernel smut on big bluestem has been observed in new prairie plantings in other areas of the state, where this fungus does not occur on big bluestem on native prairies. Mycelium of kernel smut is perennial in the diseased plant and affects not only floral production but also vegetative vigor of the plant (Snetselaar and Tiffany, 1991). The impact of this fungus on its host population in Iowa prairies is still incompletely understood.

As we establish a more complete record of the fungus parasites on plants of individual prairies, we may be in a position to use this information to develop maintenance strategies that will control them or minimize their impact, particularly on our small, widely separated, remnant prairies. At the least, we will have information on another component involved in the dynamic mix of biological and environmental factors that shape our prairies.

Literature Cited

Burdon, J. 1987. Diseases and Plant Population Biology. Cambridge University Press, London. 208 pp.

Cummins, G.B. 1971. The Rust Fungi of Cereals, Grasses and Bamboos. Springer-Verlag, New York, NY. 570 pp.

Cummins, G.B. 1978. Rust Fungi of Legumes and Composites in North America. University of Arizona Press, Tucson, AZ. 424 pp.

Davis, J.J. 1903. Third supplementary list of parasitic fungi of Wisconsin. Transactions of the Wisconsin Academy of Science 14:83-106.

Davis, J.J. 1926. Notes on parasitic fungi in Wisconsin XII, XIII, XIV. Transactions of the Wisconsin Academy of Science 22:155-192.

Dunleavy, J. 1956. Kernel smut of big bluestem. Phytopathology 46:116-120.

Farr, D.F., G.F. Bills, G.P. Chamuris and A.Y. Rossman. 1989. Fungi on plants and plant products in the United States. Publ. no. 5, Contributions from the U.S. National Fungus Collections. American Phytopathological Society, St. Paul, MN. 1252 pp.

Fischer, G.W. 1953. Manual of the Northern American Smut Fungi. Ronald Press, New York, NY. 343 pp.

Frankland, J.C., J.N. Hedger and M.J. Swift. 1982. Decomposer Basidiomycetes: Their Biology and Ecology. Cambridge University Press, London. 355 pp.

Gabel, A.W. and L.H. Tiffany. 1987. Life history of *Elsinoë panici*. Proceedings of the Iowa Academy of Science 94:121-127.

Gilman, J.C. 1932. First supplemental list of parasitic fungi from Iowa. Iowa State College of Journal of Science 6:357-365.

Gilman, J.C. 1949. Second supplementary list of parasitic fungi from Iowa. Iowa State College Journal of Science 23:261-272.

Gilman, J.C. and W.A. Archer. 1929. The fungi of Iowa parasitic on plants. Iowa State College Journal of Science 3:299-502.

Greene, H.C. 1940. Notes on Wisconsin parasitic fungi. I. Transactions of the Wisconsin Academy of Science 32:77-83.

Greene, H.C. 1968. Notes on Wisconsin parasitic fungi. XXXIII. Transactions of the Wisconsin Academy of Science 56:263-280.

Knaphus, G. and L.H. Tiffany. 1986. Kernel smut of big bluestem in Iowa. Proceedings of the Iowa Academy of Science 93:1 (Abstract).

Read, D.J., D.H. Lewis, A.H. Fitter and I.J. Alexander. 1992. Mycorrhizas in ecosystems. C.A.B. International, Wallingford, U.K. 419 pp.

Snetselaar, K. and L.H. Tiffany. 1990. Light and electron microscopy of sorus development in *Sorosporium provinciale*, a smut of big bluestem. Mycologia 82:480-492.

Snetselaar, K. and L.H. Tiffany. 1991. A Study of *Sphacelotheca occidentalis*, cause of kernel smut of big bluestem. Journal of Iowa Academy of Science 98(3):145-152.

Snetselaar, K.M. and L.H. Tiffany. 1992. Diseases of big bluestem caused by smut fungi. Pages 17-20. In: D.D. Smith and C.A. Jacobs (eds). Recapturing a Vanishing Heritage. Proceedings of the Twelfth North American Prairie Conference.

Sprague, R. 1950. Diseases of Cereals and Grasses in North America. (Fungi, except Smuts and Rusts). Ronald Press, New York, NY. 538 pp.

Trelease, W. 1884. Preliminary list of the parasitic fungi of Wisconsin. Transactions of the Wisconsin Academy of Science 6:106-144.

Tiffany, L.H., J.F. Shearer and G. Knaphus. 1990. Plant parasitic fungi of four tallgrass prairies of northern Iowa: Distribution and prevalence. Journal of the Iowa Academy of Science 97:157-166.

Webster, J. 1980. Introduction to Fungi, 2nd edition. Cambridge University Press, Cambridge. 669 pp.

Effect of a Prescribed Burn on the Small Mammals of an Old Field in the Prairie Peninsula Area of Ohio

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Abstract. The effect of fire on the meadow vole *Microtus pennsylvanicus* and the northern short-tailed shrew *Blarina brevicauda* was studied between April and October, 1993. Animals in a 16,000 m^2 field were live-trapped in April, and a 4000 m^2 plot (containing 19 of the 78 traps in the field) was burned three days later. Trapping was done periodically in the entire area through 17 October. Compared to the burned area, proportionally more individuals of both species from the unburned area were recaptured after the burn, but the difference was not statistically significant for either species. *M. pennsylvanicus* and *B. brevicauda* captures in the burned area dropped to nearly zero for 4 and 7 weeks respectively, but both species' use of the area returned to preburn levels within 3 months of the fire. These observations suggest that, in small preserves, small mammal diversity is enhanced by small fires that do not burn the entire area at one time.

Key words: Abandoned field, fire, *Microtus*, *Blarina*, small mammals, Ohio.

Introduction

The impact of fire on small mammals in grasslands has been studied extensively (Kaufman *et al.* 1990), but the fate of individuals, their survival and movements, and the pattern of reinvasion of the burned area warrant further consideration (Clark and Kaufman 1990). This study concerned the impact of fire on meadow voles (*Microtus pennsylvanicus*) and northern short-tailed shrews (*Blarina brevicauda*) in a grass-covered field in Hardin County, Ohio. The direct effect of the fire on individual persistence on the grid (a potential correlate of individual survival), the pattern of use of the burned area in the months after the fire, and differences in responses of the two species to the fire were evaluated.

Methods

The field is irregular in shape, about 1.6 ha in area, and surrounds a 0.6 ha farm pond. It is bounded by a blacktop road, mowed yards, and agricultural fields. It is dominated by fescue (*Festuca* spp.) and bluegrass (*Poa* spp.), with clumps of reed canary grass (*Phalaris arundinacea*) and patches of goldenrod (*Solidago* spp.), teasel (*Dipsacus sylvestris*), and Canada thistle (*Cirsium arvense*). The pond is fringed by willows (*Salix* spp.), cottonwoods (*Populus deltoides*), and silver maples (*Acer saccharinum*).

The grid consisted of 78 folding Sherman live-traps (9x3x3 cm), placed one per station, with 14 m spacing between stations. Each captured animal was removed from the trap, identified to species, sexed, aged, and toe clipped (or the toe clip number was read on recaptured animals) to identify the individual. Traps were set and checked six times during 25-27 April 1993, once on each of six days from 1 May-4 June 1993, once on each of three days from 7-28 July 1993, and six times during 15-17 October 1993.

A 4000 m^2 (50 m x 80 m) area of the field was burned in two afternoons, 29 and 30 April. Two days were required because rain interrupted the burn shortly after it started on the first day. The burn was even and complete except for an approximately 4 m wide strip along the pond overflow, which burned unevenly. Charred grass was left on the surface throughout the area, and 80-90% of the area burned to this charred grass condition.

A log likelihood (G) test for independence (2x2 table using William's correction factor) was run for each species to determine whether the animals captured outside the burned area before the fire survived (as indicated by persistence on the grid) better than those captured inside the burned area before the fire. Individuals captured in both areas (burned and unburned) before the fire were eliminated from the analysis. There were only two such individuals, one of each species.

The trapping sessions were divided into three time periods: the Preburn, Postburn, and Recovery periods. The Preburn period consisted of all trapping before the fire. The Postburn and Recovery periods differed for the two species. The Postburn period started with the first trapping session after the fire and ended when the species began to be captured consistently in the burned area. The Recovery period included all remaining trapping sessions.

A log likelihood test (using a 2 x 3 contingency table and William's correction factor) was run for each species to determine whether the three periods differed with respect to the proportion of individuals captured in the burned area. If so, a log likelihood test (2 x 2 table, William's correction factor) was used to determine whether the Preburn and Recovery periods differed in the proportion of individuals of each species captured in the burned area.

Results

For each species, half or fewer of the individuals captured in the burned area before the fire were recaptured after the fire. On the other hand, 70% or more of the individuals captured before the fire in the area not burned were recaptured after the fire (Table 1). The animals that moved out of the area cannot be separated from those actually killed by the fire, but the data do show greater persistence on the grid for animals that presumably were not exposed directly to the fire. However, the data are not statistically significant ($G = 1.8$, $df = 1$, $p > 0.05$ for *Blarina*, $G = 2.3$, $df = 1$, $p > 0.05$ for *Microtus*), and so are only suggestive.

Table 1. Number of short-tailed shrews and meadow voles captured in unburned and burned old field both before and after fire and only before fire.

Treatment	Shrews		Voles	
	Before and after fire	Only before fire	Before and after fire	Only before fire
Unburned	10	2	14	6
Burned	3	3	3	5

The meadow vole recovery period began 4 to 5 weeks after the fire, and only two individuals were captured (once each) in the burned area during the four trapping sessions of the Post-burn period (Table 2). The proportion of individuals captured in the burned area differed significantly among the three periods ($G = 6.5$, $df = 2$, $p < 0.05$), suggesting that the fire had an effect on the species' use of the burned area. The proportion of individuals captured in the burned area did not differ between the Preburn period and the Recovery period ($G = 0$, $df = 1$, $p > 0.05$), suggesting that the voles were using the burned area at preburn levels during the Recovery period.

Table 2. Number of individual short-tailed shrews and meadow voles captured in unburned and burned old field and the percentage of the individuals that were captured in the burned area.

Time period	Shrews			Voles		
	Unburned	Burned	% in Burn	Unburned	Burned	% in Burn
Preburn	13	7	35	20	7	26
Postburn	35	0	0	28	2	7
Recovery	41	11	21	62	23	27

Preburn was 23-25 April for both species, Postburn was 1 May-4 June for shrews and 1-21 May for voles, Recovery was 7 July-17 October for shrews and 28 May-17 October for voles.

The short-tailed shrew recovery period began between 7 and 11 weeks after the fire, and no shrews were captured in the burned area during the six trapping sessions of the Postburn period (Table 2). Again, the proportion of individuals captured in the burned area differed significantly among the three periods ($G = 17.1$, $df = 2$, $p < 0.05$), suggesting that the fire had a statistically significant effect on the species' use of the burned area. The proportion of individuals captured in the burned area did not differ significantly between the Preburn period and the Recovery period ($G = 1.3$, $df = 1$, $p > 0.05$), suggesting that shrews also used the burned area at preburn levels during the Recovery period.

Though no statistically significant difference can be shown, voles began using the burned area after the fire more quickly than did shrews. The meadow vole's proportional use of the burned area also approached its preburn use of the area more closely than did the shrew's (Table 2), though there was no statistically significant difference between Preburn and Recovery period use for either species. The fire in this abandoned field seemed to be more detrimental to short-tailed shrews than to meadow voles, but both were using the burned part of the field at or near preburn levels within 3 months of the fire.

Discussion

In general, shrews and voles responded negatively to fire, as expected from earlier studies (Kaufman *et al.* 1990, Schramm and Willcutts 1983, Springer and Schramm 1972). The greater persistence on the grid of individuals not exposed to the fire, though not statistically significant, is suggestive of mortality or emigration because of the fire. However, several reports suggest that mortality from direct effects of fire is low, except for the young of a species that uses aboveground nests and other special cases (Clark and Kaufman 1990, Erwin and Stasiak 1979, Kaufman *et al.* 1990, Schramm 1970). Perhaps the direct effects suggested in this study are artifacts of the small sample sizes, but the question bears further study. On the other hand, there is little doubt that, in keeping with other studies (Kaufman *et al.* 1990 and several studies quoted therein), shrew and vole use of the burned area decreased for several weeks after the fire.

The suggestion in the data that the short-tailed shrew's recovery was slower and less complete than that of the meadow vole seems reasonable, because the meadow vole feeds primarily on grass and can return to a burned area as soon as grass is sufficiently dense to supply cover. On the other hand, shrews are primarily insectivorous and so must await the recovery of the vegetation and the return of their invertebrate food supply, which is itself probably dependent on the recovery of the vegetation.

Despite these differences, both species' use of the burned area recovered to levels that were statistically indistinguishable from prefire levels before the end of the growing season. In studies of prairie fires, the recovery of fire negative species to prefire levels generally has taken one to several years (Kaufman *et al.* 1990 and studies quoted therein). Those studies involved larger burned areas and the authors predicted that the time required for reestablishing small mammal use of a burned area to preburn levels would be shorter for smaller areas. This study supports that contention.

This study also suggests that, if the small mammal fauna is a concern, prairie relicts should be burned in patches, with time for recovery between successive burns. Large burned areas, even those surrounded by habitat with animals available for reinvasion, are reoccupied more slowly than was the small area burned in this study. Reinvasion of completely burned, isolated prairie relicts would be even slower, because the animals would have to cross inhospitable areas to reach the prairie. Burning a fraction of the prairie allows the small mammal species a haven from which to reinvade as their habitat is restored by regrowth. As a result, the important functions small mammals perform in the prairie ecosystem (such as seed dispersal, mycorrhyzal spore dispersal, predation on insects and weed seeds, grazing, and providing food for higher-level predators) are restored quickly.

Literature Cited

Clark, B. K. and D. W. Kaufman. 1990. Short-term responses of small mammals to experimental fire in tallgrass prairie. Canadian Journal of Zoology 68:2450-2454.

Erwin, W. J. and R. H. Stasiak. 1979. Vertebrate mortality during the burning of a reestablished prairie in Nebraska. American Midland Naturalist 101:247-249.

Kaufman, D. W., E. J. Finck, and G. A. Kaufman. 1990. Small mammals and grassland fires. *In* S. L. Collins and L. L. Wallace (eds.) Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman, pp 46-80.

Schramm, P. 1970. Effects of fire on small mammal populations in a restored tall-grass prairie. *In* P. Schramm (ed.) The Proceedings of a Symposium on Prairie and Prairie Restoration. Knox College Biological Field Station, Special Publication No. 3. Galesburg, IL, pp 39-41.

Schramm, P. and B. J. Willcutts. 1983. Habitat selection of small mammals in burned and unburned tallgrass prairie. *In* R. Brewer (ed.) Proceedings of the Eighth North American Prairie Conference. Western Michigan University, Kalamazoo, pp 49-55.

Springer, J. T. and P. Schramm. 1972. The effects of fire on small mammal populations in a restored prairie with special reference to the short-tail shrew. *In* J. H. Zimmerman (ed.) Proceedings of the Second Midwest Prairie Conference. University of Wisconsin, Madison, pp 91-96.

Small-Mammal Use of Experimental Patches of Tallgrass Prairie: Influence of Topographic Position and Fire History

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Abstract. We examined the influence of topographic position and fire history on use of 44 small patches (each 0.025 ha) of tallgrass prairie by rodents and shrews. The study was conducted on the Konza Prairie Research Natural Area during 15 sampling periods from November 1982 to October 1992. We caught nine species of rodents and two of shrews on the site, but only hispid cotton rats (*Sigmodon hispidus*), deer mice (*Peromyscus maniculatus*), prairie voles (*Microtus ochrogaster*), western harvest mice (*Reithrodontomys megalotis*), and Elliot's short-tailed shrews (*Blarina hylophaga*) were common. Overall, cotton rats selected lowland prairie but showed no response to fire history, whereas deer mice selected upland and annually burned prairie. Prairie voles, white-footed mice (*Peromyscus leucopus*), and western harvest mice showed no selection for topographic position but did avoid annually burned patches. Finally, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) selected upland prairie but did not respond to fire history.

Key words. habitat selection, small mammals, rodents, shrews, fire, topography, tallgrass prairie, Kansas

Introduction

Topography and fire influence the spatial distributions and local abundances of small mammals in tallgrass prairie. For example, Peterson *et al.* (1985) assessed responses of small mammals to fire and topography in 44 small fire-treatment patches (each 0.025 ha) on an experimental site (2 ha) that contained both upland and lowland prairie. At this site, deer mice (*Peromyscus maniculatus*) were most common in burned, upland prairie, whereas western harvest mice (*Reithrodontomys megalotis*) were more common in unburned, lowland prairie. Further, prairie fires affected many species of small mammals, with some responding positively and others negatively to conditions created by fire (Kaufman, D. W. *et al.* 1983; Kaufman, D. W. *et al.* 1990b). Differential use of topographic features also was noted for small mammals living within the Flint Hills tallgrass-prairie landscape (Kaufman, G. A. *et al.* 1988; Kaufman, G. A. *et al.* this volume).

Weather conditions, environmental factors, and population abundances of individual species of small mammals can vary highly among years. Because the effects of fire and topography on individual species of small mammals can vary with those year-to-year shifts in population abundances; weather conditions (e.g., precipitation and summer temperature); and environmental conditions (e.g., primary productivity), multiannual studies of small mammals are necessary to establish general, rather than year-specific, patterns of habitat use. Because of the likelihood of temporal variation in habitat use by small mammals in prairie habitats, we periodically sampled small mammals from autumn 1982 through autumn 1992 on the site used by Peterson *et al.* (1985). In this paper, we examine the effects of topographic position and fire history on use of tallgrass prairie by rodents and shrews on this experimental site. Further, we assess temporal variation in habitat use by the four common species, the hispid cotton rat (*Sigmodon hispidus*), deer mouse, prairie vole (*Microtus ochrogaster*), and western harvest mouse, found on the site.

Methods

Our study site was located on the Konza Prairie Research Natural Area, Manhattan, Kansas (for description of Konza Prairie and mammals of the site, see Finck *et al.* 1986; Hulbert 1985; and Kaufman, G. A. *et al.* 1988). We live-trapped small mammals in 44 patches (each 10 x 25 m 0.025 ha) during 15 sampling periods from November 1982 to October 1992. Patches were arranged in four rows of 11 and separated from each other and surrounding prairie by mowed boundary strips (see Fig. 1). Two rows were in upland prairie (established in 1982), and two were in lowland prairie (established in 1980); the maximum difference in elevation between lowland and upland was about 10 m. Three patches in each row were burned annually in March (n=4), May (n=4), or November (n=4), whereas the other patches were burned in spring every other year (n=8), in spring every fourth year (n=16), in summer at irregular intervals (n=4), or remained unburned (n=4) during the study. Patches and boundary strips covered approximately 2 ha and were situated in a watershed unit (HQB) that was burned during springs in 1979, 1983-86, and 1988-92.

We live-trapped small mammals for 4 days during each sampling period. Trapping was conducted on 11-12 and 20-21 November 1982, 3-6 March 1983, 25-28 July 1983, 30 September-3 October 1983, 10-11 and 15-16 September 1987, 3-4 and 16-17 October 1989, 21-22 and 27-28 April 1990, 3-4 and 6-7 November 1990, 27-28 February and 8-9 March 1991, 14-17 May 1991, 10-13 July 1991, 6-9 September 1991, 6-9 December 1991, 3-6 March 1992, and 6-7 and 14-15 October 1992. During spring sampling periods of April 1990 and May 1991, small mammals were live-trapped after annual patches had been burned in November 1989 and March 1990 and November 1990, March 1991, and May 1991, respectively. We set four large Sherman live-traps (7.6 x 8.9 x 22.9 cm) per plot and baited them with a mixture of peanut butter and oatmeal. Nesting material (polyester fiberfill) was placed in traps during autumn, winter, and spring sampling periods.

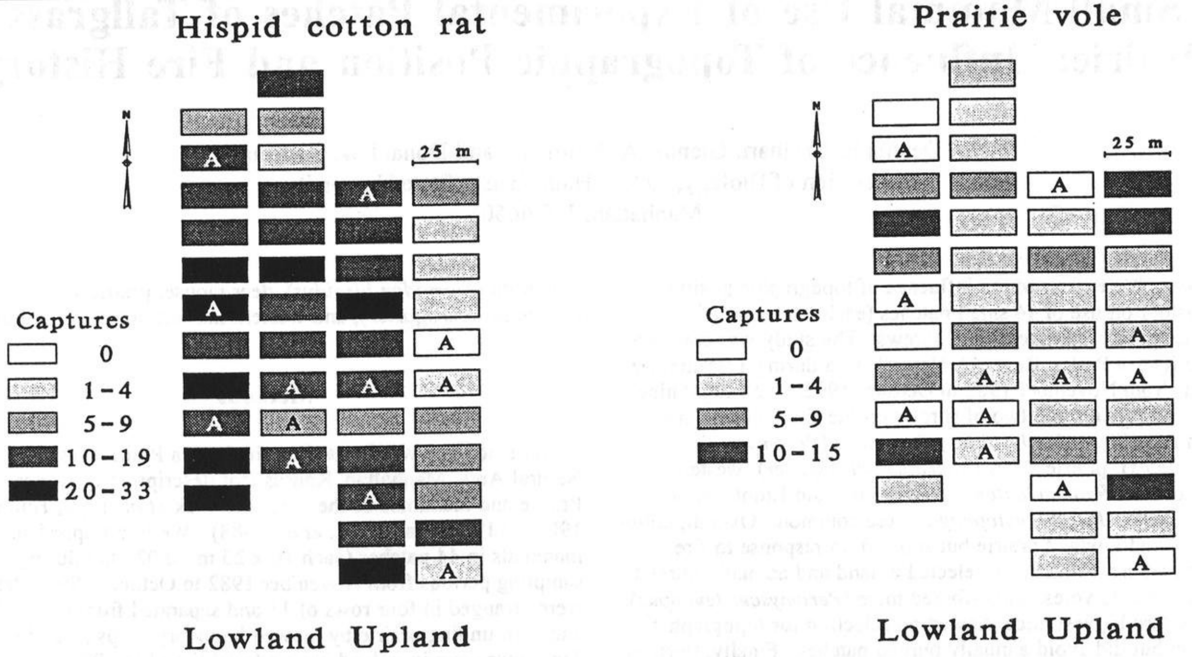

FIG. 1. Distributions of 579 captures of hispid cotton rats and 165 captures of prairie voles in experimental patches. Annually burned patches are marked with an A, and open area between patches represents mowed boundary strips.

Table 1. Numbers of captures of seven species of small mammals by topographic position and fire history on Konza Prairie. Numbers of upland and lowland and numbers of annually and nonannually burned patches are given in parentheses.

	Topography			Fire		
	Upland	Lowland	G^a	Annual	Nonannual	G^a
Species	(22)	(22)		(12)	(32)	
Hispid cotton rat	223	356	30.8***	137	442	3.9*
Deer mouse	189	75	50.9***	95	169	9.5**
Prairie vole	86	79	0.3	8	157	56.8***
Western harvest mouse	48	53	0.2	20	81	3.0
Elliot's short-tailed shrew	30	30	0.0	13	47	1.0
White-footed mouse	9	11	0.2	1	19	6.8**
Thirteen-lined ground squirrel	10	3	4.0*	3	10	0.1

[a] G = log-likelihood ratio G statistic (goodness of fit analysis results, * = $P < 0.05$, ** = $P < 0.01$, and *** = $P < 0.001$).

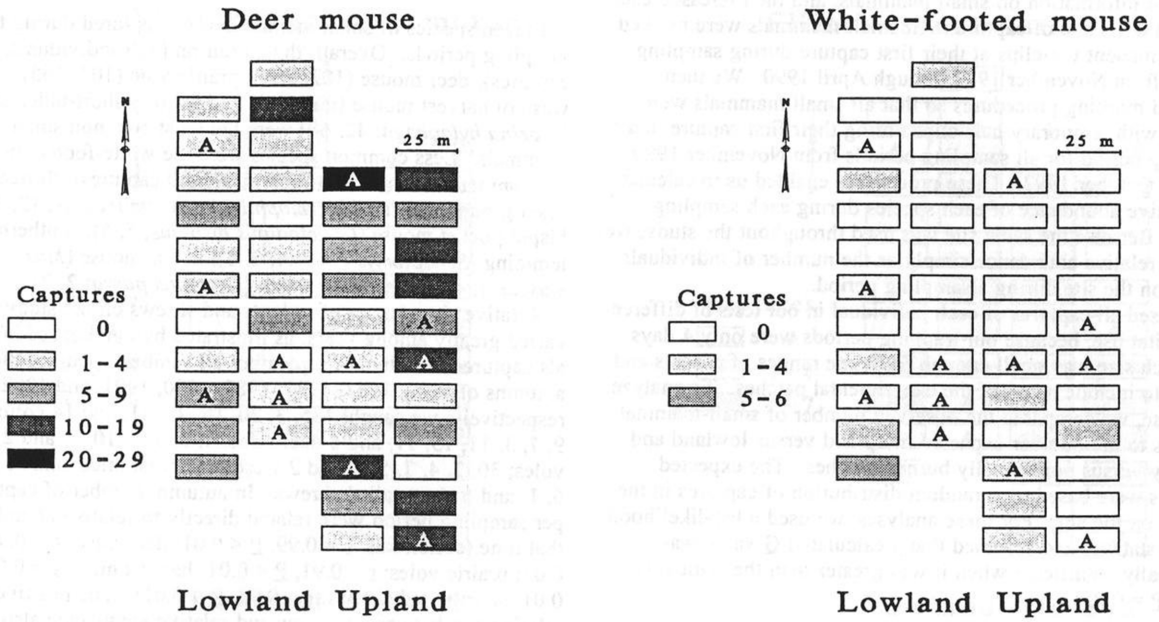

FIG. 2. Distributions of 264 captures of deer mice and 20 captures of white-footed mice in experimental patches. Annually burned patches are marked with an A, and open area between patches represents mowed boundary strips.

Table 2. Numbers of captures of hispid cotton rats and deer mice in upland and lowland prairie by sampling period. Numbers of upland and lowland patches are given in parentheses.

	Cotton rat			Deer mouse		
Sampling Period	Upland (22)	Lowland (22)	*G*[a]	Upland (22)	Lowland (22)	*G*[a]
AUTUMN						
November 1982	60	141	33.6***	22	4	13.7***
Sept/Oct 1983	0	3	NT	5	11	2.3
September 1987	8	26	10.0**	7	0	NT
October 1989	2	15	11.3***	21	4	12.7***
November 1990	55	79	4.3*	29	9	11.1***
September 1991	40	35	0.3	9	18	3.1
October 1992	9	7	0.3	7	7	0.0
WINTER						
December 1991	0	11	15.2***	3	0	NT
EARLY SPRING						
March 1983	0	0	NT	3	1	NT
Feb/March 1991	0	11	15.2***	4	0	NT
March 1992	0	4	NT	18	0	25.0***
LATE SPRING						
April 1990	10	8	0.2	16	4	7.7**
May 1991	7	5	0.3	16	13	0.3
SUMMER						
July 1983	0	5	NT	13	2	9.0**
July 1991	32	6	19.5***	16	2	12.4***

[a] *G* = log-likelihood ratio *G* statistic and NT = not tested (goodness of fit analysis results, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

We checked traps each morning, recorded location (patch type) and basic information on small mammals, and then released each mammal at its site of capture. All small mammals were marked with permanent toe-clips at their first capture during sampling periods from November 1982 through April 1990. We then switched marking procedures so that all small mammals were marked with temporary hair-clips during their first capture in a sampling period for all sampling periods from November 1990 through October 1992. These procedures enabled us to calculate the relative abundance of each species during each sampling period. Because the same site was used throughout the study, we express relative abundance simply as the number of individuals caught on the site during a sampling period.

We used all captures of each individual in our tests of differential habitat use, because our trapping periods were only 4 days and patch size was small enough for home ranges of rodents and shrews to include many of the experimental patches. To analyze patch use, we compared the observed number of small-mammal captures to the number expected in upland versus lowland and annually versus nonannually burned patches. The expected numbers were based on a random distribution of captures in the patches on the site. For these analyses, we used a log-likelihood ratio G statistic and assumed that a calculated G-value was statistically significant when it was greater than the critical G-value ($P = 0.05$).

Results

Eleven species of small mammals were captured during the 15 sampling periods. Overall, the cotton rat (359 individuals, 579 captures); deer mouse (102, 264); prairie vole (104, 165); western harvest mouse (66, 101); and Elliot's short-tailed shrew (*Blarina hylophaga*; 42, 60) were the most common small mammals. Less common species were the white-footed mouse (*Peromyscus leucopus*; 13 individuals, 20 captures); thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*; 12, 13); hispid pocket mouse (*Chaetodipus hispidus*; 5, 5); southern bog lemming (*Synaptomys cooperi*; 4, 5); house mouse (*Mus musculus*; 4, 4); and least shrew (*Cryptotis parva*; 2, 2).

Relative abundances of rodents and shrews on the study site varied greatly among years, as illustrated by numbers of individuals captured in autumn (September-November). During the autumns of 1982, 1983, 1987, 1989, 1990, 1991, and 1992, respectively, we caught 135, 3, 20, 16, 73, 41, and 14 cotton rats; 9, 7, 3, 11, 15, 11, and 6 deer mice; 4, 0, 0, 0, 10, 7, and 2 prairie voles; 30, 2, 4, 7, 5, 1, and 2 western harvest mice; and 9, 0, 3, 4, 6, 1, and 6 short-tailed shrews. In autumn, number of captures per sampling period were related directly to relative abundance at that time (cotton rats: $r = 0.99$, $P < 0.01$; deer mice: $r = 0.98$, $P < 0.01$; prairie voles: $r = 0.91$, $P < 0.01$; harvest mice: $r = 0.99$, $P < 0.01$; short-tailed shrews: $r = 0.98$, $P < 0.01$). The positive relationship between captures and relative abundance also held across all 15 sampling periods for all five species ($r > 0.92$, $P < 0.01$ in all cases).

Table 3. Numbers of captures of hispid cotton rats, deer mice, and prairie voles in annually and nonannually burned patches by sampling period. Numbers of annually and nonannually burned patches are given in parentheses.

	Cotton rat			Deer mouse			Prairie vole		
Sampling Period	Annual (12)	Nonannual (32)	G^a	Annual (12)	Nonannual (32)	G^a	Annual (12)	Nonannual (32)	G^a
AUTUMN									
November 1982	57	144	0.1	2	24	6.4*	2	2	NT
Sept/Oct 1983	1	2	NT	3	13	0.6	0	0	-
September 1987	6	28	1.7	3	4	NT	0	0	-
October 1989	3	14	0.9	9	16	0.9	0	0	-
November 1990	29	105	2.2	16	22	3.9*	2	9	0.5
September 1991	21	54	0.0	11	16	2.3	0	15	9.6**
October 1992	6	10	0.8	3	11	0.3	0	3	NT
WINTER									
December 1991	3	8	0.0	0	3	NT	0	28	17.8***
EARLY SPRING									
March 1983	0	0	NT	2	2	NT	0	0	-
Feb/March 1991	0	11	7.0*	2	2	NT	0	21	13.4***
March 1992	0	4	NT	9	9	4.3*	0	24	15.3***
LATE SPRING									
April 1990	0	18	11.5***	11	9	6.8**	0	36	22.9***
May 1991	0	12	7.6**	8	21	0.0	1	13	3.7
SUMMER									
July 1983	1	4	NT	6	9	1.1	1	0	NT
July 1991	10	28	0.0	10	8	6.4*	2	6	NT

[a] G = log-likelihood ratio G statistic and NT = not tested (goodness of fit analysis results, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).illustrated in Fig. 2.

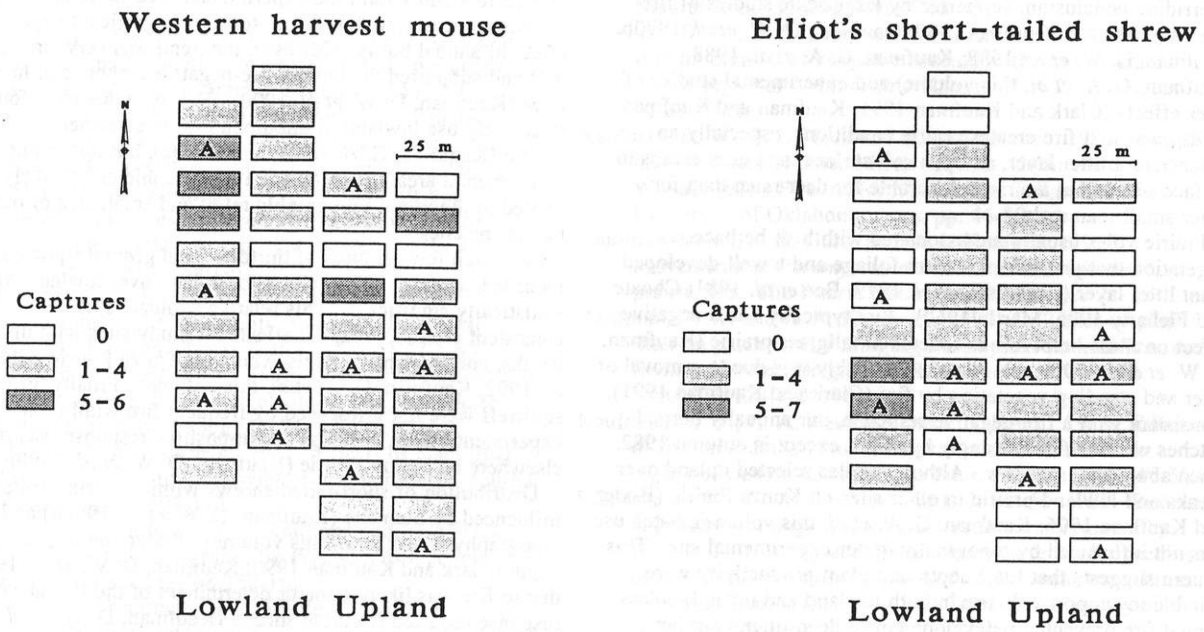

FIG. 3. Distributions of 101 captures of western harvest mice and 60 captures of Elliot's short-tailed shrews in experimental patches. Annually burned patches are marked with an A, and open area between patches represents mowed boundary strips.

Cotton rats selected lowland over upland prairie, whereas deer mice and ground squirrels selected upland over lowland prairie (Table 1; Figs. 1 and 2). However, patch use did vary among seasons and years for cotton rats and deer mice. For cotton rats, patches in lowland prairie typically were used over upland during autumn, winter, and spring; however, during summer 1991, cotton rats chose upland over lowland prairie (Table 2). Deer mice generally selected upland over lowland but did not exhibit this pattern during all sampling periods and tended to chose lowland over upland in autumns of 1983 and 1992 (Table 2).

Deer mice selected annually burned patches, whereas prairie voles and white-footed mice chose less frequently burned patches (Table 1; Figs. 1 and 2). A marginally negative effect of annual fire was noted ($0.09 > P > 0.08$) for western harvest mice (Table 1, Fig. 3). Differences in patch use associated with fire frequency occurred among seasons and years for cotton rats, deer mice, and prairie voles (Table 3). Overall, cotton rats showed no response to fire history (Table 1); however, avoidance of annually burned patches occurred in spring (Table 3). Deer mice generally selected annually burned patches during all seasons but did show variation in this response (Table 3). Prairie voles strongly avoided annually burned patches in all seasons tested, with the greatest response in winter-spring (Table 3).

Although captures of white-footed mice were unrelated to the upland-lowland pattern within the study site, captures were clustered in the southern end of the site (north half versus south half: $G = 13.3$, d.f. = 1, $P < 0.001$). The interaction of patch position and fire history on distribution of these woodland mice is illustrated in Fig. 2.

Discussion

The overall pattern for cotton rats, the most common species in our study, was selection of lowland over upland prairie and no effect of fire history. This pattern held for most, but not all summer-autumn periods. For example, cotton rats selected upland in summer 1991 and exhibited random use of upland and lowland in autumn 1991 and 1992. In contrast, habitat selection in late spring did not fit the overall or summer-autumn patterns; annual fire impacted patch use during spring, but topography did not. Summer-autumn use of lowland prairie (tall vegetation and high productivity) and spring avoidance of annual burns (little vegetative structure above a few cm) were consistent with a demonstrated association of cotton rats with tall, dense, herbaceous vegetation (Bee *et al.* 1981; Choate and Fleharty 1975; Fleharty and Mares 1973; Kaufman, D. W. *et al.* 1990a). Further, the shift by cotton rats from a fire-negative response in spring to a fire-neutral response in summer and autumn reflected the growth of abundant vegetation in both burned and unburned prairie.

Why cotton rats did not select lowland over upland prairie in summer-autumn 1991 and autumn 1992 is unknown. However, it is possible that the sutitability of vegetation for cotton rats in upland patches that were infrequently burned during summer-autumn could have increased during the study. Such changes could include increases in shrubs, forbs, and cool-season grasses (e.g., Kentucky bluegrass, *Poa pratensis*) in response to the absence of fire (Gibson and Hulbert 1987). Regardless of the causes of these atypical responses in summer-autumn 1991 and again in autumn 1992, habitat use in early spring 1991 and winter-early spring 1991-1992 suggest that lowland is the preferred habitat of cotton rats under the harsh conditions of winter-early spring. Therefore, whatever influenced habitat use during the more benign seasons of these years apparently did not impact habitat choice by cotton rats during the harsher seasons.

As expected from earlier studies on Konza Prairie (Kaufman, D. W. *et al.* 1990b; Kaufman, G. A. *et al.* 1988; Peterson *et al.* 1985), deer mice were associated positively with upland and annually burned prairie. Although these general associations were strong, distribution of captures suggested a preference for lowland in autumn 1983 and 1991, but no significant topographic selection in autumn 1992. It is interesting to note that both deer mice and cotton rats deviated from their general patterns in autumn 1991 and 1992, but the causes are unknown. Although variation in use of patches related to fire was evident, the overriding conclusion, supported by large-scale studies of fire effects (Clark and Kaufman 1990; Kaufman, D. W. *et al.* 1990b; Kaufman, D. W. *et al.* 1988; Kaufman, G. A. *et al.* 1988; Kaufman, G. A. *et al.* this volume) and experimental studies of litter effects (Clark and Kaufman 1991; Kaufman and Kaufman 1990), was that fire creates prairie conditions, especially an absence of a litter layer, an open soil surface, and easy access to surface seeds, that are more favorable for deer mice than for other small mammals.

Prairie voles usually are associated with lush herbaceous vegetation that provides abundant foliage and a well-developed plant litter layer (Abramsky *et al.* 1979; Bee *et al.* 1981; Choate and Fleharty 1975; Martin 1960). Fire typically had a negative effect on these herbivorous rodents in tallgrass prairie (Kaufman, D. W. *et al.* 1990b); this response probably was due to removal of litter and standing vegetation by fire (Clark and Kaufman 1991). Consistent with a fire-negative response, our annually burned patches were avoided strongly by voles, except in autumn 1982, when abundance was low. Although voles selected upland over breaks and lowland prairie in other sites on Konza Prairie (Bixler and Kaufman 1995; Kaufman, G. A. *et al.* this volume), patch use was not influenced by topography in our experimental site. This pattern suggests that litter depth and plant productivity were suitable to support vole use in both lowland and upland, unless annual fire prevented redevelopment of deep litter. Further, annual fire likely leads to a reduction in the abundance of bluegrass and other cool-season grasses that does not occur in less frequently burned prairie (Gibson and Hulbert 1987). Such reduction may have a negative effect on the folivorous prairie vole.

Elsewhere on Konza Prairie, white-footed mice selectively used lowland prairie (Kaufman, G. A. *et al.* this volume) but not burned or unburned prairie (Kaufman, D. W. *et al.* 1990b). Because the white-footed mouse is a woodland species (Clark *et al.* 1987; Kaufman, D. W. *et al.* 1993), the lowland response reported by Kaufman, G. A. *et al.* (this volume) probably was related to the juxtaposition of lowland prairie and wooded ravines. Shrubs and trees were present within 300 m of our study site but did not border the lowland patches and were not consistently closer to lowland than upland. As a result, white-footed mice did not select lowland over upland patches. However, use of patches in the southern portion of our study site (Fig. 2) probably was due to the distribution of shrubs and trees in the area surrounding our study site. Specifically, shrubs and trees within 300 m of our study site were more common to the south than north. Lastly, the impact of annual fire on white-footed mice was striking and related to the lack of woody vegetation in annually burned patches.

Western harvest mice on Konza Prairie were influenced by both fire (Kaufman, D. W. *et al.* 1990b) and topography (Kaufman, G. A. *et al* this volume). The fire-negative response of harvest mice occurred within a few days of an experimental burn (Clark and Kaufman 1990) and likely was due to litter removal by fire (Clark and Kaufman 1991; Kaufman and Kaufman 1990; Kaufman, D. W. *et al.* 1989), because litter provides protection and nest sites (Clark and Kaufman 1991; Webster and Jones 1982). In autumn 1982, Peterson *et al.* (1985) found that harvest mice used unburned lowland over upland and burned lowland within the experimental area examined in our study. We expected, but failed, to find a significant negative effect of annual burns. However, the trend was very strong ($\underline{P} < 0.1$) and supported the known fire-negative response of harvest mice (Kaufman, D. W. *et al.* 1990). Harvest mice were found to selectively use lowland in unburned prairie elsewhere on Konza Prairie (Kaufman, G. A. *et al.* this volume), but not in our experimental area. This lack of a topographic effect likely was related to the minor topographic relief and small size of our habitat patches.

Although few captures of thirteen-lined ground squirrels were recorded, a positive association for upland over lowland was statistically significant. This relative avoidance of lowland was consistent with topographic effects for study sites with upland, breaks, and lowland sites elsewhere on Konza Prairie (Clark *et al.* 1992; Kaufman, G. A. *et al.* this volume). Finally, ground squirrels were not influenced by frequent fire within our experimental area, although a fire-positive response was reported elsewhere on Konza Prairie (Kaufman, D. W. *et al.* 1990b).

Distribution of short-tailed shrews within prairie habitats was influenced by both fire (Kaufman, D. W. *et al.* 1990b) and topography (Clark *et al.* this volume). Reduction of plant litter depth (Clark and Kaufman 1990; Kaufman, D. W. *et al.* 1989) due to fire was likely a major determinant of the fire-negative response reported for these shrews (Kaufman, D. W. *et al.* 1990b). A well-developed litter layer provides foraging microhabitat for invertebrate prey, as well as travel paths and safe sites with moderate temperature and humidity conditions (George *et al.* 1986). Therefore, it was surprising that patch use was not influenced by annual fire, which would prevent a well-developed litter layer. As with harvest mice, the lack of a topographic effect probably was due to limited topographic relief and the contiguous nature of our small patches.

In summary, fire history, local topography, or both influenced use of our experimental habitat patches by all but one of the seven species of small mammals studied. However, it is important to note that responses within a sample or a season may diverge from an overall pattern, even when relatively strong effects of fire and topography are evident for data summed over years and seasons. Such deviations may be due to chance events or may have real biological causes; therefore, future studies of effects of fire, topography, grazing, and so forth on small mammals should be designed to gather data for multiple years, seasons, and sites to better assess the strength and causes of patterns.

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Literature Cited

Abramsky, Z., M. I. Dyer, and P. D. Harrison. 1979. Competitionamong small mammals in experimentally perturbed areas of the shortgrass prairie. Ecology 60:530-536.

Bee, J. W., G. E. Glass, R. S. Hoffmann, and R. R. Patterson. 1981. Mammals in Kansas. University of Kansas, Museum of Natural History Public Education Series 7:1-300.

Bixler, S. H. and D. W. Kaufman. 1995. Local distribution of prairie voles (*Microtus ochrogaster*) on Konza Prairie: effect of topographic position. Transactions of the Kansas Academy of Science 98:61-67.

Choate, J. R. and E. D. Fleharty. 1975. Synopsis of native, recent mammals of Ellis County, Kansas. Occasional Papers, The Museum, Texas Tech University 37:1-80.

Clark, B. K. and D. W. Kaufman. 1990. Short-term responses of small mammals to experimental fire in tallgrass prairie. Canadian Journal of Zoology 68:2450-2454.

Clark, B. K. and D. W. Kaufman. 1991. Effects of plant litter on foraging and nesting behavior of prairie rodents. Journal of Mammalogy 72:502-512.

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.

Clark, B. K., D. W. Kaufman, G. A. Kaufman, and S. K. Gurtz. 1995. Population ecology of Elliot's short-tailed shrew and least shrew in ungrazed tallgrass prairie manipulated by experimental fire. *In* D. C. Hartnett (ed.) Proceedings of the Fourteenth North American Prairie Conference, Prairie Diversity: from Molecules to Landscapes, from the Past to the Future. Kansas State University, pp.

Clark, B. K., D. W. Kaufman, G. A. Kaufman, S. K. Gurtz, and S. H. Bixler. 1992. Population ecology of thirteen-lined ground squirrels in ungrazed tallgrass prairie manipulated by fire. *In* D. A. Smith and C. A. Jacobs (eds.) Proceedings of the Twelfth North American Prairie Conference, Recapturing a Vanishing Heritage. University of Northern Iowa, pp. 51-54.

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. The Prairie Naturalist 18:153-166.

Fleharty, E. D. and M. A. Mares. 1973. Habitat preference and spatial relations of *Sigmodon hispidus* on remnant prairie in west-central Kansas. The Southwestern Naturalist 18:21-29.

George, S. B., J. R. Choate and H. H. Genoways. 1986. *Blarina brevicauda*. Mammalian Species 261:1-9.

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.

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

Kaufman, D. W., B. K. Clark and G. A. Kaufman. 1990a. Habitat breadth of nongame rodents in the mixed-grass prairie regionof north central Kansas. The Prairie Naturalist 22:19-26.

Kaufman, D. W., E. J. Finck and G. A. Kaufman. 1990b. Small mammals and grassland fires. *In* S. L. Collins and L. L. Wallace (eds.) Fire in North American Tallgrass Prairies. University of Oklahoma Press, pp. 46-80.

Kaufman, D. W., S. K. Gurtz and G. A. Kaufman. 1988. Movements of *Peromyscus maniculatus* in response to prairie fire. The Prairie Naturalist 20:225-229.

Kaufman, D. W. and G. A. Kaufman. 1990. Influence of plant litter on patch use by foraging *Peromyscus maniculatus* and *Reithrodontomys megalotis*. The American Midland Naturalist 124:195-198.

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. The Prairie Naturalist 15:49-56.

Kaufman, D. W., G. A. Kaufman and E. J. Finck. 1989. Rodents and shrews in ungrazed tallgrass prairie manipulated by fire. *In* T. B. Bragg and J. Stubbendieck (eds.) Proceedings of the Eleventh North American Prairie Conference, Prairie Pioneers: Ecology, History, and Culture. University of Nebraska Press, pp. 173-177.

Kaufman, D. W., G. A. Kaufman, and E. J. Finck. 1993. Small mammals of wooded habitats of the Konza Prairie Research Natural Area, Kansas. The Prairie Naturalist 25:27-32.

Kaufman, G. A., D. W. Kaufman, D. E. Brillhart, and E. J. Finck. 1995. Effect of topography on the distribution of small mammals on the Konza Prairie Research Natural Area, Kansas. *In* D. C. Hartnett (ed.) Proceedings of the Fourteenth North American Prairie Conference, Prairie Diversity: from Molecules to Landscapes, from the Past to the Future. Kansas State University, pp.

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 69:342-352.

Martin, E. P. 1960. Distribution of native mammals among communities of mixed prairie. Fort Hays Studies, Science Series 1:1-26.

Peterson, S. K., G. A. Kaufman, and D. W. Kaufman. 1985. Habitat selection by small mammals of the tall-grass prairie: experimental patch choice. Prairie Naturalist 17:65-70.

Webster, W. D. and J. K. Jones, Jr. 1982. *Reithrodontomys megalotis*. Mammalian Species 167:1-5.

The Effects of Spring Burns on the Western Prairie Fringed Orchid (*Platanthera praeclara*)

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Abstract. To assess the effects of spring prairie burns on the western prairie fringed orchid, *Platanthera praeclara*, in a way that would provide statistically valid replication, a number of spot burns were made. Each of 12 spot burns, performed in 1992, covered a circle 2m in diameter and included at the center an orchid plant that had flowered in 1991. Each plant in a burned plot was paired with a nearby control plant of comparable 1991 size (together referred to as focal plants). Over the course of the study, other plants were added; these were used only for analysis of emergence and growth rate. In the year of the burn (1992), no size differences between the two treatment groups were found, although the plants on the burned plots senesced sooner. In 1993, plants on plots burned in 1992 emerged sooner and grew more rapidly, although their final size was not different from that of control plants. In neither 1992 nor 1993 did any difference in flowering probability occur between the two treatment groups. In 1994, half of the study area was burned. Paired focal plants still could be compared for 1992 burn effects, because both pair members experienced the same 1994 treatment. Plants on plots burned in 1992 had greater leaf area than plants on plots unburned in 1992. Again, no difference in flowering probability occurred. From 1992 to 1994 a greater proportion of plants on unburned plots disappeared. The effects of the 1994 burn were also examined. In 1994, plants on the burned area grew more slowly and had higher rates of inflorescence abortion than plants on the unburned area. In 1995, plants on the burned area grew more rapidly, achieved larger size, and flowered sooner.

A fire/soil moisture interaction is hypothesized to explain these results. In a dry year, the removal of litter by fire adds to drought stress, resulting in slower growth rates and a higher probability of inflorescence abortion. In a wet year, the removal of litter increases photosynthesis, resulting in faster growth rates and ultimately greater plant size. The effects of litter removal are felt both in the year of the burn and the following year. The results are consistent with this hypothesis. In 1992 and 1994, when spring precipitation was very low, the effects of burning were negative. In 1993 and 1995, when spring precipitation was high, the effects were positive. Management implications are discussed.

Key words: western prairie fringed orchid, *Platanthera praeclara*, burning, prairie burns, response to fire, endangered species

Introduction

The western prairie fringed orchid, *Platanthera praeclara*, is on the a federal list of threatened species. It occurs today in scattered populations in mesic prairies in Nebraska, Kansas Missouri, Iowa, Minnesota, North Dakota, and Manitoba, . Most of the 74 known populations of the species are small, with less than 50 to 250 individuals (U.S. Fish and Wildlife Service 1994). Three large metapopulations occur in the northern part of the species' range, at Sheyenne National Grassland (North Dakota), Pembina Trail (Minnesota), and Vita (southern Manitoba). Each of these site has several thousand flowering individuals and an unknown number of vegetative individuals (U.S. Fish and Wildlife Service 1994).

The proper management of western prairie fringed orchid populations is of obvious importance to the long-term persistence of the species. Spring burning is a common prairie management tool. Fire can affect the growth rate of plants as well as the frequency and magnitude of sexual reproduction (Collins and Wallace 1990). Several studies have suggested that spring burns benefit the warm-season grasses but may have a detrimental effect on forbs (Gibson and Hulbert 1987, Hartnett 1991). Some of the information to date on the effects of fire on the western prairie fringed orchid is anecdotal; Bowles (1983) and Currier (1984) have suggested that flowering frequency increases following a fall or spring burn. One experimental study, done at the Sheyenne National Grassland, found no effect of burning on orchid densities (Sieg *et al.* 1994).

The purpose of the present study was to determine the effects of fire on the growth and flowering probability of the western prairie fringed orchid. The study focused on a population from the southern part of the species' range, at Sheeder Prairie in south central Iowa. The small size of southern populations makes them especially vulnerable to extinction and makes knowledge of fire effects more critical.

In order to determine the effects of fire on a perennial plant, such as this orchid, long-term monitoring of populations is required in conjunction with periodic burn treatments. In addition, a sufficient number of treatment (fire) and control (no fire) plots is needed to statistically test for fire-effect differences in growth or flowering (Hurlbert 1984). Some burn studies, for logistical convenience, divide the site into a burned area and an unburned area. However, treating the plants in each area as independent participants in the treatment constitutes pseudoreplication (Hurlbert 1984). The problem with having a single control and single experimental area is that observed differences among plants could be due to inherent differences between the two areas (such as soil moisture or composition of neighboring plants) rather than the treatment itself. One solution is to create a randomized patchwork of burned and unburned areas at the site. However, the small size of some prairie preserves makes this difficult to do. In addition, if one is interested in the response of a particular rare species, its distribution in the preserve may be sparse and patchy. A randomized burn/unburned patchwork may have many patches without subject plants. For the present study, which faced the problems associated with studying a rare plant on a small preserve, replication was achieved by having individual plants serve as experimental subjects. Plants were located the year prior to the experiment and then half of the spots on which plants were located were burned and half were not. In addition to the spot-burn experiment, the results of a later, large-scale burn are also reported.

Methods

Study Site

The study site was Sheeder Prairie, a 25-acre State Preserve in Guthrie County, Iowa with over 180 plant species (Kennedy 1969). The site has a rolling topography dominated by a central hill. As a whole, the prairie is characterized as a mesic, tallgrass-dominated, upland prairie (Kennedy 1969). The western prairie fringed orchids are found in a band roughly in the middle of the central hill and near the base of a slope to the north of the hill. The plants are located in a band of exposed Aftonian paleosols bracketed by Kansas till upslope and Nebraska till downslope (Kennedy 1970). Because of the clay subsoil in this band, this area has a higher soil moisture than surrounding areas (Kennedy 1970), which may explain the presence of this mesic plant.

The number of western prairie fringed orchids at this site is difficult to estimate, because only plants that are in flower can be found easily in unburned vegetation. Occasionally mass flowering years occur in this species (Bowles *et al.* 1992), which facilitates estimation of population size. At Sheeder Prairie in 1987, 160 flowering stems were located; a burn in the spring of that year also allowed the discovery of 120 vegetative individuals (M. Leoschke, unpub. data). Fewer than 50 plants had flowered in the 3 previous years and have flowered since (M. Leoschke, J. Pleasants, unpub. data).

Sheeder Prairie was mowed annually in the late fall for about 100 years prior to 1965. During that time it was also burned about every 3 years and experienced little grazing (Kennedy 1969). It became a preserve in 1961 and has since been managed with prescribed burns. The last burn prior to the present study was an arson fire on March 2, 1987, which burned virtually the entire site.

Experimental Burns, 1992

The experimental design consisted of using individual plants (called focal plants) as the experimental units. The study began in 1991, with the choosing of focal plants. The original intent was to have about 25 focal plants in the fire treatment group with another 25 focal plants as controls. However, in 1991 only 35 flowering stems could be found, forcing a reduction in sample size; 30 of these plants were marked for the study. In assigning these 30 marked plants to treatment or control groups, an attempt was made to minimize initial size differences or microsite differences between the two groups. The number of flowers was used as a size index, because inflorescence size is correlated with leaf area for this and other orchid species (Calvo 1990, Pleasants unpub. data). Plants near each other were assumed to share a microsite. Therefore, pairs of treatment and control plots were chosen which were close to each other and had approximately the same number of flowers. Of the 30 marked plants, 26 emerged in 1992, consisting of 12 treatment and 14 control plants (plots); this included only 11 of the original pairs. These pairs had been well matched for size; the mean inflorescence sizes in 1991 were 8.00 for the control plants and 9.09 for the experimental plants ($t = -1.06$, df = 20, NS).

Circular spot burns were made in the spring of 1992. To create burn patches, a 1 m high wall of aluminum flashing was placed around the perimeter of each of the 12 treatment plots (Johnson, 1987). First, 10 1.2-m electric posts were hammered into the ground in a circle of 1 m radius around the focal plant. Then the flashing was pulled around the outside of the posts and held where the ends met with two small C clamps. With the wall in place, the vegetation inside was ignited. Flappers and a portable water spray unit were used to keep the fire from creeping out from under the flashing. Then the flashing was rolled up and carried to the next plot.

Plots were burned on May 1 and May 3, 1992. Plants had already emerged at this time and were 2-5 cm tall. Prescribed burns usually are performed in April, before the orchid plants have emerged, but heavy spring rains prevented burning during this period. It was necessary to prevent fire damage to leaves in order to produce an effect as much as possible like an early spring burn. Before burning, wet clay pots were placed over each focal plant and any vegetative plants that had appeared in the plot. Unburned thatch immediately around these plants was cut and removed to simulate the effect of removal of vegetation by burning.

Prescribed Burn, 1994

In 1994, as part of the prairie management plan, half of the prairie was burned; the burned area included half of the study plots. The burn was performed on April 11, before any of the orchid plants had emerged. The original intent had been for the 1992 experiment to continue interrupted through 1994. Consequently, an attempt was made to protect study plots from burning by covering them with fire blankets, but this failed when fire crept underneath. However, it was still possible to examine 1992 burn effects (see rationale below) and it also created an additional opportunity to examine post-burn effects.

Data Collection

Several types of data were used to compare treatment effects: whether plants had emerged by a particular date, the growth rate of plants during leaf expansion (height on a particular date), final plant size (leaf area index), and the probability of flowering. The leaf area index was obtained by measuring and multiplying together the length and width of each leaf and summing over all leaves. Vegetative stems have one to three leaves but flowering stems have more than five leaves of progressively smaller size. For flowering stems, only leaves greater than 5 cm long were measured; leaves smaller than this contribute a negligible amount to the leaf area index (J. Pleasants, unpub. data). In 1992, data on emergence and growth were not gathered. Plants were measured for size, and flowering status was assessed, on July 4. In 1993, measurements of emergence and height were made on April 25, May 31, and June 15 and measurements of plant size and flowering status on July 2 and July 13. In 1994, measurements of emergence and height were made on April 23 and June 2, and measurements of plant size and flowering status on June 25 and July 6.

Data Analysis

The burn experiment in 1992 was set up as a paired comparison, and size differences between focal plants were analyzed by a paired comparisons t-test. As the study progressed, a number of nonfocal plants were included to augment sample size. Several vegetative plants appeared in the study plots in 1992; seven in treatment plots and four in controls. Outside of the plots nine new plants were found in flower in 1993 and five in 1994. Because their initial size was unknown, these nonfocal plants were not used to examine treatment differences in overall size or flowering probability. However, they were included in analyses of time of emergence and growth rate. In comparing differences in mean growth rate (height) and leaf area for the two treatments, 1-tailed t-tests were used. For statistical tests involving the analysis of frequencies the Fisher's exact test was used. For different statistical tests, the sample sizes were sometimes different. This is because some plants did not appear in a particular year or were removed by herbivores or unknown causes during the season.

The 1994 burn superimposed a second treatment/control regime on focal plants which divided them into four classes: burned92/burned94, burned92/unburned94, unburned92/burned94, and unburned92/unburned94. However, in 1994 focal plants could still be compared for 1992 burn effects because of the paired comparison experimental design. This is because both members of each pair received the same 1994 treatment.

Assessing the effects of the 1994 burn on plant size is potentially more difficult, because the burn history of plants could play a role in their response. For this analysis, plants should be divided into the four classes indicated above. However, such division results in a very small sample size for each group, ranging from three to seven, making detection of statistically significant differences difficult. Consequently, 1992 treatment history was ignored in order to examine the effects of the 1994 burn. This creates no bias because there were roughly equal numbers of plants burned in 1992 within each of the two 1994 treatment groups (five in the burned and six in the unburned area). All the plants within each treatment group, both focal plants and those added later, were considered to be replicates. This would appear to contradict the rationale presented earlier for spot burning. However, for the present study, underlying differences between the two areas, that could produce a spurious response effect, can be ruled out (see Results and Discussion).

Table 1. Summary of effects of 1992 burn on Platanthera praeclara in 1992-1994.

Variable	Burned 1992	Unburned 1992	Statistics
1992			
Mean leaf area (cm2)	47.5	40.0	t = 0.57 (pc), df = 10, NS
S.D	32.9	6.3	
n	11	11	
Probability of flowering	0.42	0.15	P = 0.22 (FET)
n	12	14	
Probability of senescence	0.72	0.29	P = 0.01 (FET)
n	18	17	
1993			
Probability of emergence, April 25	0.79	0.40	P = 0.02 (FET)
n	19	15	
Height (cm), May 31	21.2	17.5	t = 1.89, df = 21, P = 0.03
S.D.	5.7	3.5	
n	12	12	
Height (cm), June 15	27.3	26.1	t = 0.46, df = 20, NS
S.D	7.1	4.3	
n	12	10	
Mean leaf area (cm2)	80.3	73.8	t = 0.43 (pc), df = 8, NS
S.D.	40.3	22.8	
n	9	9	
Probability of flowering	0.33	0.18	P = 0.44 (FET)
n	12	11	
1994			
Mean leaf area (cm2)	137.1	101.9	t = 1.31 (pc), df = 7, P = 0.11
S.D.	70.3	33.1	
n	8	8	
Probability of flowering	1.00	0.88	P = 0.50 (FET)
n	8	8	

pc = paired comparison
FET = Fisher's exact test

Results and Discussion

Experimental Burns, 1992

1992 results. Plants had already emerged when plots were burned in 1992. The clay pots protected most plants, but some individuals did experience fire damage. Because leaf expansion had not yet occurred, damage, in most cases, was restricted to singed leaf margins because leaves are tightly wrapped together inside a conical sheath (the coleoptile) before they expand. Two plants were damaged more heavily but retained a significant proportion of their leaf tissue.

The 11 pairs of focal plants were not significantly different from each other in leaf area (Table 1). In 1992 there were no plants at the study site that successfully flowered; all inflorescences aborted. For plants with aborted inflorescences the lower leaves appeared to be normal but the upper portion of these plants, with the flower buds and subtending leaves, failed to expand; in some cases this portion turned brown and later fell off. The proportion of focal plants that attempted to flower was not significantly different between the two treatment groups (Table 1). Bowles (1983) found that flower primordia are formed in the fall, and it is possible that leaf primordia may be formed then as well. Thus burning is unlikely to affect the status or size of plants in the year in which they are burned, unless the plants are actually damaged by the fire. There was some evidence that fire might have caused early plant senescence; a greater proportion of burned plants were brown or had one brown leaf on July 4, 1992 compared with control plants (Table 1).

1993 results. Several positive effects of the 1992 burn were observed in 1993. A higher proportion of plants on burned plots had emerged by April 25 (Table 1). By May 31, all plants had emerged, but plants on burned plots were significantly taller (Table 1). Advanced phenology as a result of fire has been noted in other studies (e.g., Leoschke 1986), but in such studies the phenology effects were observed in the year of the burn rather than the year after the burn as in the present study. Earlier emergence and greater height are due to the removal of litter by burning, allowing the ground to warm up more quickly in the spring and allowing more light for early growth (Knapp and Seastedt 1986). By June 15, no significant difference in height was observed between the two treatment groups (Table 1), indicating that the emergence advantage probably lasted for about a month.

In 1993, two of the control focal plants that were members of a pair did not appear, leaving nine of the original pairs intact. For the remaining pairs, no significant differences in leaf were observed (Table 1). Several plants in both treatment groups flowered but there was no difference in the proportion that flowered (Table 1).

1994 results. The 1994 burn imposed another treatment effect on the system. However, the paired design of the study made it possible to compare size differences of plants burned and not burned in 1992, because both members of each pair experienced the same 1994 treatment. Only eight pairs of focal plants remained for this analysis. The mean leaf area for plants burned in 1992 was larger than that for plants unburned in 1992, and the difference was nearly significant (Table 1). Apparently the emergence advantage experienced in 1993 by plants on burned plots translated into larger size in 1994. All but one of the members of these pairs flowered in 1994 so the burn in 1992 did not have an effect on the probability of flowering in 1994 (Table 1).

One intriguing effect of the 1992 burn was that burned plants had significantly higher survivorship than unburned plants. All 12 focal plants that were burned in 1992 were still present in 1994, whereas only 8 of 14 control focal plants (57%) were still present (P = 0.01, Fisher's exact test). Three failed to appear in 1993, and another 3 failed to appear in 1994. The 1994 burn did not appear to have affected the disappearance in 1994 because two of the three missing control focal plants were in the unburned section.

Prescribed Burn 1994

Before analyzing the results of the 1994 burn, one question must be addressed: are there underlying differences between the two areas, apart from treatment, that could bias results. If some systematic difference between the two areas did exist we would expect plants to have behaved differently on these two areas before the treatment. Two behaviors that can be compared are emergence and early growth rate, for which data are available from 1993, the year before the prescribed burn. To analyze the 1993 data, the plants first were divided into two groups, those that had been burned in 1992 and those that had not. Within each group, plants were divided into those that were in the area that was burned in 1994 and those that were not. For the plants burned in 1992, six were on the area burned in 1994 and 13 were not. For these two sets of plants, there was no difference in the proportion which had emerged on April 25, 1993 (P = 0.64, Fisher's exact test). For the plants not burned in 1992, five were on the area burned in 1994 and nine were not. For these two sets of plants, there was no difference in the proportion which had emerged on April 25, (P = 0.34, Fisher's exact test). Comparing plant height on May 31, 1993, the two sets of plants that were burned in 1992 did not differ in their height (t = 0.71, df = 17, NS) nor did the two sets of plants unburned in 1992 (t = 1.19, df =13, NS). Thus it would appear that any differences between plants on the burned and unburned areas in 1994 would be due to treatment alone.

1994 results. On April 23, 12 days after the burn, all plants had emerged on both areas. There was no significant difference in height between plants on the burned area and plants on the unburned area at this time (t = 0.07, df = 25, NS; mean burned = 3.28 cm, mean unburned = 3.25 cm). On June 2 there was a significant difference in height between the two groups (Table 2); the plants on the burned area were smaller. However, there was no significant difference in the ultimate size achieved by flowering plants on the two areas (Table 2). In 1994, 85% of marked plants produced an inflorescence. However, a number of plants that attempted to flower aborted their inflorescences. For all plants that attempted to flower, a significantly higher proportion with aborted inflorescences occurred on the burned area (Table 2).

1995 results. In 1995, plants on the burned area were taller on April 25 and June 7 (Table 2). The ultimate size achieved by flowering plants was also greater on the burned area (Table 2). 75% of marked plants flowered in 1994 and only a few inflorescences aborted. Flowering phenology was advanced for plants on the burned area (Table 2).

Summary and Interpretation of Results

In 1992, the only effects of the 1992 burn were slightly negative; plants on burned plots senesced sooner. The 1992 burn produced positive effects in 1993; plants on burned plots emerged sooner and expanded leaves more rapidly, although their final size was no larger. The effects of the 1992 burn could even be seen in 1994; plants on burned plots were larger than those on unburned plots. Also, there was a significant difference in survivorship of focal plants; all plants on burned plots were still present in 1994 compared with only 57% of the plants on unburned plots.

Table 2. Summary of effects of 1994 burn on Platanthera praeclara in 1994 and 1995.

Variable	Burned 1994	Unburned 1994	Statistics
1994			
Height (cm), June 2	15.8	22.8	t = 5.25, df = 38, P < 0.0001
S.D	2.83	5.22	
n	20	20	
Leaf area (cm2) June 25	132.4	132.8	t = 0.02, df = 35, NS
S.D.	40.0	58.0	
n	15	22	
Probability of abortion	0.93	0.31	P < 0.001 (FET)
n	14	16	
1995			
Height (cm) April 25	5.47	2.78	t = 6.07, df = 36, P < 0.0001
S.D.	1.43	1.29	
n	18	20	
Height (cm) June 7	39.9	31.9	t = 3.16, df = 27, p < 0.001
S.D.	6.43	7.25	
n	13	16	
Leaf area (cm2) July 3	169.0	113.8	t = 2.32, df = 26, p < 0.01
S.D.	64.4	49.8	
n	10	18	
Proportion of plants with > 75% of flowers open	1.00	0.00	P < 0.0001 (FET)
n	10	14	

pc = paired comparison
FET = Fisher's exact test

In 1994, the effects of the 1994 burn were negative; plants on the burned area grew more slowly, although there was no difference in their final size. More significantly, of the many plants on both areas that attempted to flower, 93% of those on the burned area aborted their inflorescences whereas only 31% of those on the unburned area did so. In 1995, the effects of the 1994 burn were positive; plants on the burned area grew more rapidly, flowered sooner, and had a larger final size.

These results appear to be inconsistent; in some years burning has positive effects and in other years the effects are negative. But this is consistent with the hypothesis that burning and soil moisture conditions interact to produce the plant's response, as found in the study by Blankespoor and Larson (1994). The removal of litter by fire is known to reduce soil moisture (Knapp and Seastedt 1986). It is hypothesized that, when prevailing soil moisture levels are already low because of low precipitation, the further reduction in soil moisture caused by litter removal can result in plant stress. When prevailing soil moisture levels are high, litter removal can produce a positive response because of increased photosynthesis resulting from greater light reception. In the present study the effects of litter removal carried over into the year after the fire.

The four years of data from the present study are consistent with this hypothesis. Figure 1 shows the precipitation patterns during the growing season for these four years. At this study site, the plant emerges in mid April and flowers towards the end of June. Precipitation in these months is critical for the orchid's success. In 1992, May and June precipitation were well below average. This limited plant longevity; by July 4, many plants, but especially those on the burned plots, were either completely brown or had one brown leaf. It also affected reproduction; the inflorescences on all flowering plants aborted before they could mature. Thus, in 1992, burning appears to have added to the stress imposed by low moisture resulting in a negative effect on the plants. In 1993, precipitation was higher than average throughout the growing season, and all plants were green through July with no inflorescence abortion. In 1993, the plants on plots burned in 1992 had more rapid emergence and early growth which did not produce larger size in 1993 but did in 1994. In 1994 precipitation was very low in May. This appears to have stressed all plants as indicated by the high level of inflorescence abortion. However, the plants on the area burned in 1994 had 91% inflorescence abortion compared to 31% for plants on the unburned area. Plants on the burned area also experienced slower early growth. In 1995, precipitation levels were high throughout the growing season, with the exception of June. Only a few inflorescences aborted. Plants on the area burned in 1994 had faster growth and larger size.

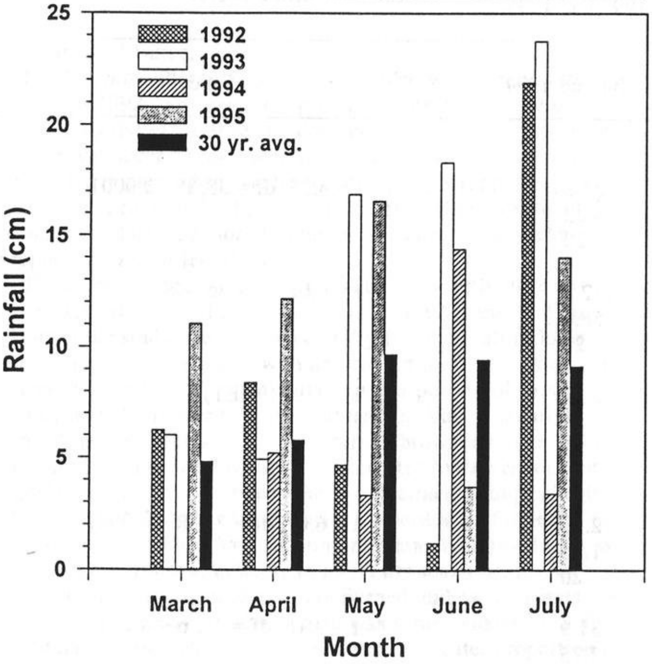

FIG. 1. Precipitation data for Guthrie Center, IA located 10km from the study site.

Some limitations of this study should be noted. First, the study was of short duration. Although results appear to be consistent with the fire/moisture interaction hypothesis, more years of study, observing other combinations of fire and precipitation, will be needed to confirm it. Second, the sample sizes were small. Often in such cases, environmental noise obscures any statistical differences that might exist between groups. In this study, the plants in the control and treatment plots were matched for initial size and microsite, in an attempt to reduce such noise. However, the number of matched pairs decreased over time because of plant disappearance, which limited the ability to detect size differences. Some plants were added to the study over time to augment sample size and it was possible to detect significant differences in emergence, growth rate and inflorescence abortion.

This study examined the effects of burning only on adult, primarily reproductive, plants. It did not examine the effects on vegetative plants or on recruitment to the population through seed germination and seedling establishment. A study at the Sheyenne National Grassland found that spring or fall burning had no statistically significant effect on orchid density, a reflection of recruitment and survivorship, or on flowering density (Sieg *et al.* 1994). Another factor, not examined in this study, that might be affected by fire is the mycorrhizae associated with orchid plants. From seed establishment through adult life, mycorrhizal relationships are important for these and many other orchids (Bowles *et al.* 1992), as well as many warm-season grasses. Little work has been done on prairie mycorrhizae but one study found increased mycorrhizal activity following a spring burn (Bentivenga and Hetrick 1991).

Management Implications

The results of this study pose a dilemma for management of western prairie fringed orchid populations. The results suggest that burning in early spring can have positive effects, if April-June precipitation levels are near or above normal. However, if precipitation during this period is below normal then burning can have negative effects. Unfortunately one cannot know at the time of a burn, in early April, what the precipitation over the next two months will be. In addition, one cannot know what precipitation conditions will be like the following year, and litter removal effects carry over into the following year. A conservative approach would be to consult the 90 day weather forecast before burning. If indications are for drier than normal conditions then the portion of the prairie with the orchids should not be burned. In addition, burning would not be recommended in a year following a very wet year because many plants will be attempting to flower (Bowles *et al.* 1994) and burning could jeopardize reproduction, which is essential to the long-term persistence of the species. Burning before orchid leaves have emerged (early to mid April for Sheeder Prairie) is also important. A study on another prairie orchid, *Spiranthes cernua,* found that burning after emergence significantly reduced leaf area in that year and the following year (A. Antlfinger, unpub. data). These management recommendations would apply to the small populations in the southern part of the species' range. For the metapopulations of the species in Manitoba, North Dakota, and Minnesota, soil moisture may be less important. These northern populations typically are found in low-lying, moist areas and may not be as vulnerable to drying as are the populations to the south, which are located in less mesic habitats. Further studies on burning effects in these populations are desirable.

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Literature Cited

Bentivenga, S. P. and B. A. D. Hetrick. 1991. Relationship between mycorrhizal activity, burning, and plant productivity in tallgrass prairie. Canadian Journal of Botany 69: 2597-2602.

Blankespoor, G. W. and E. A. Larson. 1994. Response of smooth brome (*Bromus inermis* Leyss.) to burning under varying moisture conditions. American Midland Naturalist 131:266-272.

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 towards management. Natural Areas Journal 3: 14-37.

Bowles, M. L., R. Flakne and R. Dombeck. 1992. Status and population fluctuations of the eastern prairie fringed orchid (*Platanthera leucophaea* (Nutt.) Lindl)) in Illinois. Erigenia 12: 26-40.

Collins, S. L. and L. L. Wallace, editors. 1990. Fire in North American Tall Grass Prairies. University of Oklahoma Press, Norman.

Calvo, R. N., 1990. Four -year growth and reproduction of *Cyclopogon cranichoides* (Orchidaceae) in south Florida. American Journal of Botany 77: 736-741.

Currier, P., 1984. Response of prairie fringed orchid to fire and reduction in grazing. Restoration and Management Notes 2: 28.

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.

Hartnett, D. C., 1991. Effects of fire in tallgrass prairie on growth and reproduction of prairie coneflower (*Ratibida columnifera*: Asteraceae). American Journal of Botany 78: 429-435.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological; field experiments. Ecological Monographs 54:187-211.

Johnson, L. A., 1987. The effect of fire at different times of the year on vegetative and sexual reproduction of grasses, and on establishment of seedlings. MS thesis, Iowa State University, Ames.

Kennedy, R. K. 1969. An analysis of tall-grass prairie vegetation relative to slope position, Sheeder Prairie, Iowa. MS thesis, Iowa State University, Ames.

Kennedy, R. K. 1970. Sheeder Prairie preserve: a natural prairie landscape in Guthrie County, Iowa. A report to the Iowa State Conservation Commission and to the Iowa State Preserves Board.

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

Leoschke, M. J. 1986. Fire and the life history of shooting star, *Dodecatheon meadia*, in Iowa tallgrass prairie. MS thesis, Iowa State University, Ames.

Sieg, C. H., A. J. Bjugstad, and R. Porter-Bjugstad. 1994. Exploring the role of fire in the life history of the western prairie fringed orchid (*Platanthera praeclara*). Society for Range Management, 1994 Annual Meetings Abstract, pgs 46-47.

U.S. Fish and Wildlife Service. 1994. *Platanthera praeclara* (western prairie fringed orchid) recovery plan. Technical/agency draft. U.S. Fish and Wildlife Service, Ft. Snelling, MN.

Influence of Fire Frequency and Burning Date on the Proportion of Reproductive Tillers in Big Bluestem and Indian Grass

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Abstract. Big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*) were censused for two seasons in ungrazed tallgrass prairie to investigate the influence of fire frequency and seasonality on tiller density and flowering. For big bluestem, the highest percentage of reproductive tillers (43.7%) occurred in plots burned after 3 years without burning ($P < 0.001$). As burning frequency increased, the proportion of reproductive tillers declined to 23.9% in plots burned after 1 year without burning and 14.5% in plots burned annually in late spring. The proportion of reproductive tillers was significantly lower in unburned plots than in any burn treatment. Seasonality of annual burns did not affect the percentage of reproductive tillers. For Indian grass, the proportion of reproductive tillers (14.8%) was highest in plots burned annually in late spring. Long-term unburned plots and plots burned every 4 years had the lowest percentage of tillers producing an inflorescence (0.6% and 1.4%, respectively). Results of this study indicate that annual fires in tallgrass prairie stimulate approximately 15% of big bluestem and Indian grass tillers to produce inflorescences, when ample precipitation occurs during the growing season. Burning once every 4 years reduces big bluestem tiller density compared to annual burning, but maximizes the number and percentage of reproductive tillers. In contrast, quadrennial burning drastically reduces the proportion of Indian grass tillers producing an inflorescence.

Key words: fire frequency, fire seasonality, reproductive effort, grass inflorescence, tallgrass prairie

Introduction

Reproduction by dominant, warm-season, perennial grasses in tallgrass prairie is primarily vegetative. Sexual reproductive effort varies from year-to-year, but profuse flowering of big bluestem (*Andropogon gerardii*) and Indian grass (*Sorghastrum nutans*) is infrequent, often occurring only two or three times per decade (Cornelius 1950). Removing litter with fire increases reproductive stem density (Curtis and Partch 1950; Kucera and Ehrenreich 1962; Ehrenreich and Aikman 1963; Knapp and Hulbert 1986; Hulbert 1988). However, interactions among fire frequency, fire seasonality, and independent environmental factors such as growing season precipitation can influence flowering dynamics of warm-season grasses. In native prairie, a seemingly high proportion of big bluestem and Indian grass tillers occasionally produce an inflorescence. Although various studies have examined inflorescence production in tallgrass prairie, the proportion of tillers that produce an inflorescence generally has been ignored. This study evaluated the influence of fire frequency and seasonality on tiller density and inflorescence production of big bluestem and Indian grass during 2 successive flowering years. The hypothesis was that these dominant warm-season grasses would respond to fire, particularly infrequent fire, with significant increases in both total and reproductive tillers.

Materials and Methods

An ungrazed tallgrass prairie area on Konza Prairie Research Natural Area (KPRNA) was partitioned into 10 x 25 m plots in 1982 to investigate long-term effects of fire at different seasons and intervals between fire. In addition to unburned plots, fire regimes included: annual burning in early spring (mid March), late spring (late April), and fall (mid November); late spring burning every 2 years (two different treatments for year-of-fire); and late spring burning every 4 years (four different treatments for year-of-fire). Each treatment was replicated four times across a topoedaphic gradient ranging from silty clay lowland soils to clayey upland soils. Since the initiation of treatments, seasonality and frequency of fire have visibly influenced the vegetative composition, but big bluestem and Indian grass are relatively common in most plots.

Tillers and flowering culms of big bluestem and Indian grass were censused in 10 quadrats (0.1 m^2) along a transect within each plot. To avoid edge effects, quadrats were located at least 1 m from plot borders. Tillers were counted in September 1992 and 1993.

For statistical analysis, densities of tillers and flowering culms were log transformed to equalize variances and reduce skewness within the data. The proportions of big bluestem and Indian grass tillers that produced an inflorescence were arcsine transformed before analysis (Zar 1974). Transformed data were analyzed as a two-way analysis of variance with means separated by least significant difference ($P < 0.05$).

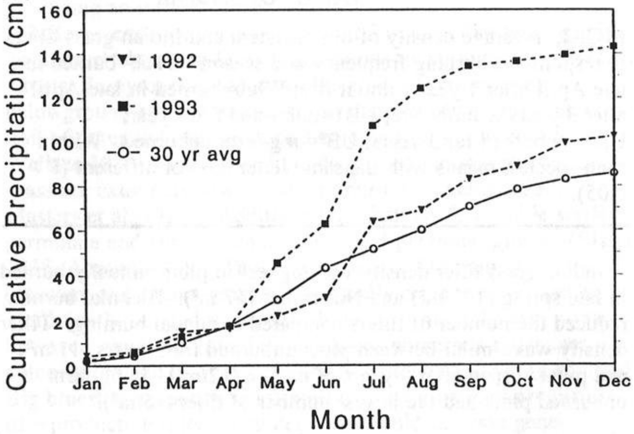

FIG. 1. Cumulative precipitation pattern of 1992 and 1993 compared with the 30-year average.

Results

Precipitation in 1992 was below the 30-year mean in the early part of the growing season (May-June). However, rainfall in July was the third highest on record (33.6 cm), and the year ended 17 cm above the long-term average (Fig. 1). In 1993, precipitation was above the 30-year mean throughout the growing season, and the year ended as the second wettest on record (143 cm).

Both 1992 and 1993 were considered "flowering years" in which perceptibly high numbers of big bluestem and Indian grass tillers produced flowering culms. However, inflorescence production was significantly higher for both grasses in 1993 than in 1992. Tiller density and the proportion of tillers producing an inflorescence also were higher for most treatments in 1993 than in 1992.

Tiller Density

Big bluestem tiller density was highest (212/m^2) in plots annually burned in late April (Fig. 2). Tillers were more numerous in plots annually burned in March (121 tillers/m^2) or November (114 tillers/m^2) than in any unburned treatment ($P < 0.001$). Biennial burning tended to increase ($P = 0.09$) tillers in the year that fire occurred (85/m^2) compared to plots unburned for 1 year (63/m^2).

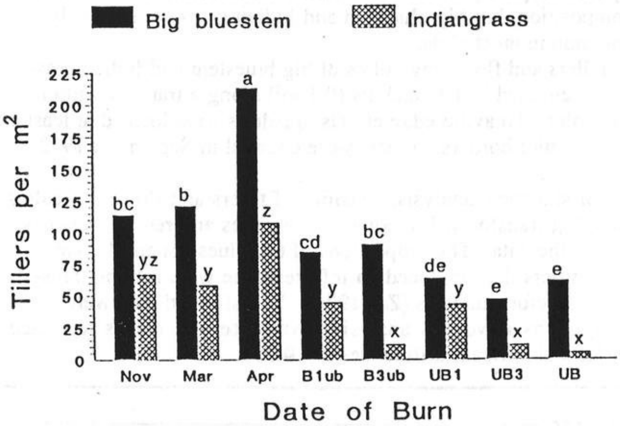

FIG. 2. Average density of big bluestem and Indian grass tillers in response to burning frequency and season. B1ub=burned in late April after 1 year without fire; B3ub=burned in late April after 3 years without fire; UB1=unburned for 1 year; UB3=unburned for 3 years; UB=long-term unburned. Within each species, means with the same letter are not different ($P > 0.05$).

Indian grass tiller density was highest in plots annually burned in late spring (107/m^2) and November (67/m^2). Biennial burning reduced the number of tillers compared to annual burning. Tiller density was similar between plots unburned for 3 years (11/m^2) and plots burned after 3 years of no fire (12/m^2). Long-term unburned plots had the lowest number of tillers (5/m^2).

Reproductive Stem Density

The greatest density of big bluestem flowering culms (39/m^2) occurred in plots burned after 3 years without fire (Fig. 3). Annual burning in late April produced more inflorescences (30/m^2) than annual burning in March or November (13/m^2 and 15/m^2, respectively). Flowering density was significantly lower ($P < 0.001$) in unburned plots than in any fire treatment.

Flowering density of Indian grass culms was greatest in plots annually burned in late April (26/m^2). In biennially burned plots, inflorescence density was 16 culms/m^2 in the year that fire occurred, but only 6 culms/m^2 in plots unburned for 1 year ($P < 0.001$).

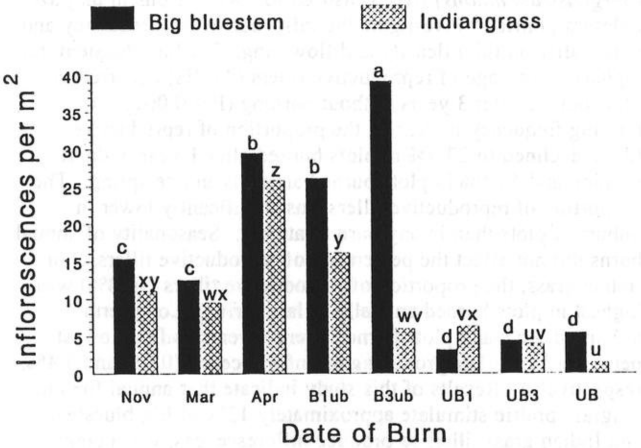

FIG. 3. Average density of big bluestem and Indian grass flowering culms in response to burning frequency and season. B1ub=burned in late April after 1 year without fire; B3ub=burned in late April after 3 years without fire; UB1=unburned for 1 year; UB3=unburned for 3 years; UB=long-term unburned. Within each species, means with the same letter are not different ($P > 0.05$).

Percentage of Reproductive Stems

The mean proportion of big bluestem tillers that produced an inflorescence (43.7%) was higher ($P < 0.001$) in plots burned after 3 years without fire than any other treatment (Fig. 4). The proportion of reproductive tillers decreased to 23.9% in plots burned after 1 year without fire and to 14.5% in plots annually burned in late spring. In unburned plots, the percentage of tillers producing an inflorescence was significantly lower than in any burn treatment. Seasonality of annual burns did not affect the proportion of reproductive tillers.

Annual burning in late April stimulated the greatest proportion of Indian grass tillers to produce an inflorescence (14.8%). Burning in different seasons reduced the percentage of tillers that flowered (5.9% in November and 3.8% in March). Long-term unburned plots and plots burned every 4 years had the lowest percentages of tillers producing an inflorescence.

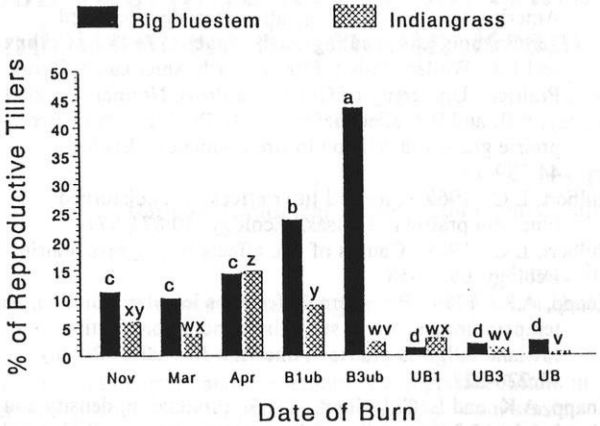

FIG. 4. Average proportion of big bluestem and Indian grass tillers producing an inflorescence in response to burning frequency and season. B1ub=burned in late April after 1 year without fire; B3ub=burned in late April after 3 years without fire; UB1=unburned for 1 year; UB3=unburned for 3 years; UB=long-term unburned. Within each species, means with the same letter are not different ($P > 0.05$).

Discussion

Annual fire, particularly in late spring, favors big bluestem (Svejcar 1990). Higher tiller density in burned than in unburned plots may be due to increased light levels from litter removal (Knapp 1984; Svejcar and Browning 1988). Although fire stimulates vegetative propagation of big bluestem, its influence is mediated by environmental conditions. Glenn-Lewin *et al.* (1990) concluded that weather is responsible for greater year-to-year fluctuations in tiller production than is fire.

Indian grass also is favored by annual fire, but tiller counts included numerous newly emerged shoots. In a separate late September census, 51.7% of all Indian grass tillers were < 10 cm tall (Table 1). These tillers arise throughout the growing season from established parent tillers and usually are short-lived (McKendrick *et al.* 1975). In unburned plots, light limitation from litter apparently is more inhibitory to the intermittently emerging tillers of Indian grass than the synchronized spring tillering of big bluestem. After 3 years without fire, litter buildup significantly reduced ($P < 0.001$) Indian grass tillers compared with other treatments. However, removing litter accumulations with quadrennial fire did not stimulate tiller or inflorescence production. Thus, Indian grass is much more dependent on frequent fire than is big bluestem.

Table 1. Height of Indian grass tillers measured in late September.

Height (cm)	Number of tillers	%
0.1 - 4.9	179	31.6
5 - 9.9	114	20.1
10 - 29.9	150	26.5
> 30	123	21.7

n = 566

Burning removes litter and usually stimulates inflorescence production in warm-season grasses (Curtis and Partch 1950; Weaver and Rowland 1952; Hulbert 1969). The flowering response is proportional to the detritus thickness and the length of time it is present (Old 1969). Inflorescence density is higher when the fire occurs in late spring than at other times. Benning and Bragg (1993) reported highest reproductive response to burning if fire occurred in mid to late May when photosynthetically active leaves were elongating. Other reports have shown that the influence of fire on inflorescence production decreased in the year after burning but remained higher than in unburned areas (Ehrenreich and Aikman 1963; Hadley and Kieckhefer 1963). In this study, however, flowering density of big bluestem was not different ($P > 0.1$) between plots unburned for 1 year and long-term unburned plots, suggesting that the stimulus of fire in the previous year did not have a carryover effect.

Although burning stimulates inflorescence production, the response is augmented by precipitation (Cornelius 1950). Generally, a wet year that follows a hot, dry year is favorable for stimulating flowering in big bluestem and Indian grass (Knapp and Hulbert 1986). Old (1969) suggested that the flowering response is controlled by environmental conditions at the beginning of the growing season. However, the high number of flowering tillers in this study suggests that precipitation during July and August, when the warm-season grasses are initiating flowering culms, may be a more critical influence. Circumstantial support for the influence of summer moisture on flowering density also can be gleaned from long-term records of inflorescence data on KPRNA. Yearly precipitation totals for 1981, 1982, 1983, and 1984 all were above the 30-year average, but only in 1981 and 1982 did profuse flowering occur. Both years received abundant moisture in July and August, with no extended periods of high temperature. In contrast, 1983 and 1984 were wet in the spring but hot and dry during the summer, and the warm-season grasses produced few or no inflorescences (Knapp and Hulbert 1986). The two successive wet years in this study stimulated a relatively high percentage of big bluestem and Indian grass tillers to produce an inflorescence, and flowering likely approached the upper limits in unfertilized native prairie. Precipitation deficits in the summer of more "typical" years presumably will dramatically reduce the proportion of tillers producing an inflorescence.

Inflorescence formation in perennial grasses that propagate vegetatively has long-term ramifications on survival of individual ramets. In pyrogenic habitats, allocation of resources to belowground storage in lieu of aerial structures is an adaptive trait of perennial grasses to conserve nutrients (Adams and Wallace 1985). Viable seed yields of big bluestem and Indian grass are extremely low in native prairie (Cornelius 1950; Masters et al. 1993). Additionally, relatively few viable seeds germinate and survive amid established perennial grasses (Blake 1935; Abrams 1988). Thus, inflorescence formation from big bluestem and Indian grass tillers usually represents wasted or inefficiently utilized resources. In quadrennially burned plots, however, removing litter buildup opens numerous microsites for colonization and may increase the likelihood of seedling survival. Big bluestem responds to infrequent fire with a high proportion of reproductive tillers, a strategy that could increase genet diversity in the population, if the probability of successful seedling establishment concomitantly increases.

Inflorescence production of big bluestem and Indian grass may reflect transient responses to recurring shifts in limiting resources. Nonequilibrium conditions created by infrequent fire stimulates the flowering response in a high proportion of big bluestem tillers, because both energy and nitrogen availability are increased (Seastedt and Knapp 1993). Nitrogen availability likely was not a limiting factor in 1992, because the previous year was relatively dry (18.3 cm precipitation below normal). Timely and abundant precipitation during the 1993 growing season saturated the soil to the point where the roots probably never experienced water stress, and the grasses responded with profuse tillering and inflorescence production.

In summary, yearly fires in tallgrass prairie stimulated approximately 15% of big bluestem and Indian grass tillers to produce inflorescences. In unburned sites, less that 3% of big bluestem and Indian grass tillers flowered. Floral induction in big bluestem is maximized (44% of the tillers) when burning occurs following 3 years without fire. However, the proportion of Indian grass tillers producing an inflorescence is reduced drastically with quadrennial burning (< 2% of all tillers).

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Alan Knapp, David Hartnett, and two anonymous reviewers provided valuable comments on the manuscript. Konza Prairie Research Natural Area is a preserve of The Nature Conservancy managed by the Division of Biology at Kansas State University. Support for this research was provided by the National Science Foundation for Long-Term Ecological Research and the Kansas Agricultural Experiment Station..

Literature Cited

Abrams, M.D. 1988. Effects of burning regime on buried seed banks and canopy coverage in a Kansas tallgrass prairie. Southwestern Naturalist 33:65-70.

Adams, D.E. and L.L. Wallace. 1985. Nutrient and biomass allocation in five grass species in an Oklahoma tallgrass prairie. American Midland Naturalist 113:170-181

Benning, T.L. and T.B. Bragg. 1993. Response of big bluestem (*Andropogon gerardii* Vitman) to timing of spring burning. American Midland Naturalist 130:127-132.

Blake, A.K. 1935. Viability and germination of seeds and early life history of prairie plants. Ecological Monographs 5:405-460.

Cornelius, D.R. 1950. Seed production of native grasses under cultivation in eastern Kansas. Ecological Monographs 20:1-29.

Curtis, J.T. and M.L. Partch. 1950. Some factors affecting flower production in *Andropogon gerardi*. Ecology 31:488-489.

Ehrenreich, J.H. and J.M. Aikman. 1963. An ecological study of the effect of certain management practices on native prairie in Iowa. Ecological Monographs 33:113-130.

Glenn-Lewin, D.C., L.A. Johnson, T.W. Jurik, A. Akey, M. Leoschke, and T. Rosburg. 1990. Fire in central North American grasslands: Vegetative reproduction, seed germination, and seedling establishment. *In* S.L. Collins and L.L. Wallace (eds.) Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman, pp 28-45.

Hadley, E.B. and B.J. Kieckhefer. 1963. Productivity of two prairie grasses in relation to fire frequency. Ecology 44:389-395.

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

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.

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. Southwestern Naturalist 31:235-241.

Kucera, C.L. and J.H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. Ecology 43:334-336.

Masters, R.A., R.B. Mitchell, K.P. Vogel, and S.S. Waller. 1993. Influence of improvement practices on big bluestem and Indian grass seed production in tallgrass prairies. Journal of Range Management 46:183-188.

McKendrick, J.D., C.E. Owensky, and R.M. Hyde. 1975. Big bluestem and Indian grass vegetative reproduction and annual reserve carbohydrate and nitrogen cycles. Agro-Ecosystems 2:75-93.

Old, S.M. 1969. Microclimate, fire, and plant production in an Illinois prairie. Ecological Monographs 39:355-384.

Seastedt, T.R. and A.K. Knapp. 1993. Consequences of nonequilibrium resource availability across multiple time scales: The transient maxima hypothesis. American Naturalist 141:621-633.

Svejcar, T.J. 1990. Response of *Andropogon gerardii* to fire in the tallgrass prairie. *In* S.L. Collins and L.L. Wallace (eds.) Fire in North American Tallgrass Prairies. University of Oklahoma Press, Norman, pp 19-27.

Svejcar, T.J. and J.A. Browning. 1988. Growth and gas exchange of *Andropogon gerardii* as influenced by burning. Journal of Range Management 41:239-244.

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

Zar, J.H. 1974. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs. 620 pp.

Soil Moisture and Temperature Differences Between Burned and Unburned Smooth Brome- and Big Bluestem-Dominated Sites

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Abstract. Soil moisture and temperature are important factors in determining productivity of prairies dominated by warm-season grasses such as big bluestem (*Andropogon gerardii*). In degraded or partially restored prairie dominated by smooth brome (*Bromus inermis*), early spring burning can stimulate growth of smooth brome tillers. Under these conditions, warm-season grasses growing in association with smooth brome would be at a disadvantage. In 1989 and 1990, a split-plot completely randomized design was used to determine differences in soil moisture and temperature between smooth brome-dominated plots and big bluestem-dominated plots both burned in early spring. Analysis of variance showed that early burning during a dry spring led to less soil moisture and lower soil temperatures on degraded sites dominated by smooth brome than on big bluestem-dominated sites. Lower available soil moisture and slower soil warming in dry years might limit big bluestem expansion in areas dominated by smooth brome.

Key words: smooth brome, big bluestem, prescribed fire, soil temperature, and moisture

Introduction

Many studies in tallgrass prairie have shown that removal in the spring of litter and standing dead biomass by burning or mowing results in increased growth of the dominant warm-season grasses (Weaver and Rowland 1952, Ehrenreich 1959, Kucera and Ehrenreich 1962, Hadley and Kieckhefer 1963, Hulbert 1969, Old 1969). Increased production in tallgrass prairie following burning has been attributed to: (1) increased availability of solar radiation to young shoots following removal of standing dead biomass, (2) increased length of the growing season from earlier warming of the site, and (3) a generally favorable early spring microclimate for growth of C_4 grasses (see Knapp 1984).

Among effects of litter removal on microclimate are changes in soil moisture and temperature. Soil moisture, measured late in the growing season, often has been reported to be lower in burned than in unburned prairie (Ehrenreich and Aikman 1963, McMurphy and Anderson 1965, Anderson 1965, Hulbert 1969, Rice and Parenti 1978). More specifically, burns at different spring dates differentially affect soil moisture. Bieber and Anderson (1961), for example, found that unburned control plots and those burned in late spring were significantly higher in soil moisture during the growing season than those burned earlier in the spring or in winter. The effect differences in soil moisture might have on plant growth was suggested by Rice and Parenti (1978), who showed that soil moisture stress at a depth of 8 cm was greater than the permanent wilting point of warm-season grasses for a total of 6 weeks during the growing season in plots burned on 22 March and mowed and for only 4 weeks in unburned control plots. Moisture stress on early-season burn sites probably is due to higher levels of evaporation from bare soil and greater transpiration from earlier growing vegetation (Hulbert 1969).

Removal of litter also has been shown to affect soil temperature. Removal of the litter layer by burning generally increases soil temperatures. Compared to untreated areas, soil temperature in areas from which litter had been removed by mowing or burning averaged as much as 20°C higher at the soil surface and up to 9°C higher at depths down to 15 cm (Steiger 1930, Ehrenreich and Aikman 1963, Peet et al. 1975, Knapp 1984). Rice and Parenti (1978) stated that the higher soil temperatures in burned and mowed plots, particularly during the first 3 months of the growing season, were primarily responsible for the increased dry matter production.

In degraded or partially restored prairie dominated by smooth brome (*Bromus inermis*), late March to early April burning can stimulate vigorous growth of smooth brome tillers (Willson 1994). Depletion of soil moisture by evaporation from bare soil and transpiration from actively growing smooth brome tillers could produce periods of soil moisture stress in the late spring when big bluestem (*Andropogon geradii*) is initiating growth. Although most native prairie species are well adapted to drought (Weaver 1968), competition with smooth brome could exaggerate naturally occurring dry periods and result in declines of native species. Also, increased leaf area from rapidly growing smooth brome tillers would replace some of the shading from litter and lower potential soil temperature (Ehrenreich and Aikman 1963). Under these conditions, warm-season grasses growing in association with smooth brome would be at a disadvantage. The objective of this study was to compare the soil moisture and temperature responses of smooth brome-dominated and big bluestem-dominated sites to early spring prescribed burning.

Methods

The study was conducted at the University of Nebraska, Agricultural Research and Development Center, near Mead, Nebraska (41° 10'N, 96° 25'W; 344 m above sea level). Climate of the study site is typical of the western limit of the tallgrass prairie region. Summers are hot and humid, with an average July temperature of 25.2°C and winds predominantly from the south. In January the average temperature is -4.3°C winds are northerly. Average annual precipitation is 690 mm with 74% falling during the growing season (Elder et al. 1965). During the 2-year study period, precipitation, measured 6 km east of the study site, varied considerably. Late winter and spring precipitation was nearly normal in 1990 but 47% below normal in 1989 (Fig. 1) (NOAA 1989 and 1990).

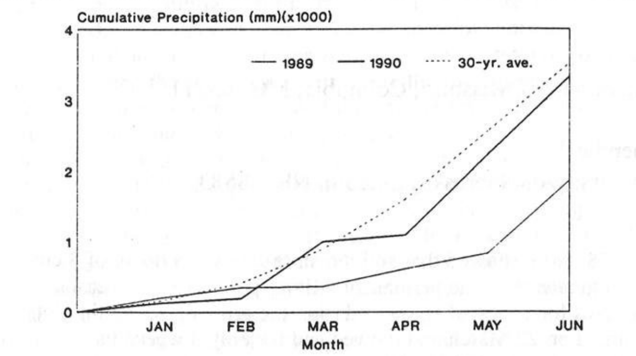

FIG. 1. Cumulative precipitation for the first 6 months of 1989 and 1990 and for the 30-year average. Precipitation was measured 6 km east of the study site.

The study area was an 8-ha field planted to big bluestem, little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*) in 1971 (J. Stubbendieck pers. comm.). The soil in the study area is a Sharpsburg silty clay loam (fine, montmorillonitic, mesic Typic Argiudoll) with slopes ranging from 0 to 12% (Elder et al. 1965). In 1982, the area was divided into 42, 250-m² plots as part of a long-term study of seasonal fire effects. Different management treatments caused some plots to become dominated by smooth brome, and others by big bluestem.

Table 1. Canopy cover for big bluestem and smooth brome in 1985 (T. Bragg pers. comm.) and visual estimates of dominance in 1989 (SB=smooth brome dominant, BB=big bluestem dominant) for plots (3, 9, 10, 16, and 27) of the long-term fire effects study area at Mead, Nebraska.

Plot	Canopy Cover, % Smooth Brome	Canopy Cover, % Big Bluestem	Dominance
3	92	38	SB
9	85	38	SB
10	2	95	BB
16	38	38	BB
27	85	38	SB

In 1989, 5 of the 42, 250-m² plots dominated by smooth brome or by big bluestem were selected for the present study (Table 1). Using these plots, treatments available for this study were smooth brome-dominated unburned, smooth brome-dominated burned, big bluestem-dominated unburned, and big bluestem-dominated burned in a split-plot completely randomized design. One randomly selected, 27-m² subplot from each smooth brome-dominatedplot and big bluestem-dominated plot was burned using a back fire on 25 March, 1989. The experiment was repeated in the spring of 1990 using five new subplots. One randomly selected subplot from each smooth brome-dominated plot and big bluestem-dominated plot was burned on 3 April. In both years, a randomly selected, 27-m² subplot was established as an unburned control in each of the five plots.

Soil moisture was measured biweekly in each subplot beginning 8 days after the burn in 1989 and on the burn date in 1990. Using a "King" tube, soil cores from a depth of 15-30 cm were obtained from three random locations in each subplot. Soil cores were stored in sealed plastic bags in the field and transferred to air-tight soil cans. Soil cores and cans were weighed and dried in a forced air oven at 55°C until a constant weight was reached. Soil moisture was expressed as the percentage of oven-dry weight of soil for each soil core and the percentages averaged in each subplot.

Soil temperature also was measured in each subplot with a Reotemp Digital Thermometer (Model FR-1) at a depth of 8 cm once a week beginning 8 days after the burn in 1989 and on the date of the burn in 1990. Five randomly selected sampling points were used to determine mean subplot soil temperatures.

An analysis of variance (ANOVA) with a means comparison test (F-protected LSD) was used to test for a significant difference between treatment means by sampling date (á = 0.10). The analyses were performed using SOLO statistical software (BMDP Statistical Software Inc. 1991).

Results and Discussion

Soil Moisture

In 1989, soil moisture did not differ until 4 May (Table 2). The burned smooth brome subplots contained the least soil moisture, the burned and unburned big bluestem subplots contained the most, and the unburned brome subplots were intermediate. This trend continued until 7 June when no significant differences occurred among treatments. Nevertheless, on 7 June, soil moisture in the burned smooth brome treatment was at a seasonal low compared to other treatments. March and April 1989 were particularly dry. Late March burning of smooth brome-dominated subplots was followed by rapid regrowth of smooth brome tillers. Elongation of smooth brome tillers in burned subplots during the first week in May was coincident with a decline in soil moisture. These concurrent events did not occur in unburned smooth brome subplots. These results suggest that smooth brome affects soil moisture in burned areas so that, in dry conditions, less soil moisture is available for later-growing species, such as big bluestem.

Table 2. Mean percent (%) soil moisture in treatment plots (BRU = brome unburned, BRB = brome burned, BBU = big bluestem unburned, and BBB = big bluestem burned) through the spring, 1989-90 at Mead, Nebraska. Numbers with the same letter by row are not significantly different at the 0.10 level (LSD).

Sample dates	Treatments BRU	 BRB	 BBU	 BBB
1989				
4-05	20.4a	19.5a	20.9a	20.3a
4-19	19.9a	19.1a	20.3a	20.2a
5-04	19.6b	16.5c	21.3a	21.0a
5-24	18.2a	13.2b	20.7a	17.6a
6-07	16.7a	12.1a	18.9a	14.6a
1990				
4-03	21.0a	20.7a	20.8a	21.2a
4-20	19.9a	19.4a	21.1a	20.2a
5-07	17.9a	19.4a	20.6a	20.3a
5-24	21.3a	20.2a	22.9a	19.6a
6-16	20.1a	18.5a	21.6a	18.5a

Hulbert (1969) thought that soil moisture differences between burned and control plots were due to both evaporation and transpiration. However, a comparison of the results of burned smooth brome and big bluestem treatments in this study indicates that transpiration from smooth brome tillers was the main cause for reduced soil moisture in burned smooth brome subplots (Table 2). This study suggests that, in burned, mixed stands of smooth brome and big bluestem, big bluestem tillers begin to grow in soil significantly drier than that encountered by tillers in stands without smooth brome (Table 2). The results of Melgoza et al. (1990) from western Nevada support this explanation. They found that plots around native plants, including a warm-season forb (*Chrysothammus viscidiflorus*), in a burned area dominated by downy brome (*Bromus tectorum*), had a faster depletion of soil water during the period of active growth of downy brome. Furthermore, they found that, once established in the open spaces around native species, downy brome was able to suppress the water potential and productivity of native species for an extended period of time.

With near normal precipitation in 1990, no significant differences in percent soil moisture occurred among treatments (Table 2). Although the response of smooth brome subplots to early burning was similar to that in 1989, soil moisture levels in 1990 in the burned smooth brome subplots did not change over the sampling period. Apparently, precipitation was adequate and distributed so that evaporation and uptake by smooth brome tillers did not deplete soil moisture. This difference between responses in 1989 and 1990 is similar to that noted on a dry-mesic to mesic Iowa prairie. Ehrenreich (1959) found that soil moisture was unaltered by burning during a wet year, whereasduring a dry year, Ehrenreich and Aikman (1963) found that burning decreased available soil moisture by 50%.

Table 3. Mean soil temperature (C°) in treatment plots (BRU = brome unburned, BRB = brome burned, BBU = big bluestem unburned, and BBB = big bluestem burned) through the spring, 1989-90 at Mead, Nebraska. Numbers with the same letter by row are not significantly different at the 0.10 level (LSD).

	Treatments			
Sample dates	BRU	BRB	BBU	BBB
1989				
4-05	4.8a	7.9b	7.7b	12.7c
4-12	4.2a	9.2c	6.1b	13.3d
4-19	6.6a	11.3b	9.7b	16.7c
4-25	14.2a	21.8c	18.8b	25.8d
5-04	11.7a	16.5c	14.4b	19.8d
5-10	11.7a	18.5c	15.5b	24.3d
5-17	13.4a	17.8c	16.0b	20.1d
5-24	17.0a	20.8c	19.5b	22.6d
5-31	16.4a	19.7c	18.0b	20.0c
6-07	17.0a	20.0b	19.5b	22.1c
1990				
4-03	4.1a	5.1ab	6.0b	4.4a
4-14	6.1a	7.8b	6.5a	8.2b
4-20	10.7a	14.2b	11.7a	14.1b
4-28	14.6a	19.9b	15.2a	20.6b
5-07	16.6a	22.6b	17.4a	23.9b
5-14	14.0a	16.9b	14.6a	17.3b
5-24	17.0a	18.9b	17.3a	19.2b
6-04	14.8a	16.6a	15.7a	19.9b
6-16	22.5a	24.4c	22.1b	23.4d

Soil Temperature

During the early portion of the 1989 growing season, burned subplots were significantly warmer than unburned subplots dominated by both smooth brome and big bluestem (Table 3). This is consistent with the response in many other studies (e.g., Hulbert 1969). Contrasting the two vegetation types, unburned smooth brome subplots were significantly cooler than unburned big bluestem subplots, most likely the result of a thicker insulating layer of thatch on the former. Unburned smooth brome subplots had been rested and not burned for over 7 years, whereas unburned big bluestem subplots had been burned annually in April for the same 7-year period. Thus, only standing dead was present. As with unburned subplots, burned smooth brome subplots were cooler than the burned big bluestem subplots (Table 3). This was probably due to a combination of two factors. First, burns in the smooth brome subplots did notcompletely consume the litter layer, thus shielding the soil surface from some incident solar radiation. Second, smooth brome tillers began to regrow immediately after the burn and shaded the soil surface in about two weeks. At the Hayden Prairie in Iowa, Ehrenreich and Aikman (1963) found that shade from vegetative regrowth following a fire became nearly as effective as litter in reducing soil temperature by early June.

In 1990, as in 1989, significant differences occurred between the burned and unburned subplots of both smooth brome and big bluestem (Table 3). However, unlike 1989, soil temperatures of burned subplots of smooth brome and big bluestem did not differ significantly until June. Similarities between the two treatments may have been due to lack of differences in soil moisture.

Conclusions

Early spring burning of degraded prairie dominated by smooth brome during a dry period can reduce soil moisture and lower soil temperatures compared to early burning of big bluestem-dominated sites. Lower available soil moisture and slower soil warming may limit big bluestem expansion in areas dominated by smooth brome.

Literature Cited

Anderson, K.L. 1965. Time of burning as it affects soil moisture in an ordinary upland bluestem prairie in the Flint Hills. Journal of Range Management 18:311-316.

Bieber, G.L., and K.L. Anderson. 1961. Soil moisture in bluestem grassland following burning. Journal of Soil and Water Conservation 16:186-187.

BMDP Statistical Software, Inc. 1991. Solo Statistical System, Los Angeles, CA.

Ehrenreich, J.H. 1959. Effect of burning and clipping on growth of native prairie in Iowa. Journal of Range Management 12:133-137.

Ehrenreich, J.H., and J.M. Aikman. 1963. An ecological study of the effect of certain management practices on native prairie in Iowa. Ecological Monographs 33:113-130.

Elder, J.A., T.E. Beesley, and W.E. McKinzie. 1965. Soil survey of Saunders County, Nebraska. U.S. Department of Agriculture-Soil Conservation Service Series 1959, Number 40.

Hadley, E.B., and B.J. Kieckhefer. 1963. Productivity of two prairie grasses in relation to fire frequency. Ecology 44:389-395.

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

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.

Kucera, C.L., and J.H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. Ecology 43:334-336.

Lamba, P.S., H.L. Ahlgren, and R.J. Muckenhirn. 1949. Root growth of alfalfa, medium red clover, bromegrass, and timothy under various soil conditions. Agronomy Journal 41:451-458.

Melgoza, G., R.S. Nowak, and R.J. Tauch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. Oecologia 83:7-13.

McMurphy, W.E., and K.L. Anderson. 1965. Burning Flint Hills range. Journal of Range Management 18:265-269.

National Oceanic and Atmospheric Administration (NOAA). 1989. Local climatological data, Mead, Nebraska. National Climatic Data Center, Asheville, North Carolina.

National Oceanic and Atmospheric Administration (NOAA). 1990. Local climatological data, Mead, Nebraska. National Climatic Data Center, Ashville, North Carolina.

Old, S.M. 1969. Microclimate, fire, and plant production in an Illinois prairie. Ecological Monograph 39:355-384.

Peet, M., R. Anderson, and M.S. Adams. 1975. Effect of fire on big bluestem production. The American Midland Naturalist 94:15-26.

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.

Steiger, T.L. 1930. Structure of prairie vegetation. Ecology 11:170-217.

Weaver, J.E. 1968. Prairie plants and their environment. University of Nebraska Press, Lincoln.

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

Willson, G.D. 1994. Burn-based smooth brome management in tallgrass prairie. Ph.D. Dissertation, University of Nebraska.

Wright, H.A., and H.W. Bailey. 1982. Fire Ecology United States and Southern Canada. John Wiley and Sons, New York. 501 pp.

Seasonal Activity of Snakes on a Kansas Floodplain Tallgrass Prairie

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Abstract. Snakes were caught in drift fence traps throughout the season of activity in a 232.9 ha floodplain tallgrass prairie in Douglas County, Kansas from 1991 through 1993. In three seasons, 6712 trap station days produced 870 captures of the five most common species of snakes: *Thamnophis sirtalis*, *Coluber constrictor*, *Thamnophis proximus*, *Lampropeltis calligaster*, and *Regina grahamii*. Most seasonal activity patterns were bimodal with a period of low activity in late July or August. Yearly variation was found to be related to food abundance, reproductive activity, or flooding.

Key Words. snakes, seasonal activity, floodplain tallgrass prairie, Kansas

Introduction

Snakes are integral parts of prairie communities. Though not as conspicuous as birds or mammals, they are important predators. Their reproduction and foraging activities are tied to optimal temperature regimes and often result in pronounced periods of inactivity during parts of the summer. Seasonal activity patterns have been considered important ecological characteristics of snakes and have been studied for nearly 70 years (Brimley 1925, Conant 1938, Klimstra 1958). A review of more recent studies by Gibbons and Semlitsch (1987) indicated two distinct patterns of seasonal activity of temperate zone snakes: bimodal patterns with peaks of activity in spring and fall and unimodal patterns with peak activity sometime between late spring and late summer. They also suggested 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. Platt (1989) studied the seasonal activity of six species of snakes over 9 years in a sand prairie in central Kansas. The present paper describes a shorter 3-year study in floodplain tallgrass prairie in eastern Kansas, in an attempt to detect not only general patterns of seasonal activity for this community but also differences between the two distinctly different Kansas communities.

Methods

The Baker University Wetlands is a 232 ha prairie tract that has been managed by Baker University since 1968. It is mostly in Sec. 18, T13S, R20E on the south edge of Lawrence, Kansas, in northeastern Kansas and lies in the Wakarusa River floodplain. A portion of the area was cultivated and most was grazed until 1958 (Boyd 1980). Native wetland prairie that has never been plowed is found in only two small areas totalling about 18 ha. These prairies were designated as a National Natural Landmark by the Department of Interior and National Park Service in 1969. Approximately 81 ha of the cultivated land has been replanted to native grasses and forbs. The grazed area has been returned to a reasonably diverse wetland prairie through burning and selective mowing. Characterisitic plant species in the native habitat areas are cordgrass (*Spartina pectinata*), eastern gammagrass (*Tripsacum dactyloides*), switchgrass (*Panicum virgatum*), big bluestem (*Andropogon gerardii*), ironweed (*Vernonia fasciculata*), coreopsis beggar-ticks (*Bidens polylepis*), Maximillian sunflower (*Helianthus maximiliani*), Jerusalem artichoke (*Helianthus tuberosa*), large-toothed sunflower (*Helianthus grosseserratus*), and numerous species of *Carex*, *Eleocharis*, *Cyperus*, and *Scirpus*. Depressions are flooded during wet seasons, and several large (0.81-2.43 ha) pools have been created to retain water for longer periods of time.

From 10 to 30 stations with live traps were operated continously from mid-April or early May to late October or early November from 1991 through 1994, except that trapping was stopped for a week in August in 2 years. A trap station consisted of an 8-m low, metal, drift fence with either four funnel traps near the ends on each side or a single funnel trap fitted on each end, modified from those described by Fitch (1951). The fence was arranged as a cross with a N-S line of 18 stations, 2 m apart along 180 m and an E-W line of 10 stations, 2 m apart along 100 m. It ran north from a random point in the center of the western half of the wetlands. A total of 6712 trap station days was completed in the 3 complete years (1991-93) covered in this paper. A trap station day is the use of one trap station for 24 hours.

Earlier studies did not standardize or quantify capture effort. Because traps did not attract snakes but merely intercepted moving snakes, capture rates are calculated as a quantitative index of snake activity. Few snakes were caught before the first of May or after the end of October. Following the example of Platt (1989), each month was divided into approximately 15-day trapping periods. For each trapping period, capture rates were calculated as the number of captures per 1000 trap station days (TSD), using the total captures and trapping effort in that trapping period in all 3 years. Proportions of sexes in the sample indicated which groups were more active and were compared with chi square tests.

Biases associated with the use of drift fences with pitfall traps were discussed by Gibbons and Semlitsch (1982), and some of their comments apply to funnel traps and drift fences used in this study. Not all members of the snake population were equally susceptible to capture. Young snakes of some species could escape through the 6mm mesh of the traps. The data reported here pertain to the trappable population.

The difference in elevation between the highest and lowest points in this part of the wetlands is less than 30 cm, so the same relative numbers of water-filled depressions were found among the trap stations. No noticeable differences occurred in trap productivity among stations. Prey organisms of snakes were captured in the funnel traps, and their numbers recorded.

All snakes were marked individually by clipping scales, weighed, measured, palpated to count eggs or young, and released at the site of capture.

Results and Discussion

A total of 870 captures was made of the five most abundant species of snakes included in this report: common garter snake (*Thamnophis sirtalis*), 474 captures; racer (*Coluber constrictor*) 157 captures; western ribbon snake (*Thamnophis proximus*), 135 captures; prairie kingsnake (*Lampropeltis calligaster*), 116 captures; and Graham's crayfish snake (*Regina grahamii*), 58 captures. Other species of snakes that make up this community but that were sampled infrequently include the rat snake (*Elaphe obsoleta*), northern water snake (*Nerodia sipedon*), and plains garter snake (*Thamnophis radix*).

Common Garter Snakes

Total capture rates for garter snakes had large seasonal variation in a bimodal pattern with peaks in late May or June (depending on the year) and early or late September (Figure 1). Low activity appears to be in early July through early August. The peak in September is very pronounced and may include a number of young that grow from 140-179 mm (snout vent lenth=SLV) at birth to about 400 mm during the summer. Few small snakes were captured during the trapping season. Platt (1989) noted that, because of variable growth, particularly in different years, first-year snakes cannot be identified in a multi-year sample.

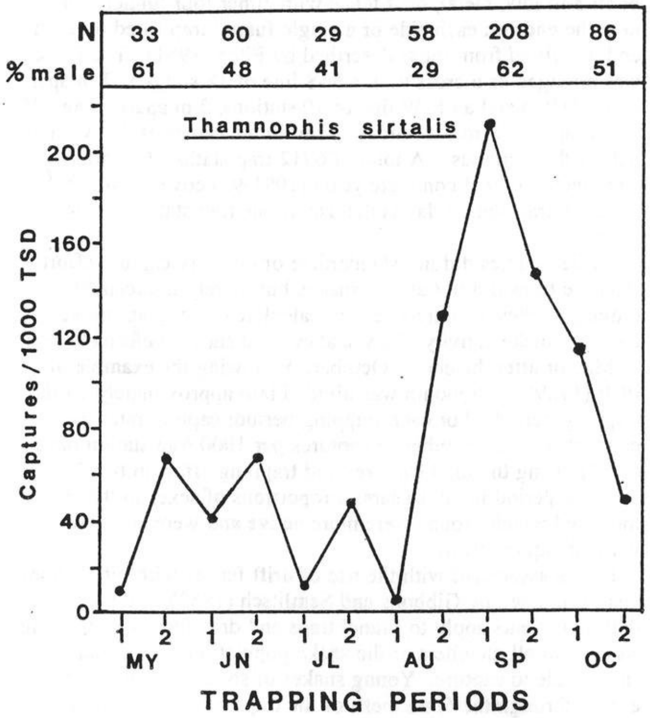

FIG. 1. Capture rates of common garter snakes in half-month trapping periods from May to October averaged over 3 years (1991-1993). "N" is sample size or total captures in month in 3 years. "TSD" is trap station days.

The higher percentages of males in May (comparison of May to July-August sample : Chi square = 13.51, P< 0.001) and September samples (comparison of September sample to July-August sample: Chi square = 14.62, P< 0.001) indicate increased male activity and perhaps both spring and fall mating (Figure 1). Fitch (1970) reported that common garter snakes mated in spring and fall.

Although Platt (1989) found that increased activity of common garter snakes in fall was due to recruitment of young snakes, causing a larger trappable population, this did not seem to be the case here. Only 3% of my August-September sample fell in the 308-490 mm SVL range, and only 7% of my October sample fell in this range. Increased activity of larger snakes, particularly males, was observed here as it was by Platt (1989).

Some variation in capture rates among years seemed to reflect abundance of food. When captures of plains leopard frog (*Rana blairi*) were low in 1991 (average of 75 frogs per 1000 TSD from mid-May to mid-July), the capture rates of garter snakes were also low (15 snakes per 1000 TSD). All but the deepest bodies of water were dry by mid July that summer. Precipitation was greater in 1992 and 1993 than 1991, and wet conditions lasted most of the summer. Frog captures were about 1000 per 1000 TSD, and garter snake numbers averaged 24 per 1000 TSD. Snakes may have withdrawn from the area around the traps during dry periods to feed on frogs concentrated in the remaining big pools.

Racers

Total capture rates of racers had a bimodal seasonal pattern with very high numbers in May, low numbers in July and early August, and higher numbers in the fall (Figure 2). This pattern is similar to the one found by Platt (1989), though his peaks were not so pronounced. Platt found that capture rates remained high in July and August in some years. The years of data in the present study may be too few to catch such a pattern.

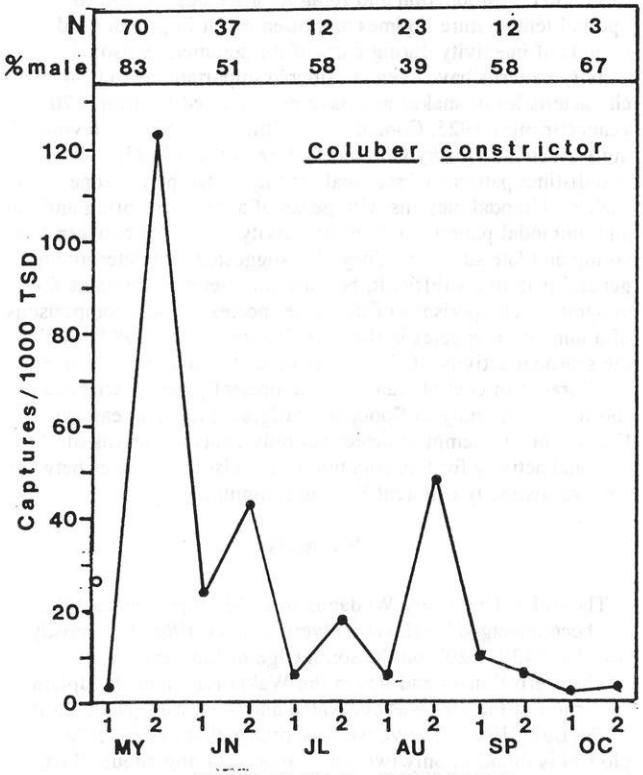

FIG. 2. Capture rates of racers in half-month trapping periods from May to October averaged over 3 years (1991-1993). "N" is sample size or total captures in month in 3 years. "TSD" is trap station days.

Because of their small size, few hatchlings were caught in the fall, so the total population of racers is probably much larger than that sampled. The high capture rate in May might have been due to activities of males searching for females (sex proportions in May sample compared to July-August: Chi square = 24.9, P< 0.001). No significant increase in males occurred in fall samples (Chi square = 1.81, P> 0.1). Fitch (1970) reported no fall mating for this species.

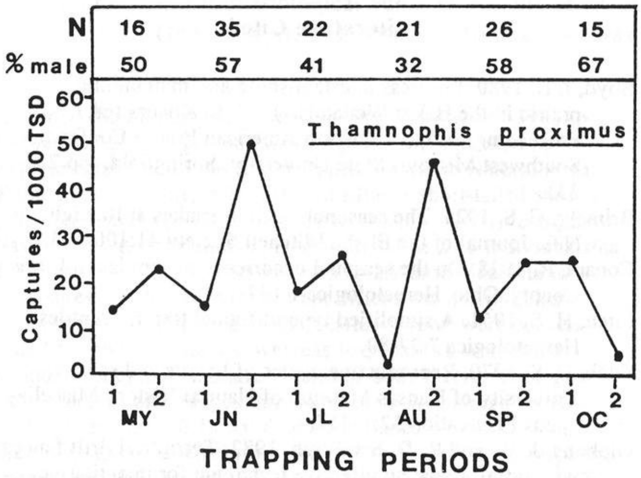

FIG. 3. Capture rates of western ribbon snakes in half-month trapping periods from May to October averaged over 3 years (1991-1993). "N" is sample size or total captures in month in 3 years. "TSD" is trap station days.

Western Ribbon Snakes

Total capture rates of western ribbon snakes shows a bimodal pattern with a peak in late June and late August and a period of reduced activity in July and August (Figure 3). The fairly large number of captures indicated for late July is largely a reflection of the data from 1993, when water levels were very high and numbers of frogs metamorphosing was also high. Total captures increased steadily over the 3-year period as more water was retained in the wetlands.

Higher percentages of males in June (comparison of June sample to July sample: Chi square = 7.67, P< 0.01) and late August (comparison of August to July sample: Chi square = 8.84, P< 0.01) indicate increased male activity. Fitch (1970) made no mention of fall breeding. Because of the narrow head in this species, even fairly large individuals (> 400 mm SVL) can work their way out of a 6-mm mesh trap and, thus, may be underrepresented in the sample. Very few young were captured in the fall (< 1%).

Prairie Kingsnakes

The data for prairie kingsnakes show only a weak indication of a bimodal pattern (Figure 4). Periods of increased activity occur in early May, in late June, and again in late August, with decreased activity in July and early August. The sample may have been too small to accurately reflect the true pattern of activity.

Males did not comprise a significantly greater proportion of the sample in May (comparison of May sample to July-August sample: Chi square = 0.08, P>.25) or in September (comparison of September sample to July-August sample: Chi square = 1.30, P> 0.25) than at midsummer. Fitch (1970) noted that this genus breeds in the spring. Few young were captured in this sample. Succeedingly fewer captures were made over the 3-year period as conditions became more mesic.

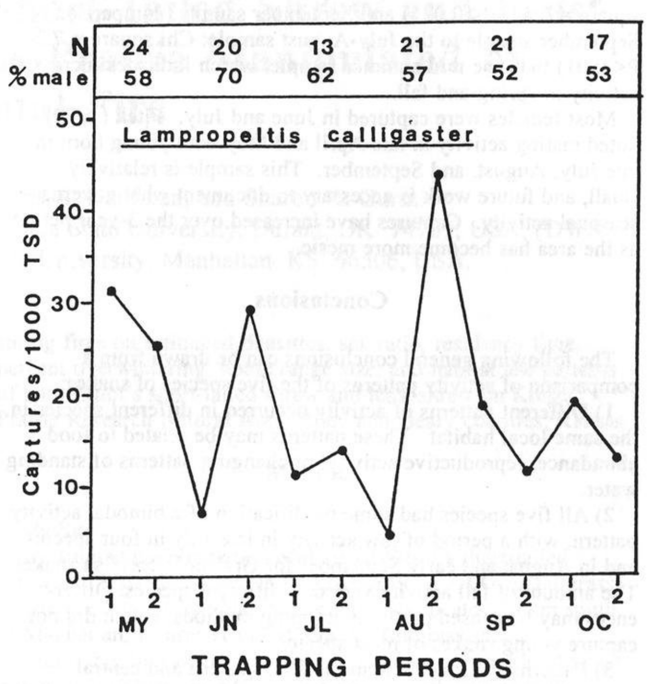

FIG. 4. Capture rates of prairie kingsnakes in half-month trapping periods from May to October averaged over 3 years (1991-1993). "N" is sample size or total captures in month in 3 years. "TSD" is trap station days.

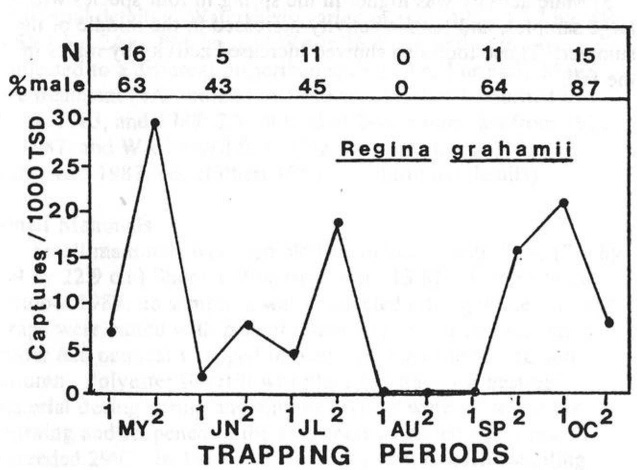

FIG. 5. Capture rates of Graham's crayfish snakes in half-month trapping periods from May to October averaged over 3 years (1991-1993). "N" is sample size or total captures in month in 3 years. "TSD" is trap station days.

Graham's Crayfish Snakes

The pattern of activity for crayfish snakes shows a peak in late May, another in late July, and a third in early October (Figure 5). A distinct period of inactivity occurred in August and early September for all 3 years. The peak in July is largely a function of data from 1993 when over 26 cm of precipitation fell in the wetlands and was retained for several weeks.

Males comprised a significantly larger portion of the May sample (comparison of May sample to July-August sample: Chi square = 6.52, P< 0.025) and September sample (comparison of September sample to the July-August sample: Chi square = 7.28, P< 0.01) than the mid-summer sample, which indicates increased activity in spring and fall.

Most females were captured in June and July. Fitch (1970) noted mating activity in late April and May with young born in late July, August, and September. This sample is relatively small, and future work is necessary to document what governs seasonal activity. Captures have increased over the 3-year period as the area has become more mesic.

Conclusions

The following general conclusions can be drawn from a comparison of activity patterns of the five species of snakes:

1) Different patterns of activity occurred in different species in the same local habitat. These patterns may be related to food abundance, reproductive activity, or changing patterns of standing water.

2) All five species had some modification of a bimodal activity pattern, with a period of low activity in late July in four species and in August and early September for Graham's crayfish snakes. The amount of fall activity varied in different species. Differences may be caused partly by trapping methods, which did not capture young snakes of most species.

3) Patterns for species found in both eastern and central Kansas are similar, with small differences in timing and extent of activity.

4) For all species, year-to-year variation existed. In common garter snakes and western ribbon snakes, much of this variability may have been due to changes in prey abundance. In Graham's crayfish snakes, it may have been a function of availability of standing water.

5) Male activity was higher in the spring in four species with large samples, and female activity increased in the middle of the summer. Those four also showed increased activity by males in the fall.

Acknowledgements

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Literature Cited

Boyd, I. L. 1980. Progress in establishing and maintaining prairie in the Baker Wetlands. In C. L. Kucera (ed.) Proceedings of the 7th North American Prairie Conference. Southwest Missouri State University, Springfield. pp 231-233.

Brimely, 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. In R. A. Siegel, J. T. Collins, and S. S. Novak (eds). Snakes: Ecology and Evolutionary Biology. Macmillan Publishing Company, New York. pp 396-421.

Klimstra, W. D. 1958. Some observations on snake activities and populations. Ecology 39:232-239.

Platt, D. R. 1989. Seasonal activity of snakes on a sand prairie. In T. B. Bragg and J. Stubbendieck (eds). Proceedings of the 11th North American Prairie Conference, University of Nebraska, Lincoln. pp 251-254.

Population Ecology of Elliot's Short-Tailed Shrew and Least Shrew in Ungrazed Tallgrass Prairie Manipulated by Experimental Fire

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Abstract. Small mammals were sampled from March 1983 to October 1987 in ungrazed tallgrass prairie manipulated by experimental fire on the Konza Prairie Research Natural Area, Kansas. We captured 806 different Elliot's short-tailed shrews (*Blarina hylophaga* Elliot) and 69 least shrews (*Cryptotis parva* Say). Estimated densities ranged from 1.7 to 24.6 individuals/ha for short-tailed shrews and from 0.5 to 2.9 individuals/ha for least shrews. The sex ratio did not differ from 1:1 in either soricid species. Captures of short-tailed shrews were concentrated in lowland habitats, whereas least shrews were most abundant in upland habitats. Males of both species had significantly larger home ranges than females (*B. hylophaga*: males = 0.26 ha; females = 0.14 ha; *C. parva*: males = 0.56 ha; females = 0.23 ha). Short-tailed shrews exhibited a fire-negative response immediately following a fire, as well as in years after a fire. We did not detect a response to fire by least shrews, but abundance was low, which may have precluded detection of any fire response. Residency time and overwintering success did not differ between females and males for either species.

Key words: *Blarina hylophaga*, *Cryptotis parva*, Elliot's short-tailed shrew, fire response, least shrew, tallgrass prairie

Introduction

Elliot's short-tailed shrew (*Blarina hylophaga*) and the least shrew (*Cryptotis parva*) inhabit a diversity of woodlands and grasslands in Kansas (Bee *et al.* 1981). Both soricid species prefer habitats with well-developed litter layers (Choate and Fleharty 1975, Davis and Joeris 1945, Kaufman *et al.* 1989); however, least shrews probably are more tolerant of xeric conditions than short-tailed shrews (Whitaker 1974). Short-tailed shrews exhibit a negative response to fire (Kaufman *et al.* 1990); response of least shrews to fire has not been studied.

Tallgrass prairie once occupied about 3% of North America (Küchler 1964). Since European settlers arrived on the Great Plains, most of this habitat has been lost or fragmented into isolated remnants except for the Flint Hills of southeastern Nebraska, eastern Kansas, and north-central Oklahoma (Hulbert 1985). The rolling topography of the Flint Hills precluded conversion to row crops, although livestock ranching occurs throughout the region. Nevertheless, native species of prairie plants persist as the dominant vegetation.

Restoration of native prairie is being promoted throughout the midwestern United States (Bragg and Stubbendieck 1989, Smith and Jacobs 1992, Wickett *et al.* 1994). Impact of management and agricultural practices, such as fire and grazing, must be better understood to ensure success of both preservation and restoration of tallgrass prairie. The objectives of this study were to assess the influence of topoedaphic conditions and prescribed spring fires on estimated densities, sex ratio, residency time, percent overwintering, home range size, and habitat use patterns of both Elliot's short-tailed shrew and least shrew on Konza Prairie Research Natural Area, Riley and Geary counties, Kansas.

Methods

Study Site

We studied the population ecology of Elliot's short-tailed shrew and least shrew on the Konza Prairie, a 3,487 ha tallgrass prairie preserve of The Nature Conservancy located 10 km south of Manhattan, Kansas (Hulbert 1985). Tallgrass species, including big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), Indian grass (*Sorgahstrum nutans*), and switchgrass (*Panicum virgatum*), are the dominant plant species. The topography of Konza Prairie is characterized by flat ridge tops, terraced hillsides, and lowland valleys (Jantz *et al.* 1975). Soils range from shallow and xeric in uplands to deep and mesic in lowlands.

Our study area included portions of two to four conterminous watersheds (see Clark 1989, Clark *et al.* 1990, Gurtz 1985 for additional details). Watersheds varied in size (4A = 17.7 ha; 4B = 55.1 ha; 2A = 29.6 ha; and WA = 26.6 ha), and each was subjected to a different prescribed spring (April or early May) fire treatment (4A: burned in 1980 and 1984; 4B: burned in 1979, 1983, and 1987; 2A: burned at 2-year intervals from 1973 to 1987; and WA burned following wet years in 1983, 1985, 1986, and 1987; see Hulbert 1985 for additional details).

Small Mammals

Small mammals were sampled periodically with large (7.6 by 8.9 by 22.9 cm) Sherman live traps from 13 March 1983 to 28 October 1987; no sampling was conducted during winter months. Traps were baited with peanut butter in summer and peanut butter and oatmeal wrapped in weighing paper in spring and autumn. Polyester fiberfill was placed in traps for nesting material during spring and autumn. Traps were closed in the morning and reopened in the afternoon when temperatures exceeded 29°C. In 1986 and 1987, traps set in each sampling period were prebaited with peanut butter placed on the open back door 2 days prior to the start of each trapping period. Traps with the back door open were left on the grid between all trapping periods. All shrews were toe-clipped uniquely and immediately released after pertinent data were recorded.

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Small mammals were sampled from 13 March to 23 November 1983 on a 5.4-ha trapping grid (10 by 24 stations; two traps per station; 15-m interstation interval) that was situated across portions of two contiguous watersheds (4A, 2.84 ha; 4B, 2.56 ha). Small mammals were sampled for 4 days every other week, except for a few weeks before and after the prescribed spring burn. During each period, alternate rows of the grid were set for 2 days and then moved to the other set of rows for 2 more days. Small mammals were sampled for 11 days between 4 February and 28 March 1984 on the same 10 by 24 station grid used in 1983. From 11-18 April 1985, a 14 by 24 station area (one trap per station; 15-m interstation interval) contiguous with the original 10 by 24 station grid was set. For 8 nights between 19-29 April 1984, the entire 13-ha grid (24 by 24 stations) was set (one trap per station). This new area included portions of four contiguous watersheds (4A, 6.91 ha; 4B, 4.58 ha; 2A, 1.17 ha; and WA, 0.34 ha). Beginning in May 1984 and continuing through October 1987, one trap per station was used on alternate rows of the grid. From 2 May to 2 December 1984, traps were set for 2 days, followed by an immediate switch to traps on the other set of rows for 2 days. Rows used first during a period alternated in each trapping period. Traps on alternate rows were set for 2 to 4 nights during 1985 (9 March-27 October) and 2 nights in 1986 (15 March-7 November) and 1987 (21 March-28 October).

Analysis

Even though trapping effort varied among years, we believe data are comparable because the entire study area was sampled in each trapping period, not all traps were used by small mammals during each period, and intensity and duration of effort were sufficient to capture most all shrews using the grid. Density (individuals/ha) of shrews was estimated by dividing number of individuals by the area of the entire grid. A sign test (corrected for ties; normal approximation Z_c) was used to assess for differences in estimated density between burned and unburned prairie for captures on watersheds 4A and 4B. We used the log-likelihood ratio test (*G*-test) to assess for heterogeneity in sex ratio, topographic use patterns, and overwinter survivorship. Yates correction for continuity was applied when appropriate; Fisher's exact test was used when sample sizes were small. Expected values for topographic use patterns were calculated from numbers of traps in each topographic position. Home range size was estimated with the minimum convex polygon method (Mohr 1947). We used the general linear models procedure (GLM, SAS Institute, Inc. 1985) to test for effects of sex, year, and interaction between sex and year on home range size. Only animals that were captured ≥ 5 times and resided on the grid for ≥ 30 days were used in this analysis. Duncan's new multiple range test was used to differentiate means ($P < 0.05$). We used the Mann-Whitney *U*-test (X^2 approx.) to assess for differences in number of days between first and last capture (residency time) between sexes.

Results

We trapped 806 individuals in the 1,486 captures of Elliot's short-tailed shrew and 69 individuals in the 136 captures recorded for the least shrew (Table 1). Estimated densities varied more than 14-fold for short-tailed shrews (individuals/ha = 1.7, 7.4, 16.9, 24.6, and 16.7 for each year from 1983 to 1987, respectively) and more than five-fold for least shrews (individuals/ha = 0.6, 0.9, 2.9, 1.0, and 0.5 for each year from 1983 to 1987, respectively). Sex ratios for short-tailed shrews did not differ significantly from 1:1 for any year or all years pooled ($G \leq 0.77$, $d.f. = 1$, $P > 0.10$). For least shrews, significantly more females were captured in 1984 ($G = 8.15$, $d.f. = 1$, $P < 0.01$); however, sex ratios did not differ from 1:1 for any other year or for all years pooled ($G \leq 3.27$, $d.f. = 1$, $P > 0.05$).

Table 1. Numbers of individuals (Ind.) and captures (Cap.) of Elliot's short-tailed shrew and least shrew on Konza Prairie from 1983 to 1987.

	1983		1984		1985		1986		1987	
Species	Ind.	Cap.	Ind.	Cap.	Ind.	Cap.	Ind.	Cap.	Ind.	Cap.
Short-tailed Shrew										
Males	2	3	40	66	103	209	162	311	114	148
Females	4	11	48	76	116	250	158	268	103	123
Least Shrew										
Males	0	0	1	1	17	49	5	6	4	4
Females	0	0	11	12	20	48	8	8	3	4

Note.--Sex was not recorded in 1983 for three individuals and three captures of short-tailed shrews and for three individuals and four captures of least shrews.

Trap mortality was high for short-tailed shrews; 29.8% of all individuals died in traps on their first capture. Similar numbers of females (125 of 408 individuals) and males (115 of 395) died in traps during the first capture ($G = 0.22$, $d.f. = 1$, $P > 0.10$); 138 short-tailed shrews also died in traps on subsequent captures (65, 71, and 2 individuals for females, males, and sex unknown, respectively). In addition to those dying in traps on their first capture, 168 females and 146 males were captured only during a single trap period. When only shrews captured during more than one trap period were considered, residency time did not differ between females and males (X^2 approx. = 0.1, $d.f. = 1$, $P > 0.10$; females: median = 58 days, range = 12-555 days; males: median = 51 days, range = 11-400 days). Additionally, 113 of 283 females and 130 of 280 males captured in more than one trap period were classified as residents during the 5 years; this pattern did not differ between males and females ($G = 2.4$, $d.f. = 1$, $P > 0.10$). Proportions of females and males that overwintered on the grid did not differ for any winter ($G \leq 1.19$, $d.f. = 1$, $P > 0.10$) or for all years combined (females: $n = 21$; males: $n = 24$; $G = 0.37$, $d.f. = 1$, $P > 0.10$; Table 2).

For least shrews, trap mortality during the first capture was 8.7%; this pattern did not differ significantly between females (4 of 40 individuals) and males (2 of 26; $G = 0.11$, $d.f. = 1$, $P > 0.10$). Six additional individuals died in traps on subsequent captures. Furthermore, 26 females and 19 males were captured only in a single trap period. Residency time did not differ between males and females when only individuals captured in more than one trap period were considered (X^2 approx. = 0.0, $d.f. = 1$, $P > 0.10$; females: median = 39 days, range = 14-378 days; males: median = 49 days, range 24-395 days). Across all years, similar proportions of females (13 of 36) and males (7 of 24) established residency on the study area ($G = 0.16$, $d.f. = 1$, $P > 0.10$). Only three least shrews, two females and one male, overwintered on the study area.

Table 2. Overwinter persistence of Elliot's short-tailed shrews on Konza Prairie.[1]

Years	Females	Males	Total
1983-1984			
# in 1983	4	2	6
# survived to 1984	0	0	0
% overwintered	0	0	0
1984-1985			
# in 1984	20	21	41
# survived to 1985	4[2]	4	8
% overwintered	20.0	19.0	19.5
1985-1986			
# in 1985	78	71	149
# survived to 1986	9[2]	6	15
% overwintered	11.5	8.5	10.1
1986-1987			
# in 1986	92	93	185
# survived to 1987	9	14	23
% overwintered	9.8	15.1	12.4
Total			
before winter	194	187	381
after winter	21	24	45
% overwintered	10.8	12.8	11.8

[1] Numbers do not include animals that died in traps.
[2] Includes an individual captured in 1984 and recaptured in 1986.

Short-tailed shrews consistently used lowlands more and uplands less than expected by chance; use of breaks on hillsides did not difffer from random expectation (Table 3). No differences in habitat use were evident among years for females (G = 6.9, $d.f.$ = 8, $P > 0.10$) or males (G = 7.8, $d.f.$ = 8, $P > 0.10$) or between females and males for all years pooled (G = 0.6, $d.f.$ = 2, $P > 0.10$). In contrast, least shrews were more abundant in upland compared to lowland prairie (Table 4). No differences were noted in use of topographic sites among years for females (G = 7.8, $d.f.$ = 6, $P > 0.10$) or males (G = 4.2, $d.f.$ = 6, $P > 0.10$) or between females and males for all years pooled (G = 1.67, $d.f.$ = 2, $P > 0.10$).

Table 3. Numbers of captures of Elliot's short-tailed shrew in three topographic sites on Konza Prairie.

Year	Category	Upland	Breaks	Lowland	G	P
1983	Observed	2	6	4	0.3	> 0.10
	Expected[1]	3.1	3.7	5.3		
1984	Observed	24	36	52	11.6	< 0.01
	Expected	36.6	39.5	36.0		
1985	Observed	71	97	112	10.0	< 0.01
	Expected	91.4	98.7	89.9		
1986	Observed	114	125	143	5.0	> 0.05
	Expected	124.7	134.6	122.7		
1987	Observed	67	89	81	2.1	> 0.10
	Expected	77.4	83.5	76.1		
Total	Observed	278	353	392	21.8	< 0.001
	Expected	333.9	360.5	328.6		

[1] Expected values calculated by using proportion of study area in each topographic class.

Table 4. Numbers of captures of least shrews in three topographic sites on Konza Prairie.

Year	Category	Upland	Breaks	Lowland	G	P
1983	Observed	0	3	0		nt
	Expected[1]	0.8	0.9	1.3		
1984	Observed	5	3	4	0.6	> 0.10
	Expected	3.9	4.2	3.9		
1985	Observed	30	17	5	18.3	< 0.001
	Expected	17.0	18.3	16.7		
1986	Observed	10	3	0	12.5	< 0.01
	Expected	4.2	4.6	4.2		
1987	Observed	5	2	0	5.6	> 0.05
	Expected	2.3	2.5	2.2		
Total	Observed	50	28	9	29.5	< 0.001
	Expected	28.4	30.7	27.9		

[1] Expected values calculated by using proportion of study area in each topographic class.

Home range size was significantly larger for male than female short-tailed shrews (F = 5.1, $d.f.$ = 1, $P < 0.05$; Table 5). Home range size was not influenced by year (F = 0.6, $d.f.$ = 2, $P > 0.10$) or interaction between sex and year (F = 0.5, $d.f.$ = 2, $P > 0.10$). Similarly, male least shrews had significantly larger home ranges than females in 1985 (F = 25.5, $d.f.$ = 1, $P < 0.01$); home range size could not be calculated for other years because of insufficient captures.

Table 5. Mean home range sizes (ha) for Elliot's short-tailed shrew and least shrew on Konza Prairie.

	1984			1985			1986		
Species	n	X	SE	n	X	SE	n	X	SE
Short-tailed Shrew									
Males	1	0.44		8	0.29	0.09	13	0.22	0.05
Females	1	0.20		13	0.13	0.02	8	0.15	0.06
Least Shrew									
Males				6	0.56	0.05			
Females				3	0.23	0.01			

Estimated densities of short-tailed shrews were greater in unburned than burned prairie during 27 of 36 trap periods in years following spring fires (1983, 1984, and 1987) on a portion of the grid (Z_c = 2.83, $P < 0.01$). This fire-negative response persisted for several years after a fire. Density of short-tailed shrews was greater for the area left unburned the longest when compared to the most recently burned portion of the study area during 45 of 66 trap periods in which shrews were captured during the 5 years (Z_c = 2.83, $P < 0.01$). In contrast, least shrews did not exhibit a response to fire; densities were similar between burned and unburned prairie during the year of a fire (Z_c = 0.27, $P > 0.10$) and between more recently and less recently burned prairie (Z_c = 1.28, $P > 0.10$).

Discussion

Short-tailed shrews vary markedly in abundance, from about 2 to 121 individuals/ha (Getz 1989, Jackson 1961, Platt 1968, Williams 1936). We also documented year-to-year variation in numbers of Elliot's short-tailed shrews; however, maximum estimated density (ca. 25 individuals/ha) on Konza Prairie was less than that recorded elsewhere. Howell (1954) estimated a density of 1.7 least shrews/ha in old-field habitats, but suggested that 5.0 shrews/ha was a more realistic value. Although we recorded lower values during 4 of 5 years, our range of densities probably does not represent significantly lower numbers, especially because our trapping methodology was not designed specifically to catch shrews.

We were surprised by the high frequency of trap mortality on the first capture (29.8%) and subsequent captures (24.4%) of Elliot's short-tailed shrews. However, Getz (1989) reported similar values (28.6% and 20.4% mortality on first and subsequent captures, respectively) for northern short-tailed shrews (*B. brevicauda*) in Illinois. Even though trap mortality was high in both studies, it did not differ between sexes or seasons. Trap mortality was markedly less for least shrews (8.7% and 9.5% mortality on first and subsequent captures, respectively). Given the high metabolic rate of least shrews (McNab 1991, Whitaker 1974), a higher incidence of trap mortality was expected, especially because we checked traps only once per day.

Average residency time of Elliot's short-tailed shrews was about 2 months and did not differ between sexes. Getz (1989) documented similar results for northern short-tailed shrews in Illinois. Maximum longevity in the wild was reported as 18 months or less (see Getz 1989, Manville 1949, Pearson 1945), similar to the maximum time between first and last captures for an individual during our study (18-19 months).

Average residency time on the study area did not differ between males and females for least shrews and averaged between 1 and 2 months; maximum time spent on our study area was 12-13 months. Pfeiffer and Gass (1963) documented that a captive least shrew lived for 21 months, and Mock (1982) reported a maximum survival time in captivity was 30 months.

Previous studies concerning northern short-tailed shrews have reported greater than 90% winter mortality (Barbehenn 1958, Gottschang 1965, Jackson 1961, Pearson 1945). The 11.8% overwinter persistence documented for Elliot's short-tailed shrews during our study was consistent with these results. Only 3 of 69 least shrews overwintered on the study area.

Mean home range size was significantly greater for male (0.26 ha) than female (0.14 ha) Elliot's short-tailed shrews on Konza Prairie. These values were less than the average home range size (2.5 ha) reported for northern short-tailed shrews (Blair 1940). Although Elliot's short-tailed shrew is somewhat smaller (13-16 g) than the northern short-tailed shrew (20-30 g; Jones *et al.* 1985), this alone probably does not account for differences in sizes of home ranges between the two species. Smaller home ranges for short-tailed shrews on Konza Prairie may be due, at least in part, to the restricted distribution and high plant productivity of lowlands (Abrams and Hulbert 1987; Abrams *et al.* 1986; Anderson and Fly 1955; Clark 1989; Gibson and Hulbert 1987; Hulbert 1986). Shallow, xeric, and poorly developed soils in uplands and along hillsides influence plant species composition, as well as reduce plant productivity and litter accumulation (see Abrams and Hulbert 1987; Abrams *et al.* 1986; Anderson and Fly 1955; Clark 1989; Gibson and Hulbert 1987; Hulbert 1986). Rate of accumulation and depth of plant litter are greatest in lowland habitats; therefore, greater abundance of Elliot's short-tailed shrew in lowlands compared to either uplands or hillsides was expected.

Female least shrews on Konza Prairie had home ranges similar in size to that reported by Howell (1954) for a single female; however, home range size for male least shrews on Konza Prairie was more than 300% greater than that reported for a single male by Howell (1954).

The fire-negative response exhibited by Elliot's short-tailed shrew was expected, because previous studies have documented that this species prefers habitats with a dense groundcover (Choate and Fleharty 1975; Clark 1989; Kaufman *et al.* 1989). Elsewhere on Konza Prairie, this shrew was more abundant on unburned than burned habitats (Clark *et al.* 1989; Finck *et al.* 1986; Kaufman *et al.* 1990). Additionally, northern short-tailed shrews in Illinois were impacted negatively by fire (Schramm 1970; Schramm and Wilcutts 1983; Springer and Schramm 1972). Greater abundance in lowland habitats on Konza Prairie is consistent with use of unburned over burned sites.

We were surprised by the lack of a fire-negative response by least shrews, especially given their preference for habitats with a well-developed ground cover (Davis and Joeris 1945). However, we captured few least shrews during years when prescribed fires burned large portions of the study area (1983, 1984, and 1987), and this may account for lack of a detectable fire response. Most least shrews (50% of the females; 65% of the males) were captured in 1985 (1 or 2 years after prescribed fires on the two main watersheds of the study area). Sufficient ground cover probably had accumulated by 1985 to provide their preferred habitat.

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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.

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.

Anderson, K. L., and C. L. Fly. 1955. Vegetation-soil relationships in Flint Hills bluestem pastures. Journal of Range Management 8:163-169.

Barbehenn, K. R. 1958. Spatial and population relationships between *Microtus* and *Blarina*. Ecology 21:284-288.

Bee, J. W., G. E. Glass, R. S. Hoffman, and R. R. Patterson. 1981. Mammals in Kansas. University of Kansas, Museum of Natural History Public Education Series 7:1-300.

Blair, W. F. 1940. Notes on home ranges and populations of the short-tailed shrew. Ecology 21:284-288.

Bragg, T. B., and J. Stubbendieck (eds.). 1989. Prairie Pioneers: Ecology, History and Culture. Proceedings of the Eleventh North American Prairie Conference. University of Nebraska Printing, Lincoln.

Choate, J. R., and E. D. Fleharty. 1975. Synopsis of native, Recent mammals of Ellis County, Kansas. Occasional Paper 37:1-80, The Museum, Texas Tech University, Lubbock.

Clark, B. K. 1989. Influence of litter and habitat structure on small mammal assemblages: experimental manipulations and field observations. Ph.D. Dissertation, Kansas State University, Manhattan.

Clark, B. K., D. W. Kaufman, E. J. Finck, and G. A. Kaufman. 1989. Small mammals in tall-grass prairie: patterns associated with grazing and burning. Prairie Naturalist 21:177-184.

Clark, B. K., D. W. Kaufman, G. A. Kaufman, S. K. Gurtz, and S. Hand Bixler. 1990. Population ecology of thirteen-lined ground squirrels in ungrazed tallgrass prairie manipulated by fire. *In* D. D. Smith and C. A. Jacobs (eds.). Proceedings of the Twelfth North American Prairie Conference. University of Northern Iowa, Cedar Falls, pp. 51-54.

Davis, W. B., and L. Joeris. 1945. Notes on the life history of the little short-tailed shrew. Journal of Mammalogy 26:136-138.

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 Konza Prairie Research Natural Area, Kansas. Prairie Naturalist 18:153-166.

Getz, L. L. 1989. A 14-year study of *Blarina brevicauda* populations in east-central Illinois. Journal of Mammalogy 70:58-66.

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.

Gottschang, J. L. 1965. Winter populations of small mammals in old fields in southwestern Ohio. Journal of Mammalogy 46:44-52.

Gurtz, S. K. 1985. Habitat selection by small mammals: seasonality of responses to conditions created by fire and topography in tallgrass prairie. M.S. Thesis, Kansas State University, Manhattan.

Howell, J. C. 1954. Populations and home ranges of small mammals on an overgrown field. Journal of Mammalogy 35:177-186.

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

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

Jackson, H. H. T. 1961. Mammals of Wisconsin. University of Wisconsin Press, Madison. 504 pp.

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. United States Department of Agriculture, Soil Conservation Service, United States Printing Office, Washington, DC.

Jones, J. K., Jr., D. M. Armstrong, and J. R. Choate. 1985. Guide to Mammals of the Plains States. University of Nebraska Press, Lincoln.

Kaufman, D. W., E. J. Finck, and G. A. Kaufman. 1990. Small mammals and grassland fires. *In* S. Collins and L. J. Wallace (eds.). Fire in North American Grasslands. University of Oklahoma Press, Norman, pp. 46-80.

Kaufman, D. W., G. A. Kaufman, and E. J. Finck. 1989. Rodents and shrews in ungrazed tallgrass prairie manipulated by fire. *In* T. B. Bragg and J. Stubbendieck (eds.). Proceedings of the Eleventh North American Prairie Conference, University of Nebraska Press, Lincoln, pp. 173-177.

Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Special Publication 36, American Geographic Society, New York.

Manville, R. H. 1949. A study of small mammal populations in northern Michigan. Miscellaneous Publication 73:1-83, Museum of Zoology, University of Michigan.

McNab, B. K. 1991. The energy expenditures of shrews. *In* J. S. Findley and T. L. Yates (eds.). The Biology of the Soricidae. Special Publication of the Museum of Southwestern Biology, University of New Mexico, Albuquerque, pp. 35-45.

Mock, O. B. 1982. The least shrew, *Cryptotis parva*, as a laboratory animal. Laboratory Animal Science 32:177-179.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223-249.

Pearson, O. P. 1945. Longevity of the short-tailed shrew. American Midland Naturalist 34:531-546.

Pfeiffer, C. J., and G. H. Gass. 1963. Note on the longevity and habits of captive *Cryptotis parva*. Journal of Mammalogy 44:427-428.

Platt, A. P. 1968. Differential trap mortality as a measure of stress during times of population increase and decrease. Journal of Mammalogy 49:331-335.

SAS Institute, Inc. 1985. SAS User's Guide: Statistics. SAS Institute, Inc., Cary, NC.

Schramm, P. 1970. Effects of fire on small mammal populations in a restored tallgrass prairie. *In* P. Schramm (ed.). Proceedings of Symposium, Prairie and Prairie Restoration. Galesburg, IL, pp. 39-41.

Schramm, P., and B. J. Willcutts. 1983. Habitat selection of small mammals in burned and unburned tallgrass prairie. *In* R. Brewer (ed.). Proceedings of the Eighth North American Prairie Conference, Western Michigan University, Kalamazoo, pp. 49-55.

Smith, D. D., and C. A. Jacobs (eds). 1982. Recapturing a Vanishing Heritage. Proceedings of the Twelfth North American Prairie Conference. University of Northern Iowa, Cedar Falls.

Springer, J. T., and P. Schramm. 1972. The effects of fire on small mammal populations in a restored prairie with special reference to the short-tailed shrew (*Blarina brevicauda*). *In* J. H. Zimmerman (ed.). Proceedings of the Second Midwest Prairie Conference, University of Wisconsin, Madison, pp. 91-96.

Whitaker, J. O., Jr. 1974. *Cryptotis parva*. Mammalian Species 43:1-8.

Wickett, R. G., P. D. Lewis, A. Woodliffe, and P. Pratt (eds.). 1994. Spirit of the Land, Our Prairie Legacy. Proceedings of the Thirteenth North American Prairie Conference. Department of Parks and Recreation, Windsor, Ontario.

Williams, A. B. 1936. The composition and dynamics of a beech-maple climax community. Ecological Monographs 5:317-408.

Feral Pigs, *Sus Scrofa*, in Kansas

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Abstract. A population of feral pigs, *Sus scrofa*, was documented on Fort Riley Army Base, Kansas during summer 1993. Reproduction occurred during spring 1993 and winter 1993-94. The population probably has existed for more than five years. Thirty-nine pigs were removed from November 1993 through February 1994. A minimum of six pigs remained in April 1994.

Key Words. Army base, feral pigs, prairie, Kansas.

Introduction

More than two million wild pigs, *Sus scrofa*, were distributed in 23 states in 1993 (Miller, 1993), and about half of them in Texas (Taylor 1993). In 1992, wild pigs were found throughout Texas, except for extreme western and northwestern regions of the state (Taylor 1993). In Oklahoma, wild pigs have occurred for many years in forested eastern and southern counties, and recently they were reported in western counties near the border with Kansas (Wagner 1995). Mr. Bill Hlavachick, Supervisor of the Wildlife Management Division of the Kansas Department of Wildlife and Parks, advised the first author that he received reports in 1985 of a group of six or seven wild pigs killed south of Lake Perry in eastern Kansas. This paper is the first documented report of wild pigs in Kansas.

Study Area

This study was conducted on Fort Riley, a 44,500 ha army base in northeastern Kansas. Most of the base is typical of tallgrass prairies found in the Kansas Flint Hills. Uplands are dominated by prairie grasses including big bluestem, *Andropogon gerardii*; little bluestem, *A. scoparius*; switch grass, *Panicum virgatum*; and Indian grass, *Sorgastrum nutans*. Hardwood forests occur in the lowlands and are dominated by bur oak, *Quercus macrocarpa*; green ash, *Fraxinus pennsylvanica*; hackberry, *Celtis occidentalis*; walnut, *Juglans nigra*; and woody shrubs.

Methods

Wild pigs were collected using three methods: live traps, sport hunting, and shooting by the study team. Distribution of pigs, population structure, and use of habitats were determined from observations of pigs and from field signs observed by the study team as well as reports by hunters, farmers, and military personnel.

Ages of pigs were estimated from tooth eruption and replacement (Matschke 1967). Females were considered adults if second molar teeth were present, they were pregnant or nursing, or if the teats were enlarged indicating they had nursed in the past. Wild female pigs reach puberty at about 10 months of age (Sweeney et al. 1979), and the second molar teeth erupt at 12 - 14 months (Matschke 1967). Males were considered adults if permanent canines were present. Wild male pigs reach puberty at five to seven months, and their adult canine teeth erupt at seven to eleven months.

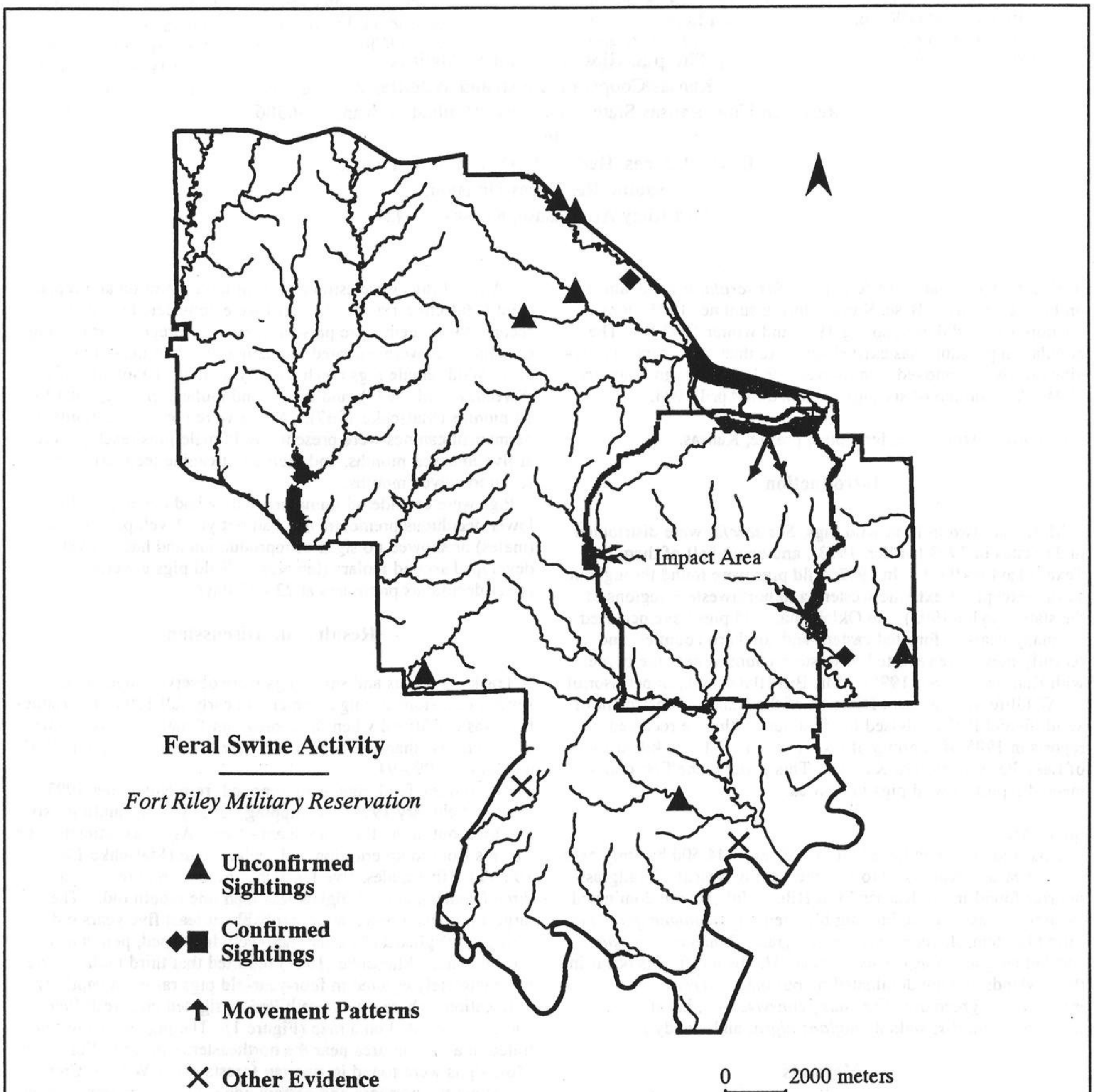
Pigs were considered immature if they had developed third lower deciduous premolars and had not yet developed canines (males) or showed no signs of reproduction and had not yet developed second molars (females). Wild pigs develop third lower deciduous premolars at 23 - 33 days.

Results and Discussion

Tracks of adults and small pigs were observed together on several occasions during summer and early fall 1993. Reproduction was confirmed when three pregnant females and two litters of piglets less than one month old were trapped during fall 1993 and winter 1993-94.

Thirty-nine feral pigs were removed from November 1993 through February 1994: by trapping - 31, by sport hunting - six, and by shooting by the study team - two. Age was estimated for 32 pigs from tooth eruption and replacement (Matschke 1967): 10 adults (five males, five females), nine immatures (six males, three females), and 13 piglets less than one month old. The largest pig taken was a male, probably at least five years old. This pig weighed 117 kg and had well developed, permanent, third molars. Matschke (1967) reported that third molars were not completely erupted in four-year-old pigs raised in captivity.

Locations where pigs were killed or sighted and fresh field signs were plotted on a map (Figure 1). The pigs were concentrated in a 45 km^2 area near the northeastern border of Fort Riley. Most signs were found in riparian forests along Wildcat Creek and along the northern and eastern edges of a large impact area that is off limits to human entry. Reports of pigs were received occasionally from other sections of the base. Signs of rooting and rubs on brush were discovered on private lands adjacent to Fort Riley, showing that pigs made forays off the base.



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FT. Riley, KS.

FIG. 1. Locations of feral pigs on Fort Riley Army Base, Kansas. Confirmed sightings were made by members of the study team. Unconfirmed sightings were reports by farmers or hunters, but not direct observations by members of the study team. Other evidence included the lower jaw of a mature male pig found by a surveying team working on a road construction project and a pig struck by an automobile. Arrows indicate trails used by pigs moving into and out of the impact area.

The status of the population is unknown, but tracks observed during April 1994 indicated at least six adult pigs were present. Katahira et al. (1993) noted that a high percentage of a feral pig population would have to be killed each year for several years in order to eradicate the population. Hone and Robards (1980) calculated that, with a 70% reduction once each year, about nine years probably would be required to eradicate an established population of 1,000 wild pigs. Assuming the Fort Riley population numbered 45 to 50 animals prior to initiation of control and that six remained after control, we achieved an 86% - 88% reduction.

The Fort Riley population possibly could be eliminated in another two to three years, if 80% or more of the pigs were killed each year. However, elimination of the population is confounded by the presence of a large impact area that provides a refuge for pigs (Figure 1). There is also a possibility that substantially more than six pigs remained on Fort Riley, but we were unable to detect their presence.

A long-term strategy for managing or eradicating this pig population is needed.

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Literature Cited

Hone, J. and G. E. Robards. 1980. Feral pigs: ecology and control. Wool Technology and Sheep Breeding 28: 7-11.

Katahira, L. K., P. Finnegan, and C. P. Stone. 1993. Eradicating feral pigs in montane mesic habitat at Hawaii Volcanoes National Park. Wildlife Society Bulletin 21: 269-274.

Matschke, G. H. 1967. Aging European wild hogs by dentition. Journal of WildlifeManagement 31: 109-113.

Miller, J. E. 1993. A national perspective on feral swine. *In* Hanselka, C. W. and

J. F. Cadenhead (eds.). Feral Swine: A Compendium for Resource Managers. Texas Cooperative Extension Service, San Angelo, TX. pp 9-16.

Sweeney, J. M., J. R. Sweeney, and E. E. Provost. 1979. Reproductive biology of a feral hog population. Journal of Wildlife Management 43: 555-559.

Taylor, R. B. 1993. History and distribution of feral hogs in Texas. *In* Hanselka, C. W. and J. F. Cadenhead (eds.). Feral Swine: A Compendium for Resources Managers. Texas Cooperative Extension Service, San Angelo, TX. pp. 17-27.

Wagner, S. 1995. Hogs. Outdoor Oklahoma January/February: 24-28.

Effect of Topography on the Distribution of Small Mammals on the Konza Prairie Research Natural Area, Kansas

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Abstract. Long-term research on small mammals was initiated on the Konza Prairie Research Natural Area in autumn, 1981. Twenty-eight permanent traplines (20 stations per line) were established in fire treatments that were burned at 1- to 20-year intervals in the spring. Small mammals were trapped in summer during 1981-1987 and spring and autumn during 1981-1991. A total of 12 species of rodents and 2 species of shrews was recorded from our prairie sites during the study period. Eight species were sufficiently common with wide distributions across Konza Prairie to warrant analyses of their use of upland, limestone-breaks, and lowland prairie. Five of eight common species were not distributed randomly across topography in burned and unburned sites on Konza Prairie. For example, deer mice (*Peromyscus maniculatus*) and thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) used more stations in limestone-breaks than in lowland and upland prairie, whereas western harvest mice (*Reithrodontomys megalotis*), white-footed mice (*P. leucopus*), and hispid cotton rats (*Sigmodon hispidus*) used more stations in lowland than in upland and breaks prairie. Fewer species were captured per trap station in upland than lowland and breaks prairie, although plant species richness and diversity are greater on uplands than lowlands on Konza Prairie.

Key words: small mammals, rodents, shrews, topography, fire, tallgrass prairie

Introduction

Although habitat distribution and use have been studied for small mammals, little information is available on the effect of local differences in topography on the distribution of small mammals. This lack of knowledge is conspicuous within the grassland biome, because a topographically rugged landscape is a prominent feature of most unplowed native prairie, including tallgrass prairie. Recent short-term studies of habitat selection of small mammals on the Konza Prairie Research Natural Area near Manhattan, Kansas suggest that topography has an effect on small mammals. For example, deer mice (*Peromyscus maniculatus*) selected limestone breaks (Kaufman *et al.* 1988) or burned uplands (Peterson *et al.* 1985), whereas western harvest mice (*Reithrodontomys megalotis*) selected unburned lowlands (Kaufman *et al.* 1988; Peterson *et al.* 1985). In contrast to these small mammals, hispid cotton rats (*Sigmodon hispidus*) were not affected by fire treatments, but selected lowland over upland prairie (Peterson *et al.* 1985). Topographic effects for other species of small mammals are poorly known.

Studies of vegetation on Konza Prairie suggest differences relative to time since fire and topography. For example, live plant biomass is greater on lowland than on upland prairie (Abrams *et al.* 1986). Plant biomass also was greater on annually burned than unburned lowland prairie, whereas no burning response was found on upland. Additionally, species richness (number of species per plot) was greater on upland than on lowland prairie in both annually burned and unburned sites (Abrams and Hulbert 1987). Differences in plant biomass, composition, and species richness likely influence spatial distributions of small mammals on Konza Prairie and, more broadly, spatial distributions of small mammals in tallgrass prairie in the Flint Hills.

During 10 years (1981-1991) of sampling small mammals along 580 traplines in prairie on the Konza Prairie, 12 species of rodents and 2 species of shrews were recorded. The common species (> 1% of the community of small mammals) were the deer mouse (4.8 individuals per trapline); western harvest mouse (2.1); Elliot's short-tailed shrew (*Blarina hylophaga*, 1.6); white-footed mouse (*P. leucopus*, 0.89); prairie vole (*Microtus ochrogaster*, 0.55); thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*, 0.33); hispid cotton rat (0.23); and southern bog lemming (*Synaptomys cooperi*, 0.11). Rare species (< 0.5% of the community of small mammals) included the hispid pocket mouse (*Chaetodipus hispidus*, 0.040 individuals per trapline); eastern woodrat (*Neotoma floridana*, 0.028); house mouse (*Mus musculus*, 0.024); plains harvest mouse (*R. montanus*, 0.021); least shrew (*Cryptotis parva*, 0.012); and meadow jumping mouse (*Zapus hudsonius*, 0.0034).

Our primary objective was to examine the effect of topography on the distributions of small mammals on Konza Prairie using a 10-year data set (1981-1991). Specific objectives were to determine (1) if one topographic position (upland, limestone-breaks, or lowland prairie) had more species present on average than others; (2) if the eight common species showed repeated patterns of use across burned and unburned prairie that were related to topography; and (3) if the six rare species showed any observable patterns that were related to topography.

Methods

Long-term research on small mammals was initiated on the Konza Prairie Research Natural Area south of Manhattan, Kansas in autumn, 1981. Konza Prairie is located within the Flint Hills and is characterized by steep-sided hills with wide valleys and flat ridges (for more detailed description, see Kaufman *et al.* 1988). Konza Prairie is divided into areas with prescribed burning treatments that vary from 1 to 20 years between spring fires (for more details on the Konza Prairie and location of treatment sites, see Zimmerman 1993). Our study utilized a total of 14 treatment sites with three experiencing annual fire for various lengths of time (1A since 1972, 1D since 1978, and N1B since 1988). Eleven treatment sites had periodic fires that were preceded and followed by various lengths of time with no fire

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(2C and 2D burned every other year since 1977 and 1978, respectively; 4B, 4D, 4F, 4G, and N4D burned once every 4 years since 1979, 1974, 1981, 1980, and 1988, respectively; and 10A and 10D burned once every 10 years since 1981 and 1986, respectively). Two treatments (20B and N20B) were not burned between 1981 and 1991, but differed in length of time with no fire in that N20B was burned in an accidental fire in 1980, whereas 20B was unburned since 1973. All study sites were ungrazed by large mammalian herbivores during our study.

Each experimental fire treatment had two permanent traplines (20 traps per station per line). Each station had two large Sherman live traps (7.6 by 8.9 by 22.9 cm) placed within 1 m of the permanent station marker. For more details on traplines, stations, and trapping procedures, see Kaufman *et al.* (1988). Because of the extensive topographical relief, we attempted to place the two traplines within an experimental treatment such that 40% of the stations would occur in upland, 20% in limestone-breaks, and 40% in lowland prairie. These percentages were attempted in our initial placement of traplines to try to standardize the number of stations in different topographic categories for the many fire treatment sites. All stations within a treatment site were categorized as occurring in either upland, breaks, or lowland prairie (for more description of topographic positions, see Kaufman *et al.* 1988).

Spring and autumn data for small mammal traplines were accumulated for 10 years from autumn 1981 to spring 1991, whereas summer data were accumulated from 1981 to 1987. These data were divided into four data sets, annual burns, periodic burns (first year after fire with more than 1 year since fire), short-term unburns (2-4 years without fire), and long-term unburns (5-20 years without fire). Some experimental fire treatments appeared in only one data set (e.g., 1D), whereas others appeared in a maximum of three data sets (e.g., N1B, Table 1). The parameter that was evaluated for each data set was the presence/absence of a species at each station during each sampling period. A value of 1 was recorded if a species was present at a station, whereas a value of 0 was recorded if a species was absent.

Table 1. Number of times a treatment site appeared in data sets for annual burns, periodic burns (2-20 year interval), short-term unburns (2-4 years), and long-term unburns (5-20 years) in summer (SU), autumn (AU), and spring (SP) on Konza Prairie Research Natural Area, Kansas.

	Annual			Periodic			Short			Long		
Site	SU	AU	SP	SU	AU	SP	SU	AU	SP	SU	AU	SP
1A	2	4	3	--	--	--	--	--	--	--	--	--
1D	6	10	10	--	--	--	--	--	--	--	--	--
N1B	--	2	2	--	1	1	--	--	--	6	7	7
2C	--	--	--	2	2	2	1	3	2	--	--	--
2	--	--	--	1	3	2	2	2	2	--	--	--
4B	--	--	--	2	2	2	4	8	8	--	--	--
4D	--	--	--	2	2	2	4	6	5	--	--	--
4F	--	--	--	1	3	3	5	7	7	--	--	--
4G	--	--	--	1	2	1	5	6	6	--	--	--
N4D	--	--	--	--	1	1	--	2	2	6	7	7
10A	--	--	--	--	1	1	3	3	3	3	5	4
10D	--	--	--	1	1	1	1	2	1	--	1	1
20B	--	--	--	--	--	--	--	--	--	6	10	10
N20B	--	--	--	--	--	--	2	2	3	4	7	7

A log-likelihood ratio test (G-test) was used to test whether proportions of stations with and without a particular species present were equal across topographic positions within each of the four data sets. G-statistics that were greater than the critical test statistic (P = 0.05) were partitioned to determine which topographic positions differed in use by each species. Results from the four data sets then were compared to look for commonality of topographic patterns among burned and unburned treatments. G-tests also were used to assess the effect of topography on the number of species present at a station. The maximum number of species that possibly could occur at a station was eight (two traps set for four consecutive nights) within each trapping period.

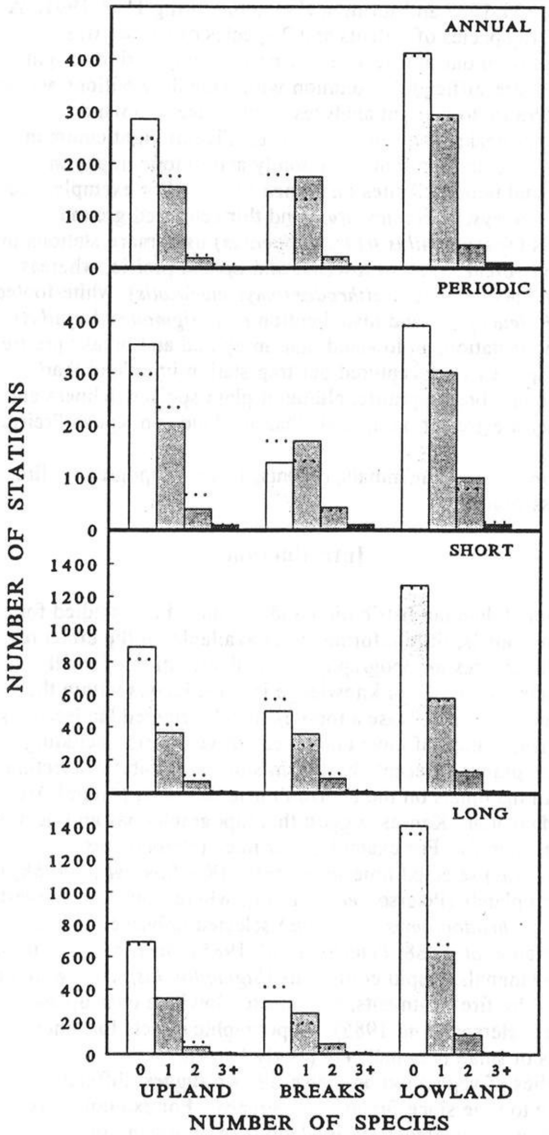

FIG. 1. Observed number of stations with zero, one, two, and three or more species present in upland, limestone-breaks, and lowland prairie in annual burns, periodic burns, short-term unburns (2-4 years), and long-term unburns (5-20 years) on the Konza Prairie Research Natural Area. Dotted lines on bars indicate the expected frequency for each category given a random distribution.

Table 2. Number of stations and number of stations used by small mammals in upland (U), limestone breaks (B), and lowland (L) in annual burns, periodic burns (first year after fire with 2-20 years unburned), short-term unburns (2-4 years), and long-term unburns (5-20 years) on the Konza Prairie Research Natural Area, Kansas.

	Annual			Periodic			Short			Long		
Category	U	B	L	U	B	L	U	B	L	U	B	L
Stations	458	342	760	606	350	804	1336	952	1992	1088	658	2174
Deer mouse	131	180	286	201	186	277	264	315	256	210	229	199
Western harvest mouse	15	4	37	40	22	57	78	78	289	72	47	268
Elliot's short-tailed shrew	14	14	23	24	15	46	73	61	144	81	54	217
White-footed mouse	2	2	20	18	25	83	22	33	116	25	22	120
Prairie vole	13	4	21	9	3	13	52	32	30	34	27	56
Thirteen-lined ground squirrel	7	12	6	8	17	23	24	27	9	25	30	26
Hispid cotton rat	7	0	13	5	10	30	2	2	14	3	0	4
Southern bog lemming	1	0	2	0	1	0	7	5	16	7	3	20

Results

A total of 14 species of small mammals was captured at 11,520 stations from 1981 to 1991 on the Konza Prairie. In descending order of the number of stations used, these species were the deer mouse (2,734 stations), western harvest mouse (1,007), Elliot's short-tailed shrew (766), white-footed mouse (488), prairie vole (294), thirteen-lined ground squirrel (214), hispid cotton rat (90), southern bog lemming (62), hispid pocket mouse (24), eastern woodrat (20), house mouse (15), plains harvest mouse (12), least shrew (7), and meadow jumping mouse (2). Statistical analyses were made for the eight common species, whereas these tests were not possible for the six rare species because of a lack of available data.

The number of species present at a station ranged from zero to five. The maximum number of species present at a station was three in upland, and five in both limestone-breaks and lowland prairie. In both burned and unburned treatments, the proportion of stations with zero, one, two and ≥ three species of small mammals was not equal across the three topographic positions (annual burn: G = 41.7, d.f. = 6, P < 0.01; periodic burn: G = 52.9, d.f. = 6, P < 0.01; short-term unburn: G = 55.0, d.f. = 6, P < 0.01; long-term unburn: G = 62.3, d.f. = 6, P < 0.01). In both burned treatments (annual and periodic), upland was overrepresented in stations with no species present, breaks in stations with one species present, and lowland prairie in stations with two and three or more species (Fig. 1). Short-term unburned sites mirrored results for burned sites, whereas in long-term unburned sites, lowland was overrepresented in stations with no species present and limestone-breaks prairie in stations with one or two species present (Fig. 1).

Deer mice did not use topographic positions randomly in either burned or unburned prairie (Table 2; annual: G = 47.9, periodic: G = 44.3, short-term unburn: G = 159.7, long-term unburn: G = 233.9; all d.f. = 2 and all P < 0.01). In both burned and unburned prairie, deer mice selected breaks over upland and lowland, although relative use of breaks was lower in unburned than in burned prairie (Fig. 2). Use of lowland was greater than that of upland in annually burned prairie, whereas upland was used more than lowland in unburned prairie. Upland and lowland were not used differentially in periodic burns.

Western harvest mice selectively used topographic sites in annually burned and unburned prairie (Table 2; annual: G = 11.2, short-term unburn: G = 72.8, long-term unburn: G = 34.3; all d.f. = 2 and all P < 0.01), but not in periodic burns (G = 0.3, d.f. = 2, P > 0.05). In short- and long-term unburns, western harvest mice selected lowland over upland and limestone-breaks prairie (Fig. 2). For annual burns, they also used lowland more than limestone-breaks, but not significantly more than upland.

White-footed mice also did not use topographic positions randomly in either burned or unburned prairie (Table 2; annual: G = 12.7, periodic: G = 31.0, short-term unburn: G = 40.5, long-term unburn: G = 21.5; all d.f. = 2 and all P < 0.01). White-footed mice used lowland more than upland and breaks in both burned and unburned prairies, except that lowland was not used more than breaks in periodic burns (Fig. 2). Additionally, white-footed mice used breaks over upland in periodic burns and short-term unburns.

Thirteen-lined ground squirrels differentially used topographic sites in all four types of burned and unburned prairie (Table 2; annual: G = 9.8, periodic: G = 10.5, short-term unburn: G = 30.0, long-term unburn: G = 25.0; all d.f. = 2 and all P < 0.01). Ground squirrels selected limestone breaks over lowland except in periodic burns (Fig. 2). Additionally, breaks was selected over upland prairie in periodic burns and long-term unburns.

Cotton rats selectively used topographic positions in burned and short-term unburned prairie (Table 2; annual: G = 10.0, periodic: G = 13.9, short-term unburn: G = 7.5, long-term unburn: too few stations used to test statistically; d.f. = 2 and P < 0.01 for burn treatments and P < 0.05 for short-term unburns). Lowland was selected over upland by cotton rats in periodic burns and short-term unburns, but not in annual burns (Fig. 2). In contrast, lowland was selected over breaks in annual burns, but not in periodic burns or short-term unburns.

Other common species (Elliot's short-tailed shrews, prairie voles, and southern bog lemmings) tended to use the topographic positions according to the frequency of availability (Table 2). Exceptions to this random pattern were shrews in long-term unburns (G = 6.4, d.f. = 2, P < 0.05) and voles in short-term unburns (G = 20.7, d.f. = 2, P < 0.01). In these situations, short-tailed shrews selected lowland over upland, whereas prairie voles selected upland and breaks over lowland (Fig. 2).

Table 3. Mean percentage of stations used in upland, limestone-breaks, and lowland prairie by rare species on Konza Prairie Research Natural Area, Kansas.

Species	Upland	Breaks	Lowland
Hispid pocket mouse	0.09 (0.08)	0.61 (0.06)	0.13 (0.05)
Eastern woodrat	0.09 (0.11)	0.36 (0.31)	0.10 (0.07)
House mouse	0.06 (0.05)	0.10 (0.08)	0.22 (0.08)
Plains harvest mouse	0.14 (0.10)	0.15 (0.18)	0.08 (0.03)
Least shrew	0.12 (0.06)	0.03 (0.03)	0.03 (0.04)
Meadow jumping mouse	0.02 (0.02)	--	0.03 (0.04)

Standard errors are given in parentheses.

Of the rare species, hispid pocket mice were observed in limestone-breaks prairie proportionally more than in upland or lowland prairie, although variability (*SE*) of use of stations was similar between topographical positions (Table 3). Similarly, eastern woodrats used breaks stations more frequently than those in upland and lowland, but use of breaks also had the greatest variability. The house mouse, a nonnative species, was the only rare species that was observed in lowland more frequently than upland or breaks. Variability in use by house mice was similar across upland, breaks, and lowland prairie. Least shrews were observed more in upland than in breaks and lowland with similar levels of variability. The plains harvest mouse was the only rare species that showed similar use of two topographic positions (upland and breaks) with a slightly lower use of lowland prairie. Meadow jumping mice were observed once each in upland and lowland, but never in limestone breaks.

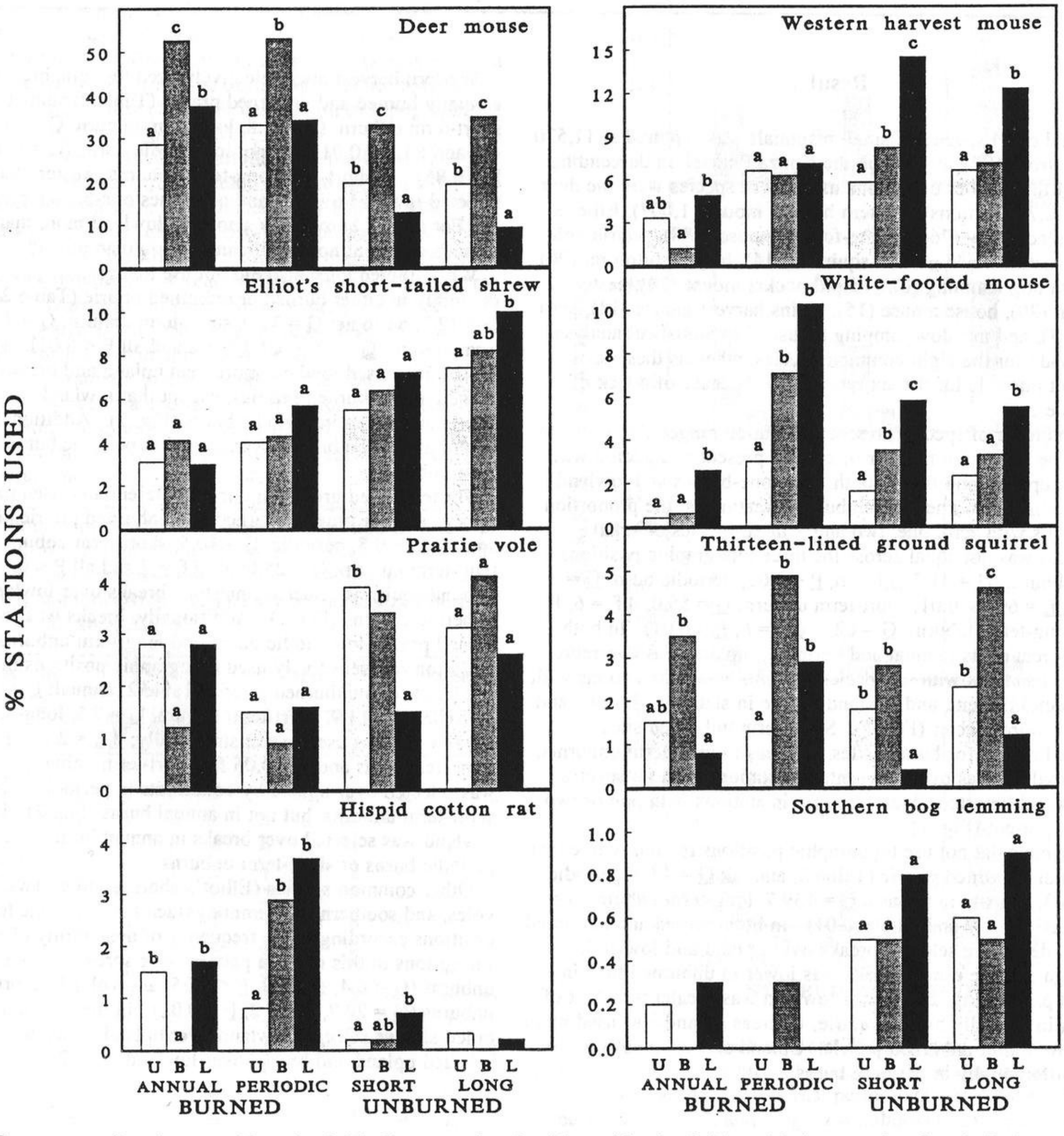

FIG. 2. Percentage of stations used in upland (U), limestone-breaks (B), and lowland (L) prairie in annual and periodic burns and short-term (2-4 years) and long-term (5-20 years) unburns by eight common small mammal species on the Konza Prairie Research Natural Area. Letters above bars within each fire treatment that are not the same indicate significant differences.

Discussion

When we initiated our long-term study of small mammals in tallgrass prairie, we expected unique species-specific patterns in use of local topographic conditions because of major differences in the natural history of rodents and shrews found in eastern Kansas (Bee *et al.* 1981). Our results support this general expectation for common species such as deer mice and thirteen-lined ground squirrels, which selectively used the limestone breaks, and western harvest mice, white-footed mice, and hispid cotton rats, which selectively used lowland. However, differential use was statistically nonsignificant for Elliot's short-tailed shrews, prairie voles, and southern bog lemmings. Differential association with topographic position was suggested by patterns of station use for rare species, but abundance and station use were too low to test statistically.

Lowland prairie was selected more than other habitats by western harvest mice, white-footed mice, and hispid cotton rats. Harvest mice used lowland prairie at a landscape scale (our study) and at a microscale (Peterson *et al.* 1985), although Brillhart *et al.* (this volume) failed to demonstrate differential use of lowland and upland on small experimental plots. Selective use of lowlands by cotton rats was evident at a microscale in small experimental patches (Brillhart *et al.* this volume, Peterson *et al.* 1985) and at a landscape scale on Konza Prairie (our study). However, cotton rats may select upland over lowland prairie in summer (Brillhart *et al.* this volume). Our pattern for cotton rats primarily represents autumn use, because 81% of the stations used by cotton rats occurred during autumn sampling periods. Selective use of lowland by white-footed mice likely was due to wooded ravine habitats, which they prefer (Clark *et al.* 1987), being spatially closer to lowland than upland and breaks. Use of trap stations in our study also suggested greater use of lowland over upland and breaks by house mice. This species, which is most common around human habitation (Kaufman and Kaufman 1990), may use ravines and nearby lowland as dispersal corridors more frequently than other topographic features.

Limestone-breaks prairie was used selectively more than other habitats by deer mice and thirteen-lined ground squirrels. Kaufman *et al.* (1988) reported that deer mice selected limestone breaks in unburned prairie, but exhibited no differential use of topography during the first year after fire. In contrast to results reported in the 1-year study by Kaufman *et al.* (1988), deer mice selected breaks over upland and lowland prairie in both annually and periodically burned prairie in our 10-year study. When only upland and lowland prairie were available in small experimental patches, deer mice used upland over lowland stations (Brillhart *et al.* this volume, Peterson *et al.* 1985). The overall pattern of habitat use for deer mice is selection of limestone-breaks habitat over uplands or lowlands, regardless of the burn history of the site. However, the change from secondary use of lowlands in the first year after fire to secondary use of uplands in years following the first year postburn likely reflects the deterioration of the lowlands from a habitat of high productivity and no litter in the first year after fire (Abrams *et al.* 1986, Kaufman *et al.* 1988) to a habitat with standing dead vegetation and an increasing amount of litter present on the soil surface (Kaufman *et al.* 1988). Our results for thirteen-lined ground squirrels were similar to results from a 13-ha grid on Konza Prairie (Clark *et al.* 1990) where ground squirrels selected limestone breaks and avoided lowland prairie.

Use of trap stations also suggested greater use of limestone breaks over other habitats by hispid pocket mice and eastern woodrats. Pocket mice likely used breaks because of the lack of litter and the large amount of exposed soil surface (Kaufman *et al.* 1988). Higher use of limestone breaks by woodrats probably reflects availability of the rocky outcrop and shrubs that provide the resources for dens.

Prairie voles differentially used upland over lowland in short-term unburned prairie; however, no preferences were shown on burned sites or long-term unburns in our study. Selection of upland by voles also was shown on a 13-ha grid on Konza Prairie following 2-4 years after a fire (Bixler and Kaufman 1995). Use of trap stations also suggested greater use of upland over other habitats by least shrews. Least shrews were associated with upland communities in tallgrass (Clark *et al.* this volume) and mixed grass prairie (Choate and Fleharty 1975).

Elliot's short-tailed shrews and southern bog lemmings showed little differential use of upland, limestone-breaks, and lowland prairie. Elliot's short-tailed shrews were shown to select lowland and avoid upland prairie on a site 2-4 years after fire (Clark *et al.* this volume), whereas our study showed this pattern only in long-term unburns and not in short-term unburns. For southern bog lemmings, only 62 of 11,520 stations (0.5%) were used during our study, so selective use of lowland prairie may become evident as data continue to accumulate from ongoing, yearly, spring and autumn sampling.

The repeatability of patterns of small mammal use of topographic positions on Konza Prairie shows the strength of the topographic effect on habitat selection by small mammals given the complex management plan and the variability in climate, soil, spatial scale, and parameters evaluated in this and other studies. Our study used the presence/absence of a species at a station to assess use of topography, whereas other studies used individual captures of each species (Bixler and Kaufman 1995, Brillhart *et al.* this volume, Clark *et al* 1990 and this volume, Peterson *et al.* 1985). Spatial scales of studies included small experimental patches (0.04 ha) in upland and lowland prairie on a 2-ha site (Brillhart *et al.* this volume, Peterson *et al.* 1985); in three microhabitats from upland to lowland prairie on a 13-ha grid (Bixler and Kaufman 1995, Clark *et al.* 1990 and this volume); and in three microhabitats in spatially explicit traplines scattered across the landscape of Konza Prairie (Kaufman *et al.* 1988 and our study). However, studies of topographic associations at additional sites are required to ascertain whether the patterns we observed are universal across tallgrass prairie and other topographically diverse grasslands.

Finally, number of species of small mammals recorded per station ranked, in ascending order, as upland, breaks, and lowland. In contrast, shallow, rocky upland had more species of plants than deep-soil lowland prairie on Konza Prairie (Abrams and Hulbert 1987, Gibson and Hulbert 1987). A pattern of high richness and diversity of plant species on upland and low richness and diversity on lowland prairie and the opposite pattern for use by small mammals appears counterintuitive. Rather, one might expect higher diversity in plants to promote greater diversity of small mammals in these topographic sites. However, plant biomass is higher in lowland than in upland prairie (Abrams *et al.* 1986), suggesting that patterns shown in small mammal use may be influenced more by productivity than by the diversity of vegetation. Currently, small mammal use and vegetation cannot be compared on limestone breaks of Konza Prairie, because no measure of plant biomass or species richness and diversity is available.

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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.

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.

Bee, J. W., G. E. Glass, R. S. Hoffmann and R. R. Patterson. 1981. Mammals in Kansas. University of Kansas, Museum of Natural History Public Education Series 7:1-300.

Bixler, S. H. and D. W. Kaufman. 1995. Local distribution of prairie voles (*Microtus ochrogaster*) on Konza Prairie: effect of topographic position. Transactions of the Kansas Academy of Science 98:61-67.

Brillhart, D. E., G. A. Kaufman and D. W. Kaufman. 1995. Small-mammal use of experimental patches of tallgrass prairie: influence of topographic position and fire history. *In* D. C. Hartnett (ed.) Proceedings of the 14th North American Prairie Conference, Prairie Diversity: from Molecules to Landscapes, from the Past to the Future. Kansas State University, pp. .

Choate, J. R. and E. D. Fleharty. 1975. Synopsis of native, recent mammals of Ellis County, Kansas. Occasional Papers, The Museum, Texas Tech University, Lubbock 37:1-80.

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.

Clark, B. K., D. W. Kaufman, G. A. Kaufman and S. K. Gurtz. 1995. Population ecology of Elliot's short-tailed shrew and least shrew in ungrazed tallgrass prairie manipulated by experimental fire. *In* D. C. Hartnett (ed.) Proceedings of the 14th North American Prairie Conference, Prairie Diversity: from Molecules to Landscapes, from the Past to the Future. Kansas State University, pp. .

Clark, B. K., D. W. Kaufman, G. A. Kaufman, S. K. Gurtz and S. H. Hand. 1990. Population ecology of thirteen-lined ground squirrels in ungrazed tallgrass prairie manipulated by fire. *In* D. D. Smith and C. A. Jacobs (eds.) Proceedings of the 12th North American Prairie Conference, Recapturing a Vanishing Heritage. University of Northern Iowa, pp. 51-54.

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.

Kaufman, D. W. and G. A. Kaufman. 1990. House mice (*Mus musculus*) in natural and disturbed habitats in Kansas. Journal of Mammalogy 71:428-432.

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 69:342-352.

Peterson, S. K., G. A. Kaufman and D. W. Kaufman. 1985. Habitat selection by small mammals of the tall-grass prairie: experimental patch choice. Prairie Naturalist 17:65-70.

Zimmerman, J. L. 1993. The Birds of Konza: The Avian Ecology of the Tallgrass Prairie. University Press of Kansas, Lawrence. 186 pp.

Species Richness of Insects on Prairie Flowers in Southeastern Minnesota

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Abstract. I systematically collected 3784 flower-visiting insects representing 287 species from 59 forb species in 4 prairie remnants and 4 prairie reconstructions (farm fields replanted to prairie plants) during 3 summers. Flower visitors included nectar and pollen feeders, parasitoids, and predators. Size of the site, time since planting of reconstructions and total flower number did not appear to influence the species richness of flower visitors on the sites. The presence of flowers throughout the summer and the presence of forb species that supported specialist insects appeared to increase insect species richness of sites. Certain forb species supported more than their share of insect visitors. Insect species richness was highest on sites of intermediate forb species richness. The native remnants had slightly higher insect species richness than the reconstructions when collection effort was equalized, but the reconstructions also supported many flower visitors. Of the 287 insect species, 105 were found on only one site, implying that even small remnants and reconstructions can contribute to the conservation of prairie insect species.

Key words: prairie insects; prairie forbs; prairie restoration; flower visitors; bees; species richness; insect phenology

Introduction

Many factors may be expected to influence species richness, i.e., the number of insect species present on a site. Many flower visitors are highly mobile (Johnson 1969); thus a landscape-level pool of species is available to colonize new sites, and to recolonize old ones if the sites meet the insectsquirements.

Large sites are expected to support more species than smaller ones, based on the greater variety of microhabitats on larger sites (Usher 1987). The degree of isolation of a site from other sites with established insect populations may influence species richness, because other sites are needed as sources of colonists for reconstructions or replacements of populations that have become locally extinct on native sites (Samways 1994).

Even for highly mobile flower visitors, the colonization and establishment processes take time: so native prairie sites are expected to have more insect species than reconstructions, and older reconstructions are expected to have more insect species than those that were planted recently.

Flower visitors include nectar and pollen feeders and their predators and parasites, so flowers themselves are the basic resources for the group. Differences in the forb community are expected to have strong effects on the insect community. The site resource level (number of flowers present) is a rough measure of the energy which is available for use by the flower visitors and is expected to limit the number of individual insects that can survive on a site (Bowers 1985). As the species richness of the forb community as a whole increases, insect species richness potentially can increase, but when many habitats are compared, the relationship between forb and insect species richness has been inconsistent (Neff and Simpson 1993). To elucidate this relationship in any habitat, we must examine the ways in which forb species serve as resources for different types of flower visitors. Many insect species complete their active life during only a few weeks of the summer; one way in which increased forb species richness can increase insect species richness on sites is by increasing the number of flowers in bloom throughout the season (Rathcke 1988).

On single sites, the relationship between forb and insect species richness is based in the forb species that are actually present and their visitors. Certain forb species may be especially valuable contributors to the insect species richness of their sites because they support specialists, are especially attractive to certain insect groups, and/or support unique species not found on other forbs. If certain forbs do increase the insect species richness of their sites, it may be possible to increase the insect species richness of reconstructed prairies by planting these forbs.

A variety of methods has been developed for estimating insect species richness on sites (Coddington et al. 1991). A major issue is collection effort. Making identical numbers of collections on each site is rarely possible when several sites are sampled, so site species richness is compared using the rates at which new species are found on the various sites. On any site, the first few collections will yield many species not seen before; as collections continue, fewer new species will be found per collection, yet it is unlikely that all the species on the site will be found. This diminishing return per collection can be displayed in a species accumulation curve like Figure 1. The slope of the curve indicates the rate at which additional collections yield additional species, and the extent of flattening of the curve with increasing number of collections indicates the completeness of sampling (Connor and McCoy 1979). Estimates of site species richness can also be made using truncated species accumulation curves (Janzen 1971).

Methods

Study Sites

All the sites are located in eastern Minnesota, USA, and all are managed. The sites vary in prairie plant area and number of forb species present (Table 1). The majority of the forb species are prairie plants but alien weeds are also present (Table 1). Plant names follow Great Plains Flora Association (1986).

Prairie Reconstructions. These are former agricultural areas that have been replanted to prairie vegetation.

Afton State Park (ASP), Washington County, contains several reconstructions. I sampled a 4.8 hectare field located at the NE 1/4 of section 10, T27N R20W, containing prairie grasses and four forb species planted 9 years before the study and managed by controlled burning. The soil is Ripon silt loam. The prairie area is bounded by old fields, second-growth woodland, and overgrown oak savanna remnants. The most recent burn was in the spring of 1989.

Table 1. Area, forb species number, age, total flower number in 1992, number of collections, total insect species, insect species in 17 randomly selected collections (mean of 5 values), and number of unique insect species collected for each site.

Site	Area, hectares#	Plant Spp##	Age in years	Total flower number 1992	No. of coll.	Total insect species	Ins spp. in 17 coll.**	Unique insect species***
Reconstructions								
ASP	4.8/4.8	6	9	113,600	17	33	33	2
CARP	32.4/16.2	25	1-4	93,000	89	128	55	15
CHR	243/10.0	31	1-15	40,500	107	112	46	12
LLRP	2.8/2.8	29	4	35,000	76	100	41	15
Native Sites								
AREM	1.6/1.6	13	11,000	47	86	51	14	
CC	60.7/8.0	15	9,500	62	118	55	23	
CEM	0.4/0.4 15	22,800	50	88	52	8		
LV	13.5/7.5	22	16,000	57	95	50	16	

Area that supported prairie plants/Area from which collections were made
Includes only those species with at least 100 flowers or infloresences blooming on at least one sampling date
**Number of insect species in 17 randomly selected collections
*** Number of insect species found on this site only

Carpenter Nature Center (CARP) in Washington County contains a 32.4-hectare reconstructed prairie at the NE 1/4 of Section 8, T27N R20W. One-quarter of the area was planted in 1988, one-quarter in 1989, one-quarter in 1990, and the remaining area in 1991. The reconstructions are managed by mowing during the first 2 years, followed by regular burning. The soil is Ripon silt loam. The area is bounded by agricultural fields. The site was burned in the spring of 1991.

Crow Hassan Park Reserve (CHR) in northwestern Hennepin County includes 243 hectares of reconstructed prairie replanted into former agricultural fields over the last 15 years. Forbs have been planted densely in a 10-hectare portion of the prairie area, located in the NW 1/4 of section 19, T120N R23W; new forb species have been added frequently since reconstruction began. The area is managed by controlled burning of parts of the area in different years. The soil is Hubbard loamy sand. The prairie area is bounded by restored deciduous woodland. The site was burned in the spring of 1991.

Long Lake Regional Park (LLRP) in Ramsey County contains a 2.8-hectare prairie reconstruction planted in 1987, located at the SE 1/4 of section 17, T30N R23W, and bounded by wetlands, trails, and an overgrown oak savanna remnant. A railroad right-of-way 100 meters from the site supports some prairie plants. This area is managed by burning, most recently in early spring of 1992. The soil is Zimmerman fine sand. I collected at LLRP in 1992 only.

Native Prairies. These are relatively undisturbed remnants.

Afton Remnant (AREM) is a 1.6 hectare remnant located on a bluff top in Afton State Park, Washington County at the N 1/2 of section 35, T28N R20W. It was somewhat overgrown but has been managed by brush cutting and burning since 1987; the most recent burn was in the spring of 1989, and extensive brush cutting was done in 1991. The soil is Ripon silt loam. The remnant is bounded by the bluff above the St. Croix river and by second-growth decidous forest.

Cedar Creek Natural History area (CC), Anoka County, contains a 60.7 hectare oak savanna area with two open meadows (approximately 5 and 3 hectares in area) containing many prairie plants located at the S 1/2 of section 34, T34N R 23W. Portions are burned in different years; the collection area was burned in 1990. The soil is Zimmerman fine sand. The meadows are bounded by oak savanna, and the area includes some wetlands.

Point Douglas Cemetery (CEM) is a 0.4 hectare pioneer cemetery directly adjacent to the Carpenter Nature Center Reconstruction at the SE 1/4 of section 5, T27N R20W. It has never been plowed, and the entire site was burned in 1989. The soil is Ripon silt loam. The site is bounded by agricultural fields and the section of the Carpenter Nature Center reconstruction that was planted in 1991.

Lost Valley State Natural area (LV), in Washington County is a protected area of 40.5 hectares including bluff prairie, shrubs, old field vegetation, and a small area still cultivated; about 1/3 of the area, the rocky bluff tops, supports prairie plants, at the S 1/2 of section 21 and the N 1/2 of section 22, T27N R20W. I sampled about half of this area, in the southern part of the site. Management of the area began in 1991 with brush cutting and burning of part of the site; this was continued extensively in 1992. The prairie areas are located on the Doreton rock outcrop complex, with very shallow loamy soil. The site is surrounded by agricultural areas and suburban development.

Collections

I counted the flowers or inflorescences of each forb species blooming on each site on each sampling date, using quadrat and line transect methods, and summed these for the entire year as an index of total resource level. I collected insects from the flowers by hand netting between 9 am and 4 pm on sunny or partly cloudy days when the temperature was between 20 and 35o C. The first collections were made in late May, and the last collections in late September. I made one 15-minute collection from the flowers of each forb species with at least 100 flowers or inflorescences open, from all forb species in all sites during 1991 and 1992, and limited collections in 1990, for a total of 505 collections (Table 1). From 1 to 53 collections were made from each forb species, depending on the length of blooming period and the number of sites on which it was present. I attempted to minimize overlap in collecting to avoid depleting the insect populations on the sites. All specimens were labelled according to site, date, and forb species, and were identified or confirmed by specialists.

Insect species were classified as predators, parasitoids, pollen feeders, pollen collectors, or cleptoparasites, and as specialists or generalists on plant species, genera, or families using standard references: Borror et al. 1989, Krombein et al. 1979, Opler and Krizek 1984, Scott 1986, Stone et al. 1965 (Table 2). Flower visitors were also defined as specialists if at least eight individuals were collected from only one plant species.

Table 2. Forb species presence on the eight sites, season, total collections made from each forb, total insect species collected, insect species unique to each forb, and ratio of percent insect species collected from each forb to the percent of total collections which were made from this forb.

	Plant Species				Site					Season	Total	Total	Unique	Pctspp/
		ASP	CARP	CHR	LLRP	AREM	OC	CEM	LV		Col	Spp	Spp	Pctcol
Apiaceae														
	Zizia aurea		x		x				x	early	8	34	5	
Asteraceae														
	Achillea millefolium*		x	x	x	x			x	early-mid	10	18	4	3.15
	Aster ericoides		x	x	x			x	x	v. late	11	46	3	6.15
	Aster ontarionis								x	v. late	3	13	1	
	Aster oolentangiensis			x	x	x	x	x	x	v. late	20	57	3	4.98
	Aster sericeus			x	x				x	late	4	17	0	
	Aster simplex		x		x			x		v. late	5	25	1	
	Chrysopsis villosa			x	x					mid	5	12	1	
	Cirsium arvense*		x							mid	2	9	2	
	Cirsium discolor		x			x			x	late	9	21	2	
	Coreopsis palmata			x						mid	3	4	0	
	Crepis tectorum				x					early	5	8	0	
	Erigeron strigosus		x		x					early	3	5	1	
	Grindelia squarrosa				x					mid	2	6	0	
	Helianthus rigidus		x	x	x		x	x	x	mid-late	27	39	7	2.63
	Helianthus tuberosus		x	x				x		late	7	13	2	
	Heliopsis helianthoides		x	x	x			x		early-mid	15	18	0	2.10
	Liatris aspera			x			x		x	late	10	27	0	4.70
	Liatris punctata								x	late	1	3	1	
	Liatris pycnostachya			x						late	1	1	0	
	Ratibida pinnata	x	x	x				x	x	mid	30	38	1	2.24
	Rudbeckia hirta	x	x	x	x	x	x			mid	30	40	4	2.36
	Solidago canadensis		x	x	x	x	x	x	x	late	20	62	7	5.40
	Solidago nemoralis				x	x	x			mid-late	10	40	3	6.95
	Solidago rigida		x	x	x		x	x	x	mid-late	20	62	2	5.40
	Solidago speciosa		x	x	x	x		x	x	late	11	30	3	4.77
	Vernonia fasciculata								x	mid	1	8	0	
Boraginaceae														
	Lithospermum canescens						x			early	2	3	0	

Table 2 cont.

Brassicaceae													
Berteroa incana*				x					early	3	13	2	
Campanulaceae													
Campanula rotundifolia								x	early	1	4	1	
Fabaceae													
Amorpha canescens			x	x	x	x		x	mid	10	41	7	7.15
Dalea purpurea	x	x	x	x		x			mid	19	53	6	3.55
Dalea villosa				x					mid	2	7	1	
Desmodium canadense				x			x		mid	4	8	0	
Lupinus perennis			x						early	2	7	0	
Melilotus alba*			x	x					mid	9	19	0	
Melilotus officinalis*		x	x	x					early	7	15	2	
Trifolium pratense*		x							mid	1	2	0	
Vicia americana							x		v. early	1	4	0	
Iridaceae													
Sisyrinchium campestre			x						v.early	1	5	0	
Lamiaceae													
Agastache foeniculum		x	x	x	x				mid	31	48	4	2.74
Monarda fistulosa	x	x	x	x	x	x	x	x	mid	57	60	13	1.76
Nepeta cataria*					x			x	mid	6	18	0	
Pycnanthemum virginianum				x	x	x		x	mid	26	87	17	5.94
Stachys palustris		x				x			mid	4	12	0	
Liliaceae													
Allium canadense		x	x	x					mid-late	4	13	3	
Nyctaginaceae													
Mirabilis nyctaginea			x						early	1	3	0	
Polemoniaceae													
Phlox pilosa			x			x			early-mid	4	6	1	
Ranunculaceae													
Anemone canadensis			x						early	1	1	0	
Aquilegia canadensis								x	early	1	2	0	
Rosaceae													
Potentilla arguta		x	x						mid	2	8	0	

Table 2 cont.

	Potentilla recta*	x	x							early-mid	3	15	0	
	Rosa blanda		x	x				x		early-mid	4	8	0	
	Rubus occidentalis								x	v.early	1	4	0	
Rubiaceae														
	Galium boreale							x		early	1	6	3	
Scrophulariaceae														
	Penstemon grandiflorus			x	x		x			early	15	36	5	4.46
Verbenaceae														
	Verbena hastata	x				x				mid	5	13	1	
	Verbena stricta		x							early-mid	5	10	0	
Total Plant Species on Site		6	25	31	29	13	15	15	22					
		ASP	CARP	CHR	LLRP	AREM	OC	CEM	LV					

X = presence of at least 100 flowers on that site on at least one sampling day
* = alien plant species

Tests of Factors Related to Insect Species Richness

I performed three analyses to determine whether native sites had more flower-visiting insect species than reconstutions. First, I looked at all the collections in all the sites. I constructed separate species accumulation curves for all native sites and all reconstructions combined by randomizing the collections and recording the cumulative number of species as each new collection was added (Figure 1). This method compares the rates at which additional collections added species to the total species lists for native sites and reconstructions (Coddington et al.1991). I compared the slopes of the curves by log-log transformation and regression (Connor and McCoy 1979); a higher slope indicates a more species-rich site (Figure 1).

Second, I treated the native sites and the reconstructions as replicates and compared mean species number per site using a 2-tailed t-test (unequal variances). To equalize collection effort among sites to the lowest collection effort (17 collections at ASP), I randomly selected 17 collections from each site (except ASP) and counted the species in this subsample. I repeated the randomization five times and used the mean species number as the site value for the t-test (values for 17 collections are shown in Table 1).

Third, I compared individual plant species that were found in both native and reconstructed sites. There were 28 species from which insect collections were made in both types of sites (Table 2). I equalized the collection number in native and reconstructed sites by using all collections from the type that had the lower number, and randomly selecting an equal number of collections from the type that had the higher number. This method made use of 282 of the 505 collections. I counted the insect species per plant species in the selected number of collections and compared the number in native and reconstructed sites using the Wilcoxon Signed-Rank test (Remington and Schork 1970).

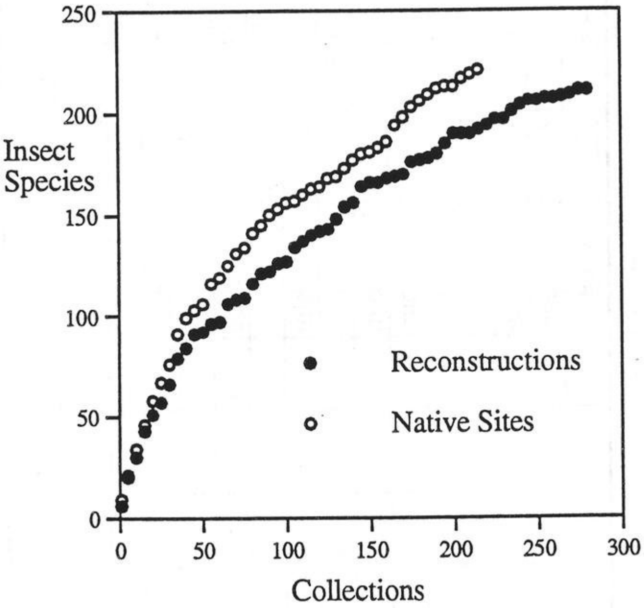

FIG. 1. Species accumulation curves for allnative sites combined and all reconstructions combined. Slopes of the log-log transformed curves are 0.599 for native sites, range 0.579-0.619; and 0.529, range 0.512-0.547 for the reconstructions.

Distance from Sources of Colonists

I identified possible sources of insect colonists using maps and by exploration near sites. At least 125 prairie and oak savanna remnants large enough to be mapped (about 8000 m2, or 90 X 90 meters appears to be the minimum size shown) exist in Washington County. (Source: Minnesota County Biological Survey Map Series no 1 (1990) Washington County). There are many more remnants too small to map, especially along the river bluffs and railroad tracks.

The rural/suburban Hennepin County site, CHR, is probably similar to the Washington County sites in having many remnants not too far away. This county has not yet been mapped by the Biological Survey. The LLRP site seems much more isolated by four-lane highways, heavy and light industry, trucking companies, and a few suburban developments, but it is separated by only a few hundred meters of woods from a remnant containing some prairie plants. A nearby railroad right-of-way contains some prairie plants. Only 21 mappable native vegetation remnants occur in Ramsey county, whereas Anoka County has at least 50 remnants, the largest one covering four sections (Minnesota County Biological Survey Map Series, Ramsey and Anoka Counties (1994)). The Cedar Creek site is the least isolated of the sites, because it is located in a less developed and less agricultural area than the others.

Phenology

I charted the phenology of all the insect species for which eight or more individuals were collected by listing the first and last dates of collection (Table 3). I noted the first and last date of collection from each forb species and recorded each as an early-, mid-, or late-season forb.

Insect and Forb Species Richness on Sites

I graphed insect species richness vs. forb species richness for each site, using both total insect species collected and insect species in 17 collections, fitted the curves, and calculated r2 for each (Figure 2).

Insect Species Richness Associated with Individual Forb Species

The number of unique insect species (insect species found on that forb only) are listed for all forbs in Table 2. As a measure of species richness, I calculated the percent of total insect species collected from the forb and divided this by the percent of all collections made from it. I limited this procedure to forb species with at least 10 collections, because the results become increasingly erratic with fewer collections ; this forced me to pool all the collections from each plant species, rather than examining all the plant species on a site-by-site basis. A high value indicates high insect species richness relative to other forbs from which insects were collected.

Table 3. Phenology of insects visiting prairie forbs.

Species	June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25	
1. Bombus affinis			X	-----	-----	-----	-----	X	1.
2. Bombus auricomus			X	-----	-----	-----	-----	X	2.
3. Bombus bimaculatus		X	-----	-----	-----	X			3.
4. Bombus fervidus			X	-----	-----	-----	-----	X	4.
5. Bombus griseocollis			X	-----	-----	-----	X		5.
6. Bombus impatiens			X	-----	-----	-----	-----	X	6.
7. Bombus pennsylvanicus					X	-----	-----	X	7.
8. Bombus ternarius				X	-----	-----	X		8.
9. Bombus vagans			X	-----	-----	-----	X		9.
10. Andrena wilkella	X								10.
11. Andrena cressonii	X								11.
12. Andrena crataegi	X								12.
13. Andrena rudbeckiae				X	X				13.
14. Andrena placata						X	-----	X	14.
15. Andrena hirticincta						X	X		15.
16. Andrena helianthi						X	X		16.
17. Andrena simplex						X	X		17.
18. Andrena nubecula						X	X		18.
19. Andrena asteris							X	X	19.
20. Anthophora furcata terminalis		X	-----	-----	-----	X			20.
21. Ceratina calcarata or dupla			X	-----	-----	-----	-----	X	21.
22. Tetralonia dubitata	X								22.
23. Melissodes subillata			X	-----	-----	X			23.
24. Svastra obliqua o.				X	-----	X			24.
25. Melissodes trinodis				X	-----	-----	X		25.
26. Melissodes agilis					X	X			26.
27. Melissodes rustica						X	X		27.
28. Melissodes desponsa						X	X		28.
29. Melissodes dentiventris							X	X	29.
30. Hylaeus mesillae m.			X	-----	-----	-----	-----	X	30.
31. Hylaeus affinis			X	-----	-----	-----	-----	X	31.
32. Colletes susannae					X-----X				32.
33. Colletes simulans armatus							X	X	33.
	June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25	

Table 3 cont.

Species	June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25	
34. Lasioglossum paraforbesii	X	-	-	-	-	X			34.
35. Halictus ligatus			X	-	-	-	-	X	35.
36. Halictus confusus	X	-	-	-	-	-	-	X	36.
37. Evylaeus pectoralis	X	-	-	-	-	-	-	X	37.
38. Dialictus vierecki	X	-	-	-	-	-	-	X	38.
39. Dialictus rowheri	X	-	-	-	-	-	X		39.
40. Dialictus pruinosus	X	-	-	-	-	-	X		40.
41. Dialictus pilosus	X	-	-	-	-	-	-	X	41.
42. Dialictus pictus	X	-	-	X					42.
43. Dialictus lineatulus	X	-	-	-	-	-	-	X	43.
44. Agapostemon virescens	X	-	-	-	-	-	-	X	44.
45. Augochlorella striata	X	-	-	-	-	-	-	X	45.
46. Dialictus imitatus	X	-	-	-	X				46.
47. Dialictus albipennis	X	-	-	X					47.
48. Dufourea monardae				X	-	X			48.
49. Dialictus heterognathus				X	-	-	X		49.
50. Dialictus anomalus				X	-	-	X		50.
51. Agapostemon sericeus				X	-	-	-	X	51.
52. Agapostemon texanus	X	-	-	-	-	-	-	X	52.
53. Megachile relativa	X	-	-	-	-	-	-	X	53.
54. Megachile latimanus	X	-	-	-	-	-	-	X	54.
55. Hoplitis pilosifrons	X								55.
56. Heriades carinata				X	-	X			56.
	June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25	

Table 3 cont.

Species	June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25	
57. Hylemya sp.	X	---	---	X					57.
58. Systoechus sp.				X	X				58.
59. Exoprosopa caliptera					X	---	X		59.
60. Sphaerophoria sp.	X	---	---	---	---	---	---	X	60.
61. Lejops stipatus	X	---	---	---	X				61.
62. Allograpta obliqua			X	---	X				62.
63. Eristalis transversus			X	---	---	---	X		63.
64. Helophilus fasciatus			X	---	---	---	---	X	64.
65. Toxomerus germinatus			X	---	---	X			65.
66. Toxomerus marginatus			X	---	---	---	X		66.
67. Syrphus sp.			X	---	---	---	---	X	67.
68. Eristalis latifrons			X	---	---	---	---	X	68.
69. Metasyrphus sp.				X	---	---	---	X	69.
70. Sphaerophoria contigua					X	---	---	X	70.
71. Helophilus latifrons					X	---	---	X	71.
72. Eristalis tenax							X	X	72.
73. Eristalis dimidiatus							X	X	73.
74. Vanessa cardui	X	---	---	---	---	X			74.
75. Atrytone delaware				X	X				75.
76. Satyrium edwardsii				X	X				76.
77. Cisseps fulvicollis				X	---	---	X		77.
78. Colias sp.				X	---	---	---	X	78.
79. Polistes fuscatus	X	---	---	---	---	---	---	X	79.
80. Euodynerus foraminatus f.	X	---	---	---	---	---	X		80.
81. Myzinum quinquecinctum				X	---	X			81.
82. Philanthus ventilabris					X	X			82.
83. Myzinum maculatum					X	---	X		83.
84. Chauliognathus pennsylvanicus					X	---	---	X	84.
85. Epicauta pennsylvanica					X	---	X		85.
86. Luperaltica fuscula					X	---	---	X	86.
	June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25	

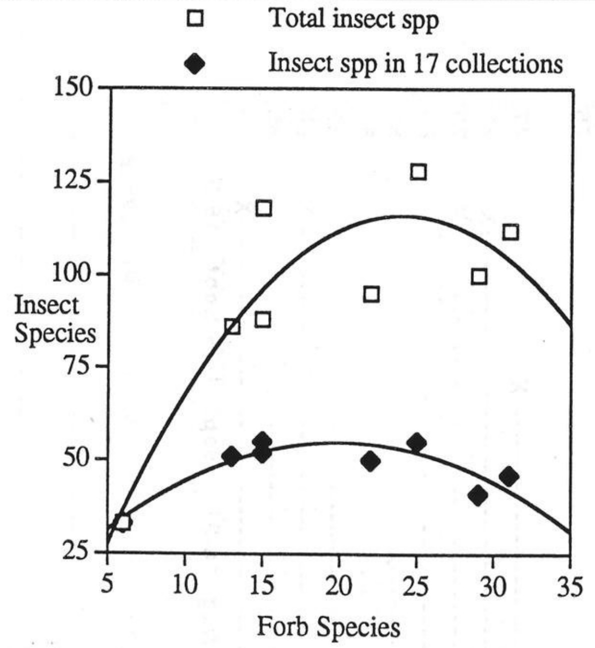

FIG. 2. Forb and insect species richness. Each symbol represents one site. For total insect species collected, $r^2 = 0.785$; for insect species richness based on 7 randomly selected collections (mead of 5 values), $r^2 = 0.789$.

Results and Discussion

I collected 3784 insects representing at least 287 species, including predators, parasitoids, pollen feeders and collectors, and cleptoparasites. The pollen collectors included specialists and generalists (Table 4). Eighty-five insect species were found on native sites only, 67 species on reconstructions only, and 135 species on both native and reconstructed sites. One hundred and five insect species were found on one site only; 112 species were found on one plant only. Of the 287 species, 88 were represented by only one individual, 98 had from 2 to 5 individuals, 36 species had from 6-10 individuals, 22 had from 11 to 20 individuals, 26 species had from 21-50 individuals, and 17 species had more than 50 individuals.

Area of Sites

Little relationship existed between the area of a site and the number of insect species collected from it (Table 1). Many species were found on even the smallest sites. Area does not directly measure the amount of insect habitat, because resources (flowers and nesting sites) are distributed in an extremely patchy and variable manner within sites. The study sites were not isolated physically, and probably insects moved on and off of them.

Table 4. Ecological categories of flower visitors

Ecological category	Taxonomic group	Number of species
Nectar feeders	Lepidoptera	27
Pollen feeders	Syrphidae (Diptera)	28
	Coleoptera (Beetles)	3
Pollen collectors	Apoidea (Hymenoptera)	116
Cleptoparasites	Apoidea (Hymenoptera)	9
Parasitoids of flower visitors	Conopidae (Diptera)	6
	Chrysidoidea (Hymenoptera)	2
	Chalcidoidea (Hymenoptera)	1
Parasitoids of other insects	Bombyliidae (Diptera)	14
	Ichneumonoidea (Hymenoptera)	5
	Tiphioidea (Hymenoptera)	3
	Scolioidea (Hymenoptera)	3
	Calliphoridae (Diptera)	1
Predators	Sphecoidea (Hymenoptera)	40
	Vespoidea (Hymenoptera)	12
	Tachinidae (Diptera: larvae are predators)	8
	Pompiloidea (Hymenoptera)	4
	Hemiptera	2
	Matispidae	1

Comparison of Species Richness of Native Sites and Reconstructions

Cumulative collections from all native sites combined yielded more species than cumulative collections on reconstructions; for example, 215 collections yielded 221 insect species in the native sites but only 192 insect species in the reconstructions (Figure 1).The slopes of the log-transformed species accumulation curves showed no overlap using an estimate of slope with 95% confidence intervals, indicating higher insect species richness in collections from the native sites overall, with statisical significance at the 0.05 level.

When the mean number of insect species per site for the four native sites and the four reconstructed sites (based on the means of five randomly selected groups of 17 collections) were compared using a 2-tailed t-test with unequal variances, the probability was 0.171. No significant difference occurred in insect species richness in native sites compared to reconstructions. The lack of statistical significance may be related to the much lower insect species richness at ASP compared to the other reconstructions, which caused a large variance in species richness values for the reconstructions.

Insect species richness of plant species growing in both native and reconstructed sites was compared. Of the 28 plant species with equivalent collection effort in native sites and reconstructions, 14 plants had more insect species in the native sites, 12 plants had more insect species in the reconstructions, and two had the same number of species in both. The difference was not significant based on the Wilcoxon Signed-Rank test.

Over all, more insect species were collected from all the native sites combined than from all the reconstructions combined, and fewer hours of collection were needed to find them (Figure 1). More insect species were found on native sites only than on reconstructions only. On the other hand, some of the reconstructions, especially CARP, had high insect species richness, even though more collections were required to find all these insects. Also, two of the three statistical approaches showed no statistically significant difference in insect species richness between the native and reconstructed sites. These results suggest that native sites had slightly higher insect species richness than reconstructions.

Distance from Possible Sources of Colonists

This variable was difficult to quantify. The CC site seemed to be the least isolated, and the LLRP site the most isolated from other prairie insect populations, but the other sites could not be compared on this basis.

Age of Reconstructions

No obvious relationship occurred between age of reconstruction and insect species richness (Table 1). Total Resource Level The reconstructions had more total flowers in 1992 than did the native sites (Table 1). No obvious relationship existed between total flowers and insect species richness. However, the measure of total resource level did not correspond with the ways flower visitors subdivided the resource, as discussed below.

Insect Phenology and Specialization

Phenology records were noted for the 86 species that had eight or more individuals: 20 species were collected during 1 month or less: six bee species, two flies, and two butterflies (Table 3). Thirty-two long-season species were present from June into September (24 bee species, six flies, and two wasps).

Fifty-seven bee species could be charted. The majority of the species fell into one of four groups:

1. Early-season bees. These were the first species seen, starting with the first collection date (May 29), and were not seen after mid-June. They were associated on my sites with certain early plant species, though they are recorded in the literature as visiting other plants. *Andrena wilkella*, *A. cressonii*, and *A. crataegi* were collected mainly from *Zizia aurea*, and *Tetralonia dubitata* and *Hoplitis pilosifrons* from *Penstemon grandiflorus*.
2. Mid-season bees were *Andrena rudbeckiae* on *Ratibida pinnata*, *Colletes susannae* on *Dalea purpurea*, *Dufourea monardae* on *Monarda fistulosa*, and *Heriades carinata* (generalist).
3. Late-season bees included *Andrena placata, A. helianthi, A. hirticincta, A. simplex, A. nubecula, A. asteris, Melissodes agilis, M. rustica, M. desponsa, M. dentiventris*, and *Colletes simulans armatus*. Most of these species are Asteraceae specialists.
4. Long-season bees were collected from June through August. All *Bombus* species were long-season bees, as were many halictids. All these species are generalists and shifted from plant to plant as the season progressed. Bumblebee numbers usually peaked on sites when the midseason flowers, especially *Monarda fistulosa*, bloomed, then dropped and increased again late in the season when the goldenrods and asters were in full bloom. Honeybees were generally rare on the prairie but visited the white and yellow sweetclovers early in the season, *Verbena stricta* and occasionally *M. fistulosa* in midseason, and the goldenrods and asters in the late summer.

Fly phenology: 17 species had eight or more individuals. The majority of the species were present for 8 weeks or more; no apparent patterns were related to subfamilies. In general, flies were more numerous late in the season. Syrphid flies, the most common flower visitors, were common from the end of June to the end of September.

Wasp phenology: only five species had eight or more individuals. Wasps were common in mid to late summer, except for *Polistes fuscatus* and *Euodynerus foraminatus*, which were present earlier.

Five Lepidoptera species had eight or more individuals. Only *Vanessa cardui* was seen early in the season; the remaining species were seen first in early to mid-July. *Cisseps fulvicollis* and *Colias spp.* persisted into mid-September, whereas *Satyrium edwardsii* and *Atrytone delaware* were not seen after early August. The sphinx moths, *Hemaris* spp., were seen mainly on *Monarda fistulosa.* during its blooming season, mid-July through August.

The beetles *Chauliognathus pennsylvanicus* and *Epicauta pennsylvanica* increased rapidly in early August to peak in late August and persisted into early September; they forage and mate in flowers of Asteraceae. The ambush bugs, *Phymata pennsylvanica*, also were seen in August.

Forb Species Richness

Insect species richness was highest at intermediate forb species richness on these sites (Figure 2). The relatively low insect species richness of the sites with the highest forb species richness is a bit surprising and may be related to unique site features.

Forb Phenology

There were 22 early species, (flowering during May and June), 24 mid-season species (July-mid August), and 13 late or very late species (mid August through September) (Table 3). The ASP site had only mid-season flowers, CARP and LLRP were especially rich in early flowers, and CEM and LV were especially rich in late flowers. The AREM site had few fall flowers.

Relationship of Forb Phenology and Insect Species Richness on Sites

Presence of flowers over a longer portion of the summer tended to increase the insect species richness of sites. Early generalist bees were found only on sites with early-season plants; for example, early andrenids such as Andrena commoda and A. crataegi, visited spring flowers at CARP, but were not found at CEM where early flowers were very limited. Most Asteraceae specialists were absent from AREM because of its lack of fall flowers, which are mainly Asteraceae; predators and parasites also tended to be found less frequently on sites with fewer fall flowers. ASP had only mid-season flowers and was very poor in insect species, lacking both specialists and many common generalists.

Insect Species Richness of Individual Forb Species

Insects that are specialists on my sites include *Osmia distincta, Tetralonia dubitata*, and *Hoplitis pilosifrons* on *Penstemon grandiflorus*; *Hoplitis cylindrica* on *Amorpha canescens*; *Colletes susannae* and *C. wilmattae* on *Dalea purpurea*; *Melissodes desponsa* on *Cirsium discolor*; *Andrena helianthi, Melissodes agilis*, and *Perdita albipennis* on *Helianthus* spp.; *Dufourea monardae* on *Monarda fistulosa*; *Andrena rudbeckiae* on *Ratibida pinnata*; *Andrena placata* on *Solidago* spp.; *Melissodes dentiventris* on *Aster* spp.and the *Hemaris* spp. on *Monarda fistulosa.* These insects are not found on sites without their plants.

Pycnanthemum virginianum and *Monarda fistulosa* supported the most unique insect species (those not found on any other forb); *Solidago canadensis, Amorpha canescens*, and *Helianthus rigidus* also supported many unique insects; unique insect species were collected from 33 of 59 plant species (Table 2).

Forbs that are especially species rich in visitors can be identified by a high ratio of percent of insect species collected to percent of total collections, if collection number is adequate for this test (Table 2). For example, *Amorpha canescens* had 2.0 % of the collections made, and 14.1 % of the total insect species, for a ratio of 7.1, whereas *Heliopsis helianthoides*, was poorer in insect visitors; it had 3.0 % of the collections and only 6.3 % of the insect species, giving a ratio of 2.1. *Amorpha canescens, Solidago nemoralis, Aster ericoides*, and *Pycnanthemum virginianum* had the highest ratios of visitors to collections, and *Rudbeckia hirta, Ratibida pinnata, Heliopsis helianthoides*, and *Monarda fistulosa* had the fewest insect visitors relative to the numbers of collections made. (The species to collection ratio may be a bit low for *M. fistulosa* because of the high number of collections thath were made from this plant).

Finally, some forb species are especially attractive to certain insect groups. For example, half the wasp species in the entire collection were found on *Pycnanthemum virginianum*; 37 bee species were collected from *Dalea purpurea*; *Liatris aspera* and *Monarda fistulosa* were the sources of the majority of bombyliids collected. Many syrphid flies were collected from *Heliopsis helianthoides*. *Lepidoptera* were found most commonly on *Monarda fistulosa, Liatris aspera*, and *Solidago speciosa*

Other forb species were visited rarely in these sites, especially *Phlox pilosa*, *Coreopsis palmata*, and *Desmodium canadense*.

Relationship of Forb Insect Species Richness to Site Insect Species Richness

Certain forb species listed above support specialist insects, others are attractive to generalists, some have strikingly rich insect visitor lists often including insects collected from no other plant, and other forbs are especially attractive to certain insect groups. Thus, forb species make unique contributions to the insect species richness of the areas in which they grow; experimental testing will be needed to determine the extent to which the presence of individual forb species affects insect species richness on a variety of prairie sites.

Conclusions

The species richness of the flower-visiting insect community on prairie sites was not related to the size and age of the site, number of individual flowers,or total forb species richness. Insect species richness of sites was increased by the presence of forb species that supported specialist insects and by the presence of flowers throughout the summer. Prairie forb species could be identified as resources for spring generalists, resources for fall generalists, and resources for specialists. Individual forb species supported unique portions of the flower visitor community on these sites. Over a variety of sites and with ample collections to sample visitor species richness, certain forb species are consistently more attractive to insects in general and to certain insect groups, than are other forbs. These results suggest that the insect species richness of reconstructions can be increased by the introduction of forb species that attract a wide variety of insect visitors.

Species tended to accumulate in older sites, as indicated by the slightly greater species richness in the native sites over all. The presence of many species on only one site indicates that even small prairie remnants should be preserved as insect conservation sites, and the presence of many unique insect species on reconstructions implies that reconstructed prairies also can be valuable sites for insect conservation.

Voucher Specimens and Species List

Voucher specimens are located in the authorollection and will be archived at the University of Minnesota Insect Museum and the University of Minnesota Herbarium. For a copy of the complete insect species list, write to the author.

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Literature Cited

Borror, D. J., C. A .Triplehorn and N. F. Johnson. 1989. An Introduction to the Study of insects. Sixth edition. Saunders Publishing Co, Philadelphia. 875 pp.

Bowers, M A. 1985. Bumblebee colonization, extinction and reproduction in subalpine meadows in NE Utah. Ecology 66: 914-927.

Coddington, J. A., C. E. Griswold, D. S. Davila, E. Penaranda and S. F. Larcher. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. In E. C. Dudley, ed. The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematics. Dioscorides Press, Portland OR. Vol 1 pp 44-59.

Connor, E. F. and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. American Naturalist 113: 791-833.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence, KS. 1402 pp.

Janzen, D H. 1971. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54: 687-708.

Johnson, C. G. 1969. Migration and Dispersal of Insects by Flight. Methuen and Co, London. 402 pp.

Krombein, K. V., P. D. Hurd Jr., D. R. Smith and B. D. Burks. 1979. Catalog of Hymenoptera in America North of Mexico. Smithsonian Institution Press, Washington, D C. 3 Vols.

Neff, J. L. and B. B. Simpson. 1993. Bees, pollination systems and plant diversity. In J. LaSalle and I. D. Gould, eds. Hymenoptera and Biodiversity. CAB International, Wallingford UK, pp 143-167.

Opler, P. A. and G. O. Krizek.1984. Butterflies East of the Great Plains. Johns Hopkins University Press, Baltimore. 294 pp.

Rathcke, B. 1988. Interactions for pollination among coflowering shrubs. Ecology 69:446-457.

Remington, R. D. and M. A. Schork. 1970. Statistics with Applications to the Biological and Health Sciences. Prentice-Hall. Englewood Cliffs, NJ. 418 pp.

Samways, M. J. 1994. Insect Conservation Biology. Chapman and Hall, London. 358 pp.

Scott, J. A. 1986. The Butterflies of North America. Stanford University Press, Stanford, CA. 585 pp.

Stone, A., C. W. Sabrosky, W. W. Wirth, R. H. Foote and J. R. Coulson. 1965. A Catalog of the Diptera of America North of Mexico. USDA, Washington DC. 1696 pp

Usher, M. B. 1987. Effects of fragmentation on communities and populations: A review with applications to wildlife conservation. *In* D. A. Saunders, G. W. Arnold, A. A. Burbidge, and A. J. M. Hopkins, eds. Nature Conservation: the Role of Remnants of Native Vegetation. Surrey Beatty and Sons, pp 103-21.

Prairie Voles Impact Plants in Tallgrass Prairie

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Abstract. Experimental enclosures were maintained with high abundance of prairie voles (*Microtus ochrogaster*) or no voles to test their effects on plants of the tallgrass prairie. Enclosures were situated in burned upland prairie on the Konza Prairie Research Natural Area, and field work was conducted during 1984-1986. Total plant biomass was not impacted by voles. However, Kentucky bluegrass (*Poa pratensis*), Indian grass (*Sorghastrum nutans*), and heath aster (*Aster ericoides*) responded negatively to voles. The nine additional plants studied were not significantly affected by voles, but large nonsignificant increases strongly suggest that voles had positive effects on little bluestem (*Andropogon scorparius*) and Scribner dicanthelium (*Dicanthelium oligosanthes*). The negative responses of Kentucky bluegrass, Indian grass, and heath aster undoubtedly were caused by selective foraging. In contrast, the possible positive effects of voles on little bluestem and Scribner dicanthelium likely resulted from loss of competition by plants negatively impacted by voles, but actual mechanisms are unknown. Finally, cuttings of flowering stalks demonstrated that voles harvested seeds from a variety of plants, including Indian grass, big bluestem, little bluestem, tall dropseed, and round-headed lespedeza (*Lespedeza capitata*).

Key words: prairie vole, *Microtus ochrogaster*, hervivory, animal disturbance, tallgrass prairie, Konza Prairie, Kansas

Introduction

Prairie voles (*Microtus ochrogaster*) are selective foragers (Cole and Batzli, 1979), and, at high densities, should influence plant composition in perennial grassland systems. For example, microtine (= arvicoline) rodents in alpine tundra reduced flowering frequency and size of *Ranunculus glacialis* within a 5-year period (Jarvinen, 1987). Further, voles may influence plant abundance by clipping vegetation during runway and burrow construction (Carroll and Getz, 1976), disturbing plants and soil by burrow construction and maintenance (Gibson, 1989), and creating germination sites by various digging activities. Therefore, voles are expected to impact vegetation, but little is known about the effects of prairie voles on grassland plants (Rose and Birney, 1985).

To test the effects of voles on plants of the tallgrass prairie, one of us (DWK) established experimental enclosures on the Konza Prairie Research Natural Area in 1983 as part of a larger study (designed by T. R. Seastedt, E. W. Evans, L. C. Hulbert, and D. W. Kaufman) that was focused on the effects of aboveground arthropods, belowground arthropods, and voles. Relative to prairie voles, Kentucky bluegrass (*Poa pratensis*) was expected to decline in abundance, because it is an uncommon cool-season (C3) grass in tallgrass prairie and it is eaten by prairie voles (Zimmerman, 1965). In contrast, voles were expected to have little impact on big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), and little bluestem (*A. scoparius*) because of their relatively high abundance, although voles do feed on all three of these warm-season (C4) grasses (Menhusen, 1963; field observations on Konza Prairie). Finally, food use by voles (Menhusen, 1963; Zimmerman, 1965; Fleharty and Olsen, 1969) suggested that voles would negatively impact sedge (*Carex* spp.) but not Louisiana sagewort (*Artemesia ludoviciana*), western ragweed (*Artemesia psilostachya*), and heath aster (*Aster ericoides*).

Using data from the experimental enclosures, Gibson *et al.* (1990) found few effects of aboveground and belowground invertebrates and prairie voles on the biomass of 23 plant species examined. The impacts of voles were a significant reduction in Kentucky bluegrass and marginal reductions in heath aster and purple lovegrass (*Eragrostis spectabilis*). Our analyses differed from those of Gibson *et al.* (1990) and were based on the expectation that vole impacts would be scattered within the enclosures and that the best evidence for vole impacts would be the comparison of the average vegetative conditions in enclosures with and without voles. Further, our intrepetation of results focused on characteristics of prairie voles and, therefore, the integration of food habits and other behavior with effects of voles on plants.

Study Site and Methods

In spring 1983, six experimental enclosures were established in upland prairie on the Konza Prairie Research Natural Area. Vegetation in all enclosures was burned in early April during 1983-1986. Each enclosure contained 16 4 x 4 m sites (each site contained an inner 3 x 3 m research plot with a 0.5 m boundary strip) fenced with sheet metal that was embedded into the ground (about 20 cm into the ground and about 90 cm above the ground).

Part of the plots in each enclosure was treated with pesticides to reduce aboveground arthropods (four plots), belowground arthropods (four plots), and both aboveground and belowground arthropods (four plots); four plots served as untreated controls (Seastedt *et al.*, 1987; Evans, 1991). However, Gibson *et al.* (1990) found that the arthropod treatments had few effects on plant biomass, so we used biomass in the 16 plots to estimate g biomass/m^2 in each enclosure for our tests of vole effects.

Peak aboveground biomass was sampled by clipping 0.5 m^2 subplots in each 3 x 3 m plot in 1984 and 1986. Plant samples, sorted to species, were collected in late September to early October, and then oven-dried and weighed. Average plant biomass (g/m^2) for each enclosure was estimated from the 16 subplots that were sampled. The 12 common plants included seven grasses, big bluestem, Indian grass, little bluestem, tall dropseed (*Sporobolus asper*), Kentucky bluegrass, Scribner dicanthelium, and sideoats grama (*Bouteloua curtipendula*). The nongrasses were sedge, western ragweed, lead plant (*Amorpha canescens*), heath aster, and Louisiana sagewort.

Two enclosures were assigned to zero (control), high, and very high densities of voles. Very high and high density treatments were set at 350-400 and 150-200 g of prairie vole per enclosure (24 x 24 m or 0.06 ha), respectively. However, we could not capture voles in 1983 and, finally, cotton rats (*Sigmodon hispidus*) were introduced to enclosures in September. The cotton rats could not be maintained and were gone by early winter. In 1984, cotton rats had crashed and were rare on Konza Prairie, but prairie voles were common enough to be introduced to enclosures by mid-June 1984.

Voles were censused weekly from spring to late autumn using one large Sherman trap (7.6 x 8.9 x 22.9 cm) set in each 3 x 3 m plot. Voles were marked with unique toe-clips before introduction or at their first capture when born in enclosures. Trap location and body mass were recorded at each capture. Voles were added or removed to maintain biomass from spring to autumn during 1984, 1985, and 1986. Voles then were added in spring 1985 and spring 1986, because most did not survive the winter in either 1984-1985 or 1985-1986.

Prairie voles cut flowering stalks of big bluestem, Indian grass, little bluestem, and tall dropseed in autumn-winter and ate seeds and possibly foliage from the clipped stems. In March 1986, standing and clipped stalks were counted but not all cut stalks could be assigned to species. Therefore, we counted standing and clipped stalks of big bluestem + Indian grass and of little bluestem + tall dropseed in a 1-m^2 subplot in each of the 96 3 x 3 m plots. Finally, cut flowering stems were counted in two experimental enclosures when vegetation was sampled in October 1986.

Although we tried to maintain high and very high biomasses of voles per enclosure, temporal variation of vole biomass in the enclosures was high because of deaths, births, and escapes. For our analyses, therefore, we considered voles in our four enclosures to be four replicates of abundant populations. We then tested for differences in biomass between years and between vole and control enclosures. Because biomass of some plant species varied greatly among enclosures and years, we also calculated standardized plant biomass by dividing plant-specific biomass in 1986 by that in the same enclosure in 1984. This standardized estimate was the g biomass produced in 1986 for each g biomass produced in 1984. Further, standardized biomass was expected to differ between experimental and control enclosures if voles had continuing negative or positive impacts on plants, but not if the voles simply removed some vegetation each year with no accumulative effect on future plant productivity. By considering biomass in 1984 and 1986, we also eliminated or at least reduced any confounding effects from the use of cotton rats in the experimental enclosures in autumn 1983.

Differences in biomass associated with year, vole abundance (present versus absent), and interaction between year and abundance were tested using a two-way analysis of variance. For tests of differences in standardized biomass between vole enclosures and control enclosures, we used a one-way analysis of variance. Standardized estimates of biomass were relativized estimates and not proportions (values could range from 0 to greater than 1); therefore, they were not transformed before analysis. Also, the vole-induced responses of any one plant species was not independent of changes in plant biomass and growth in other species. However, we did not know the magnitude of dependence between pairs of species and could not alter probability levels to correct for the magnitude of dependence. For this reason, we feel that it is important to interrelate plant responses to the natural history characteristics of voles.

Results

Plant biomass differed significantly between 1984 and 1986 for six of the 12 plants examined (Table 1). Of these, sedge, western ragweed, heath aster, Kentucky bluegrass, and Louisiana sagewort decreased significantly from 1984 to 1986, whereas little bluestem increased significantly. In contrast, only Kentucky bluegrass differed between enclosures, with biomass significantly lower in vole than control enclosures.

Standardized biomass (Table 2) was significantly lower in vole than control enclosures for Kentucky bluegrass ($P = 0.025$) and Indian grass ($P = 0.019$) and marginally lower in vole than control enclosures for heath aster ($P = 0.055$). Standardized biomasses in vole enclosures relative to that in control enclosures were 40%, 43%, and 69% for heath aster, Kentucky bluegrass, and Indian grass, respectively.

Biomasses of total plant species and the remaining nine plant species did not exhibit significant differences between vole and control enclosures. However, tests of standardized biomass between vole and control enclosures suggested increases in biomass for Scribner dicanthelium ($P = 0.10$) and little bluestem ($P = 0.11$). Although probability values were nonsignificant, standardized biomass was much greater in vole than control enclosures (57% and 30% greater for little bluestem and Scribner dicanthelium, respectively). We also should note that the four estimates of standardized biomass from vole enclosures all were greater than the two estimates from control enclosures for both little bluestem (control enclosures: 1.45-1.87; vole enclosures: 2.02-3.40) and Scribner dicanthelium (control enclosures: 0.71-0.74; vole enclosures: 0.76-1.09).

From late summer 1985 to spring 1986, voles cut 38% of 582 flowering stalks of big bluestem/Indian grass and 45% of 531 flowering stalks of little bluestem/tall dropseed in the four vole enclosures combined. In autumn 1986, nine of 16 subplots in each of two vole enclosures surveyed yielded vole cuttings. Of the 18 subplots, 16 contained cuttings of Indian grass, 4 of big bluestem, 4 of little bluestem, and 3 of round-headed lespedeza (*Lespedeza capitata*).

Discussion

As expected from Gibson *et al.* (1990), both Kentucky bluegrass and heath aster were affected negatively by prairie voles. These impacts were large, because standardized biomasses in vole enclosures was only 40% and 43% of those in control enclosures for Kentucky bluegrass and heath aster, respectively. In contrast to Gibson *et al.* (1990), however, we found a negative effect of voles on Indian grass because standardized biomass in vole enclosures was only 69% of that in control enclosures. Finally, no significant effects of voles were evident for total plant species, big bluestem, little bluestem, sedge, western ragweed, tall dropseed, lead plant, Louisiana sagewort, Scribner dicanthelium, and sideoats grama; this also agreed with the analyses of Gibson *et al.* (1990). However, probability values of 0.10-0.11 coupled with a large difference in standardized biomass were suggestive of a positive effect of voles on little bluestem and Scribner dicanthelium.

Both actual and standardized biomasses in vole and control enclosures demonstrated a large decrease in Kentucky bluegrass by voles. This decrease was consistent with voles readily feeding on bluegrass (Zimmerman, 1965) and its low abundance in tallgrass prairie (Table 1). Also, actively growing foliage of Kentucky bluegrass is physically available to foraging voles because of the low growth form of individual plants.

No studies of food habits of prairie voles have examined the use of Indian grass, but we expected voles to feed on this common C4 grass as they do on big bluestem and little bluestem.

Because Indian grass represented over 20% of the aboveground biomass in vole enclosures in 1984, the large negative impact indicated that prairie voles frequently ate or otherwise impacted this dominant grass. Although voles clipped numerous flowering stems and then ate seeds of Indian grass, most of this activity occurred during autumn-winter when plants were dormant. Therefore, herbivory during the growing season probably was the primary cause of the negative impact of voles on Indian grass.

A negative effect on heath aster by prairie voles was not expected, because a related aster was avoided by voles in Indiana (Zimmerman, 1965). However, the large decrease was consistent with heath aster being less abundant on communal burrow mounds of voles than in adjacent undisturbed prairie (Gibson, 1989). The negative effect on heath aster likely was due to foraging, but we have no documentation of vole herbivory on heath aster on Konza Prairie.

Although increases in abundance were nonsignificant for little bluestem ($P = 0.11$) and Scribner dicanthelium ($P = 0.10$), proportional differences in standardized biomasses between vole and control enclosures were large for both species. Further, standardized biomasses of both species were greater in each of the four vole enclosures than either of the two control enclosures. Considered together, these patterns strongly suggest that vole activity influenced both grasses. Little bluestem was selected by prairie voles in feeding trials (Menhusen, 1963) and was harvested after senescence in our enclosures; however, little bluestem did not differ between communal burrows of voles elsewhere on Konza Prairie (Gibson, 1989). In contrast to little bluestem, Scribner dicanthelium was less common on communal burrows than undisturbed prairie (Gibson, 1989). The positive responses associated with voles suggest that little bluestem and Scribner dicanthelium were released from competition with plants that were impacted negatively by voles, but this hypothesis remains to be tested.

Lack of changes in western ragweed, Louisiana sagewort, sideoats grama, and lead plant was consistent with avoidance of these or congeneric plant species by prairie voles (Menhusen, 1963; Zimmerman, 1965). In contrast, big bluestem and tall dropseed, which did not respond to voles, are eaten by prairie voles (Menhusen, 1963; Fleharty and Olson, 1969), but the magnitude of use in tallgrass prairie is unknown. Stem cutting of big bluestem and tall dropseed was common, but occurred after senescence and should have had little effect on future growth of these grasses. Finally, sedge was not impacted, although we expected it to be negatively influenced because heavy sedge (*Carex gravida*) was selectively eaten by voles (Menhusen, 1963).

General observations of the cutting of flowering stalks by prairie voles indicated that seeds of grasses and forbs often were eaten after the flowering stalks were pulled to the ground. We also have observed the use of seeds from clipped flowering stalks elsewhere on Konza Prairie. This use of seeds was consistent with the observations of Cole and Batzli (1979) that seeds are an important component of the diet of prairie voles.

Overall, our analyses and those of Gibson *et al.* (1990) demonstrated that voles influence prairie vegetation. In addition to Kentucky bluegrass, Indian grass, heath aster, little bluestem, and Scribner dicanthelium, biomasses of several other plant were numerically quite different between vole and control enclosures, but the patterns were nonsignificant. Further, the annual fire regime employed in the enclosures would have influenced vegetation (Abrams and Hulbert, 1987) and possibly the responses of plants to voles. These kinds of patterns suggest that long-term experimental studies both in the presence and absence of frequent fire are needed to more fully understand both negative and positive plant responses to voles. Therefore, the results of this short-term study of voles and vegetation on Konza Prairie should not be interpreted to mean that the impacts of small mammals on grassland vegetation are minor and unimportant (Gibson *et al.*, 1990; Gurevitch and Collins, 1994).

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Literature Cited

Abrams, M., 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.

Carroll, D., and L. L. Getz. 1976. Runway use and population density in *Microtus ochrogaster*. Journal of Mammalogy 57:772-776.

Cole, F. R., and G. O. Batzli. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. Journal of Animal Ecology 48:455-470.

Evans, E. W. 1991. Experimental manipulation of herbivores in native tallgrass prairie: reponses of aboveground herbivores. American Midland Naturalist 125:37-46.

Fleharty, E. D., and L. E. Olson. 1969. Summer food habits of *Microtus ochrogaster* and *Sigmodon hispidus*. Journal of Mammalogy 50:475-486.

Gibson, D. J. 1989. Effects of animal disturbance on tallgrass prairie vegetation. American Midland Naturalist 121:144-154.

Gibson, D. J., C. C. Freeman, and L. C. Hulbert. 1990. Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. Oecologia 84:169-175.

Gurevitch, J., and S. L. Collins. 1994. Experimental manipulation of natural plant communities. Trends in Ecology and Evolution 9:94-98.

Jarvinen, A. 1987. Microtine cycles and plant production: what is cause and effect? Oikos 49:352-357.

Menhusen, B. R. 1963. An investigation of the food habits of four species of rodents in captivity. Transactions of the Kansas Academy of Science 66:107-112.

Rose, R. K., and E. C. Birney. 1985. Community ecology. *In* R. H. Tamarin (ed.) Biology of New World *Microtus*. Special Publication 8, American Society of Mammalogists, pp 310-339.

Seastedt, T. R., T. C. Todd, and S. W. James. 1987. Experimental manipulations of the arthropod, nematode and earthworm communities in a North American tallgrass prairie. Pedobiologia 30:9-17.

Zimmerman, E. G. 1965. A comparison of habitat and food of two species of *Microtus*. Journal of Mammalogy 46:605-612.

Table 1.--Mean ± 2 SE for g biomass/m² in two control and four vole enclosures for total plants and 12 plant species, ranked from most to least common in control enclosures in 1984.

Species	Control enclosures		Vole enclosures		F values		
	1984	1986	1984	1986	Year	Voles	YxV
Total plants	463.2 ±10.3	461.2 ±77.8	481.5 ±31.6	463.5 ±49.0	0.16	0.17	0.10
Big bluestem	145.2 ±42.8	147.4 ±50.4	132.4 ±26.6	140.3 ±33.5	0.05	0.22	0.02
Indian grass	70.6 ±52.3	101.4 ±55.3	112.2 ±46.3	116.0 ±54.7	0.35	0.92	0.66
Little bluestem	63.5 ±6.4	104.4 ±16.5	47.0 ±9.8	119.8 ±23.3	33.37***	0.00	2.62
Sedge	39.4 ±16.8	15.7 ±0.1	45.1 ±13.1	16.6 ±9.1	13.93**	0.22	0.12
Western ragweed	28.0 ±10.1	2.0 ±1.8	19.6 ±7.1	0.6 ±0.4	53.12***	2.56	1.31
Tall dropseed	27.8 ±5.0	32.2 ±14.4	19.9 ±7.3	15.6 ±14.4	0.00	3.56	0.45
Lead plant	23.2 ±27.2	21.0 ±22.5	10.8 ±10.7	16.6 ±14.5	0.05	0.96	0.21
Heath aster	16.2 ±0.9	4.8 ±0.1	15.6 ±2.9	1.7 ±1.9	93.50***	2.00	0.77
Kentucky bluegrass	14.7 ±6.0	4.2 ±0.9	9.1 ±3.3	1.1 ±0.3	35.40***	8.08*	0.61
Louisiana sagewort	14.6 ±7.0	1.1 ±1.0	22.3 ±8.5	3.8 ±2.5	19.13**	1.97	0.46
Scribner dicanthelium	10.8 ±1.9	7.8 ±1.6	11.5 ±6.4	10.3 ±3.9	0.51	0.32	0.09
Sideoats grama	7.1 ±4.9	7.8 ±5.0	4.0 ±2.5	5.6 ±4.8	0.23	1.12	0.03

*P < 0.05, **P < 0.01, ***P < 0.001

Table 2.--Mean ± 2 SE for standardized biomass (1986 biomass/1984 biomass) in control and vole enclosures for plant species ranked as in Table 1.

Species	Control enclosures	Vole enclosures	F*	P*
Total plants	1.00±0.19	0.96±0.09	0.13	0.734
Big bluestem	1.01±0.07	1.09±0.32	0.13	0.737
Indian grass	1.50±0.32	1.03±0.10	14.30	0.019
Little bluestem	1.66±0.43	2.61±0.60	4.19	0.110
Sedge	0.44±0.26	0.35±0.14	0.46	0.535
Western ragweed	0.08±0.09	0.04±0.04	0.86	0.405
Tall dropseed	1.19±0.73	0.69±0.35	2.04	0.226
Lead plant	0.95±0.14	2.34±1.22	2.33	0.202
Heath aster	0.29±0.01	0.12±0.09	7.24	0.055
Kentucky bluegrass	0.30±0.06	0.13±0.06	12.35	0.025
Louisiana sagewort	0.07±0.05	0.17±0.09	2.00	0.230
Scribner dicanthelium	0.73±0.03	0.95±0.14	4.53	0.100
Sideoats grama	1.13±0.12	1.33±0.60	0.19	0.688

*Values of F and probability levels (P) for one-way analysis of variance.

The Influence of Crowding and Pocket Gopher Disturbance on Growth and Reproduction of a Biennial, *Tragopogon dubius*

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Abstract. Comparisons between the effects of plant density and pocket gopher (*Geomys bursarius*) disturbance (burrows and mounds) on the growth and reproductive output of a biennial, *Tragopogon dubius*, revealed that the former has a greater influence than the latter. Simulated burrow treatments in areas of high vegetation density differentially affected plant mortality, whereas burrows in low-density areas did not. Conversely, total plant biomass and measures of reproductive output differed significantly in areas of low plant density but showed no differences in high-density areas. Occupied natural burrows yielded higher plant biomasses than vacant natural burrows, and both produced higher biomasses than adjacent controls. No effects of mounds on the growth and reproductive output of *T. dubius* were evident.

Key words: burrows, fossorial herbivore, *Geomys bursarius*, mounds, oldfield vegetation, Pocket gopher, *Tragopogon dubius*

Introduction

Most individual plants are subjected to the dual influences of competition and herbivory. Adjacent individuals may compete for sunlight, water, nutrients, and mutualists, and virtually all plants are fed upon at some point in their life cycle. Investigations of such interactions are complicated and difficult and so have tended to concentrate on one aspect or the other. Further complications exist because some herbivores have both direct (e.g., consumption) and indirect (physical disturbance) effects on plants, and very little is known about the relative influence of these factors.

This study was undertaken to concurrently analyze the effects of a subterranean mammalian herbivore the plains pocket gopher (*Geomys bursarius*) and plant density on the growth and reproduction of *Tragopogon dubius*, a biennial plant species. The study followed an earlier investigation of the effects of these factors on an annual species, *Berteroa incana* (Reichman, 1988). *Tragopogon dubius* is common in old fields, where it often is subject to the influences of high densities of other early-successional plant species. In addition, it can be subject to the direct (consumption; Williams and Cameron, 1986; Behrend and Tester, 1988) and indirect (physical disturbance via burrows and mounds; Andersen 1987, 1988; Gibson 1989; Reichman and Smith 1985; Reichman 1988; Reichman et al. 1993) effects of pocket gophers, effects that can significantly alter plant density and community structure (Huntly and Inouye 1988; Huntly, 1991). *Tragopogon dubius* is a favored dietary item for pocket gophers (Behrend and Tester, 1988), and studies have revealed the effects of simulated gopher herbivory of this species (Reichman and Smith 1991).

This study was designed to determine the joint impacts of the presence of potentially competing vegetation and pocket gopher activity (mounds and burrows) on *T. dubius*. Analyses were made of the impact of simulated pocket gopher burrows, in the presence and absence of additional vegetation, on the growth and reproduction of *T. dubius*. Simulated burrows were constructed to provide more effective control over burrow variables, and treatments included open ("vacant") burrows and burrows refilled with soil to mimic backfilling behavior by pocket gophers. The effects of natural occupied and vacant burrows and mounds, also were analyzed by comparing their influence on *T. dubius* to paired controls in old-field vegetation directly adjacent to the pocket gopher disturbances.

Methods

The experimental arrangement is that of Reichman (1988). Two sets of experiments, termed Pen experiments and Field experiments, were conducted in Field 44 at Cedar Creek Natural History Area 45 km north of Minneapolis, MN. Pen experiments involved simulated burrows within gopher exclosures whereas Field experiments were outside the pens and employed naturally occurring pocket gopher mounds and vacant and occupied burrows.

Pen Experiments

The pens were 14 m in diameter, extended 1.6 m above the ground and into the ground, and had complete wire bottoms, thereby totally excluding pocket gophers. Two pens contained background old-field vegetation (32.2 and 38.6 stems/0.1m^2; these densities are similar to those in the surrounding fields) and were termed "vegetated" pens. Two other pens (termed "devegetated") were sprayed with Roundup at the initiation of the experiment in May, effectively denuding the surface.

Fourteen replicates of each of four treatments and 14 controls with no treatment were established in the vegetated and devegetated pens. The four treatments initially imposed were:

Vacant - simulated burrows with no further manipulation (simulating vacant burrows)
Occupied - simulated burrows from which emerging roots were to be trimmed (simulating occupied burrows from which pocket gophers trimmed the roots)
Top - burrows refilled with soil from the upper 10 cm of soil (simulating backfilling with the most nutrient-rich of the locally nutrient-deficient soils; Inouye et al., 1987)
Deep - burrows refilled with soil from a depth > 60 cm (soil especially nutrient-deficient; Inouye, et al., 1987)

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In the two latter treatments, the soil was packed to a density equivalent to that measured for gopher burrows at Cedar Creek (Reichman, 1988). No substantial root growth occurred in the Trimmed treatment, so it was combined with the Vacant treatment to yield three treatments (Vacant, Top, Deep) and one control, each having 14 replicates, except for the Vacant treatment with 28.

Simulated burrows were constructed by driving an 8-cm-diameter PVC pipe horizontally 1 m through the ground at a depth of 12.5 cm. and extracting the soil plug. This diameter and depth are similar to those of burrows found in Field 44 (Reichman, 1988). The simulated burrows radiated from a central pit like spokes from a hub, and each pen (two vegetated and two devegetated) contained two pits. Treatments were assigned randomly to spokes within vegetated and devegetated pens. Plugs were inserted in the open end of the simulated burrows to reduce moisture loss.

Four individual *Tragopogon dubius* rosettes were transplanted evenly and directly over each spoke after burrow construction in July and served as repeated measures for each treatment (for statistical analysis, the values for the four repeated measures/replicate were averaged). The transplanted rosettes had germinated in small pots that spring and were statistically indistinguishable in size at the time of transplantation (10-15 cm tall; ANOVA for size differences between treatments - F = 0.06, df = 3,279, P > 0.75). A 10-cm swath was cut over treatment sites in vegetated pens to facilitate initial success during transplantation. These manipulations yielded an arrangement of 14 replicates of two treatments (Top and Deep) and the controls plus 28 replicates of the Vacant treatment (after combining the Vacant and Occupied treatments), each with four repeated measures (transplanted *T dubius*), for a total of 280 individual plants.

Field Experiments

Similar *T. dubius* rosettes were transplanted onto fresh (< 2 weeks old) mounds and over vacant and occupied burrows (as determined by whether an excavated opening was plugged within 24 hrs). Burrows were located by probing the soil, a difficult technique in the loose sandy soil of Cedar Creek. Therefore, when the plants were harvested the soil below was excavated to confirm the presence of a burrow and whether it was vacant or occupied (again, based on whether the opening went unplugged for 24 hrs).

Fifty-three mounds and 50 locations over both vacant and occupied burrows received transplants. Controls also were established 25 cm from each experimental transplant. Subsequent mortality from an extreme drought over the 2 years of the investigation substantially reduced survivorship, in some cases yielding sample sizes too small to promote confidence in statistical results (see results).

Analysis

Entire plants were harvested from all experimental units in August, slightly over 2 years after they were planted. The number remaining alive for each experimental unit was recorded. Root crown diameter, plant height (both of which are accurate indicators of reproductive output for *T. dubius*; Gross 1981, 1984; Gross and Werner 1982), and the total number of capitula also were recorded. Specimens were oven dried at 60 C. for 72 hours. Subsequently, the masses of the root and stem tissue were recorded separately and summed to yield total biomass of the plant.

Model II regression analyses (using the Bartlett three-group method) were applied to relate plant height, number of capitula, stem biomass, and root biomass to total biomass. Calculations were made by treatment and for values combined for all replicates. Replicated goodness of fit test (G-statistic) was used to compare mortality (number of repeated measures/replicate alive) in the Pen experiments.

Two-way ANOVA was used to compare the effects of treatment and vegetation density on plant growth and reproduction in the Pen experiments (variances for the variables were homogeneous). Where significant treatment effects were detected, a Tukey-Kramer a posteriori separation procedure was applied to determine which treatments differed significantly from each other (Sokal and Rohlf, 1981). No significant differences in total plant biomass occurred between the two vegetated pens or between the two devegetated pens (F = 2.02, df = 1,29, P > 0.05 and F = 0.78, df = 1,64, P > 0.05 respectively). Therefore, the data for each set of two pens were combined for the analyses.

Mortality in the Field experiments was extremely high. Therefore, the controls for all treatments (mounds, vacant and occupied burrows) were combined and compared to each treatment with a Student's t-test.

It should be noted that the 14 or 28 replicates of each simulated burrow treatment were arrayed in only two pens each for vegetated and devegetated manipulations and that transplants in the field experiments were placed over just a few separate burrow systems. This could be considered a form of pseudoreplication (Hurlbert, 1984). The required effort, expense, and disturbance precluded constructing 140 separate gopher exclosures or finding 50 separate burrows systems. The results should be considered in light of this caveat.

Results

All of the measures of plant growth and reproduction were correlated significantly with total plant biomass and exhibited the same pattern of response, in both direction and magnitude, between controls and treatments (Table 1). Therefore, total plant biomass will be used as the primary measurement variable for comparisons between treatments.

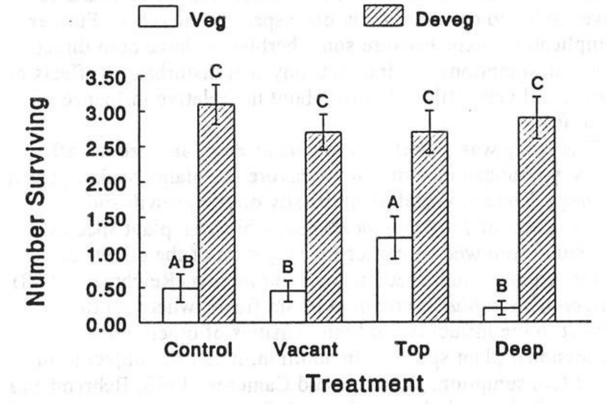

FIG. 1. Average number of plants alive (out of four initially transplanted) after 2 years for controls and treatments in vegetated and devegetated pens (vertical bars = S. E.'s). Bars sharing letters are statistically indistinguishable from each other. Sample size for each from left to right = 6, 14, 9, 25, 11, 13, 4, 13.

Pen Experiments

The number of individuals alive 2 years after transplantation was significantly lower in vegetated pens than in devegetated pens (F = 255.4, df = 1,139, $P < 0.0001$; Fig.1). Within vegetated pens, plants over the Top treatment survived in significantly greater numbers than plants over Vacant and Deep treatments; survival of the controls was intermediate and statistically indistinguishable from survival of the treatments (Fig. 2; F = 5.38, df = 3,29, $P < 0.01$). No significant differences occurred in survival between treatments within devegetated pens (Fig. 1).

The average plant biomass was significantly greater in devegetated than in vegetated pens (F = 12.68, df = 1, 94, $P < 0.001$; Fig. 1). Within devegetated pens, control plants were significantly smaller than those in the three treatments (F = 2.86, df = 3, 94, $P < 0.05$; Fig. 2; stem and root biomass, root crown diameter, and plant height showed statistically similar patterns), but no significant differences occurred among controls and treatments within vegetated pens (F = 0.92, df = 3, 29, $P > 0.05$; Fig. 2).

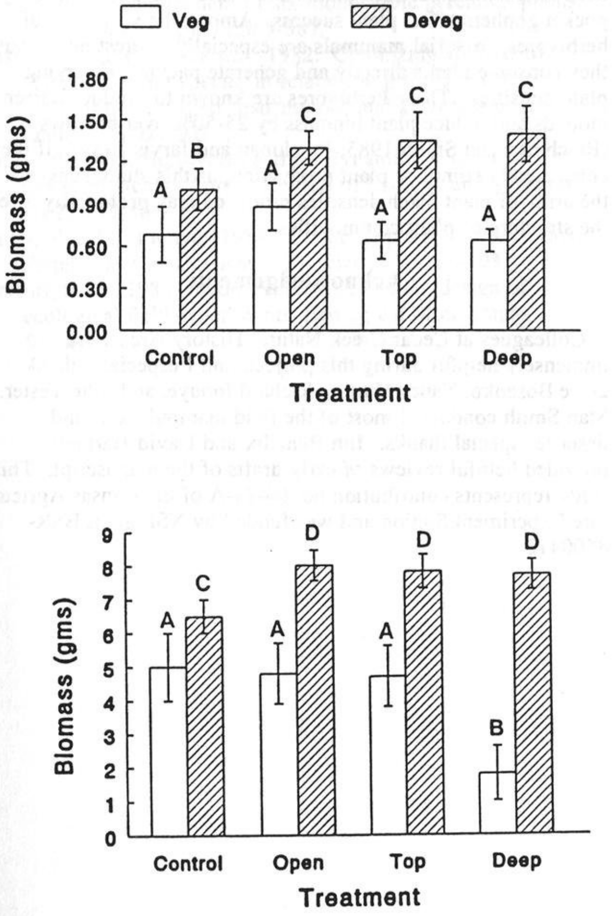

FIG. 2. Average total plant biomass (top) and total number of flowers produced (bottom) for controls and treatments in vegetated and devegetated pens (vertical bars = S. E.'s). Bars sharing letters within either graph are statistically indistinguishable from each other. See Fig. 1 for sample sizes.

A similar pattern was exhibited for the total number of flowering heads produced (Fig. 2). Significantly more were produced in the devegetated pens than the vegetated pens (F = 11.22, df = 1, 94, $P < 0.001$), and the controls in the devegetated pens produced significantly fewer flowers than plants in any of the treatments (F = 2.99, df = 3, 94, $P < 0.001$). Within the vegetated pens, plants over burrows refilled with top soil produced fewer flowering heads (F = 3.68, df = 3, 94, $P < 0.001$) than plants in other treatments (unlike values for total biomass, where no differences were exhibited within the vegetated pens).

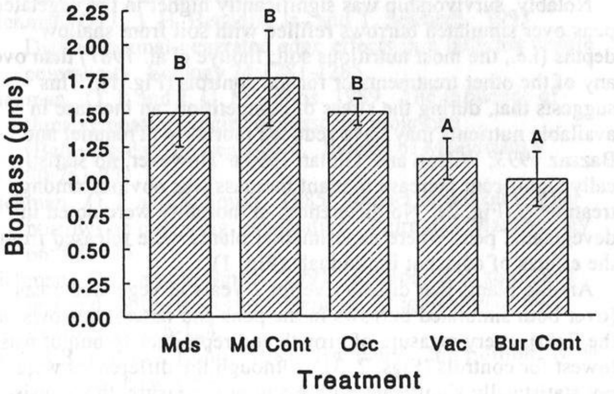

FIG. 3. Total biomass of plants on mounds and adjacent controls and over occupied and vacant burrows and their controls (vertical bars = S. E.'s). Bars sharing letters are statistically indistinguishable from each other.

Field Experiments

Total biomass of individual *T. dubius* plants on mounds and adjacent controls did not differ significantly (Fig. 3). However, significant differences occurred among plants growing over occupied burrows, those over vacant burrows, and control plants, with those on occupied burrows exhibiting the highest biomass response (F= 5.41, df = 1, 38, $P < 0.01$; Fig. 3). These differences are in spite of very small sample sizes, which resulted from high mortality during the experiments. Mortality did not differ between plants on mounds and their controls or between plants on the occupied and vacant burrows and their controls However, many more plants over burrows, whether occupied or vacant, and their controls died than did compared to plants on the mounds or their controls.

Table 1. Product moment correlations between total plant biomass and other variables measured in the study. Df = 94, all $P < 0.001$

Variable	r
Stem Biomass	0.982
Root Biomass	0.873
Root Crown Diameter	0.785
Heigh	0.637
Total Number of Flowers	0.693

Discussion

Under certain circumstances, the simulated and natural pocket gopher disturbances analyzed in this study did affect experimental plants. Furthermore, Reichman and Smith (1991) showed that *T. dubius* was affected significantly more by herbivory simulating pocket gopher foraging than by aboveground herbivory. However, as with an earlier investigation of an annual species (Reichman and Smith 1985), the survival, growth, and reproduction of individuals was affected more by the presence of nearby plants than by specific gopher generated disturbances (Figs. 1, 2, 3).

Notably, survivorship was significantly higher in the vegetated pens over simulated burrows refilled with soil from shallow depths (i.e., the most nutritious soil; Inouye et al. 1987) than over any of the other treatments or for the controls (Fig. 1). This suggests that, during the stress of competition, an increase in available nutrients may have reduced mortality (Tremmel and Bazzaz 1993; Wilson and Tilman 1993). However, no statistically significant increase in plant biomass was obvious among treatments (Fig. 2). No differences in mortality were noted in devegetated pens where experimental plants were released from the effects of adjacent individuals (Fig. 1).

Among plants that did survive for 2 years in vegetated areas (over both simulated burrows in the pens and natural burrows in the field), every measure of growth and reproductive output was lowest for controls (Figs. 2, 3). Although the differences were not statistically significant within any one measure, this consistent pattern suggests that controls tended to have particularly low values for all aspects of growth and reproduction. This pattern is the opposite of what was found in a similar experiment using an annual species (*Berteroa incana*; Reichman 1988), where control plants tended to be the largest.

The disparity between the annual and biennial species may be related to several characteristics of these growth forms. Initially, the annual species may not have had enough time to recover from the trauma of transplantation and respond to the treatments before flowering. The biennial species could overcome the transplantation trauma in the first year and respond to the imposed gopher disturbances in the following year when it flowered. Additional factors associated with growth form (upright for the annual and low for the first year biennial) and root structure probably contributed to the differences exhibited by the two types of plants.

Total plant biomass in the devegetated pens was significantly lower for control plants than for any of the treatments (Fig. 2). A comparison of the patterns of mortality and total biomass between vegetated and devegetated pens reveals an example of the relationship between pocket gopher disturbances and the influences of plant density in this particular system. Differences in mortality between treatments occurred under regimes of high plant densities, whereas no differences occurred in areas relieved of potential competition. Conversely, differences in biomass occurred only in devegetated areas. Thus, the effects of gopher disturbances on mortality were manifested under high plant density (i.e., competition) for the reasons discussed above. Pocket gopher effects on biomass occurred only at low competitor densities, perhaps because only under these circumstances would any burrow effect be directed primarily at the experimental plants and not diluted by numerous adjacent neighbors.

The biennial species did not show any statistically significant response to mounds. Because mounds are more ephemeral than burrows (especially in the sandy soils of Cedar Creek), any potential effects of mounds may have been ameliorated by the second year as the mounds eroded.

Reichman and Smith (1985) found that plant biomass was significantly greater directly adjacent to burrows than in random samples taken from the surrounding field. This was interpreted as an ability by foraging pocket gophers to locate areas of highest resource concentration. Results from the current experiments suggest the alternative explanation, i.e., that gophers actually might increase productivity by generating disturbances via their burrowing activities. In the current study, not only was plant biomass greater over all of the burrows treatments than for controls, but the highest values were recorded over occupied burrows, suggesting that ongoing activity stimulates plants even more than the past construction of a burrow. Other authors have noted that disturbances can break up soil aggregates and increase the surface area available for nitrification processes (Jenny 1930). This may partly explain why Grant et al. (1980) found a net increase in plant production where gophers occurred, even though the animals ate vegetation and killed it with their mounds. Furthermore, Reichman et al. (1993) found that the influence of pocket gopher burrows and mounds extends up to 0.5m from the disturbance.

Many of the sample sizes in these experiments were quite small (because of the extreme drought in central Minnesota during the 2-year investigation), perhaps obscuring treatment effects or skewing results. Nevertheless, the results suggest that both interactions between plants and disturbances generated by pocket gophers affect plant success. Among the vast array of herbivores, fossorial mammals are especially interesting because they consume plants directly and generate patches of varying plant densities. These herbivores are known to produce barren mounds and reduce plant biomass by 25-50% over burrows (Reichman and Smith 1985; Reichman and Jarvis 1989). If they concurrently stimulate plant production, as this study suggests, the array of plant patch densities produced may profoundly affect the structure of plant communities.

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Literature Cited

Andersen, D.C. 1987. Below-ground herbivory in natural communities: a review emphasizing fossorial animals. Quarterly Review of Biology 62:261-286.

Andersen, D.C. 1988. Tunnel-construction methods and foraging path of a fossorial herbivore, *Geomys bursarius*. Journal of Mammalogy 69:565-582.

Behrend, A. and J. Tester. 1988. Feeding ecology of the plains pocket gopher (*Geomys bursarius*) in east-central Minnesota. Prairie Naturalist 20:99-107.

Gibson, D. J. 1989. Effects of animal disturbance on tallgrass prairie vegetation. American Midland Naturalist 121:144-154.

Grant, W. E., N. French, and L. J. Folse. 1980. Effects of pocket gopher mounds on plant production in a shortgrass prairie ecosystem. Southwestern Naturalist 25:215-224.

Gross, K.L. 1981. Predictions of fate from rosette size in four "biennial" plant species: *Verbascum thapsus, Oenothera biennis, Daucus carota*, and *Tragopogon dubius*. Oecologia (Berlin) 48:209-213.

Gross, K.L. 1984. Effect of seed size and growth form on seedling establishment of six monocarpic perennial plants. Journal of Ecology 72:369-387.

Gross, K.L. and P. A. Werner. 1982. Colonizing abilities of "biennial" plant species in relation to ground cover: implications for their distributions and a successional sere. Ecology 63:921-931.

Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. Annual Review of Ecology and Systematics 22:477-503

Huntly, N and R. Inouye. 1988. Pocket gophers in ecosystems: Patterns and mechanisms. Bioscience 38:786-793

Hurlburt, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Inouye, R. N., N. Huntly, D. Tilman, and J. Tester 1987. Pocket gophers, vegetation, and soil nitrogen along a successional sere in eat central Minnesota. Oecologia (Berlin) 72:178-184.

Jenny, H. 1930. A study of the influence of climate upon the nitrogen and organic matter of content of the soil. University of Missouri Agricultural Experiment Station Research Bulletin #152.

Reichman, O. J. 1988. Comparison of the effects of crowding and pocket gopher disturbance on mortality, growth, and seed production of *Berteroa incana*. American Midland Naturalist 120:58-69.

Reichman, O. J., J. H. Benedix, Jr., and T. Seastedt. 1993. Distinct animal-generated edge effects in a tallgrass prairie community. Ecology 74:1281-1285.

Reichman, O. J. and J. U. M. Jarvis 1989. The influence of three sympatric species of fossorial mole-rats (Bathyergidae) on vegetation. Journal of Mammalogy 70:763-771.

Reichman, O. J. and S. Smith. 1985. Impact of pocket gopher burrows on overlying vegetation. Journal of Mammalogy 66:720-725.

Reichman, O. J. and S. Smith. 1991. Responses to simulated leaf and root herbivory by biennial, *Tragopogon dubius*. Ecology 72:116-124.

Sokal, R.R. and F. J. Rohlf. 1981. Biometry. 2nd Edition. W. H. Freeman, New York

Tremmel, D. C., and F. A. Bazzaz. 1993. How neighbor canopy architecture affects target plant performance. Ecology 74:2114-2124.

Williams L. R. and G. Cameron. 1986. Food habits and dietary preferences of Attwater's pocket gopher, *Geomys attwateri*. Journal of Mammalogy 67:489-496.

Wilson, S. D., and D. Tilman. 1993. Plant competition and reseource availability in response to disturbance and fertilization. Ecology 74:599-611.

Vegetation of Sandhills Under Grazed and Ungrazed Conditions

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Abstract. An understanding of the effects of livestock grazing on long-term vegetation changes is basic to developing sustainable, natural-resource, management systems. In this study of sandhills rangeland in western Oklahoma, eight pastures moderately grazed by cattle and eight adjacent exclosures ungrazed by livestock for 50 years were compared. Little bluestem (*Andropogon scoparius*) and sand bluestem (*A. halli*) produced more biomass and had greater frequency on the ungrazed areas, whereas blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*), and western ragweed (*Ambrosia psilostachya*) were more frequent and produced more biomass on the grazed areas. Species richness within sampling quadrats was not different ($P>0.05$) on the moderately grazed pastures (21 species ± 3 SE) compared to the ungrazed sites (18 ± 2). Herbage production was not different ($P>0.05$) on grazed and ungrazed grassland. This study supports the hypothesis that species differences can exist without marked differences in ecosystem function (i.e., production) and that moderate grazing as used in this study is a sustainable management system for the mixed prairie in the semi-arid central plains area where some level of sagebrush control is maintained.

Key words: Southern Plains, species composition, frequency, mixed grass prairie, grazing.

Introduction

Understanding the impacts of livestock on vegetation is fundamental to developing sustainable grazing systems. If such knowledge comes from long-term studies, greater confidence accrues in the sustainability of the management practices. The interpretation of ecosystem response to grazing, global changes, or other effects is dependent upon understanding the principles determining vegetation structure at the species level.

Changes in species composition can occur without acute perturbations such as grazing, fire, or drought. These changes can occur without significant disruption of ecosystem function (Johnson and Mayeux 1992). Thus, ecosystems can persist and function even with somewhat unstable, but resilient, species populations (Holling 1973). Changes in rangeland vegetation often have been attributed solely to livestock grazing (Branson 1985, Tomanek and Albertson 1953, Voigt and Weaver 1951). However, others concluded that exclusion of large herbivores is a modification of the natural system (Sims et al. 1978), and that grazing shifts ecosystems from a biotically to a more abiotically controlled system (Sims and Singh 1978).

A review of the effects of grazing on vegetation (Milchunas and Lauenroth 1993) indicates that species composition changes by grazing were dependent on site productivity, grazing history, and the intensity of grazing, in that order. The dominant species were more sensitive to environmental dynamics than to intensity of grazing, and bunch grasses were more likely to decrease under increasing grazing intensity than other plant types. However, primary production did not necessarily change with changes in species composition.

A number of studies, often short-term, have determined species responses to climate and grazing effects. Hyder et al. (1975) found that year effects were three times more likely than repeated heavy grazing to cause species change in a central plains shortgrass prairie. Albertson and Weaver (1946) described the devastation of native rangeland by severe droughts without any association with grazing. In general, tall and mid-grasses decreased, whereas the short grasses and sideoats grama increased.

In the northern Great Plains, White et al. (1978) found that certain species, needle-and-thread (*Stipa comata*) and prairie Junegrass (*Koleria cristata*), were less drought tolerant than blue grama and threadleaf sedge (*Carex filifolia*). Although grazing treatments varied from light to heavy across the study areas, no plant responses were attributed to grazing effects. Coupland (1992) concluded that grazing of southern mixed prairie by livestock caused the mid and tall grasses, particularly little bluestem and Indiangrass (*Sorghastrum nutans*), to decrease, and blue grama to increase. Big bluestem (*Andropogon gerardii*) was resistant to grazing at Hays, Kansas (Lewis 1971), perhaps because its short rhizomes make it difficult for cattle to graze all of the remnants of this species.

Big bluestem and little bluestem declined with increasing grazing pressure and with increasing length of heavy grazing on a loamy, upland prairie, rangeland site in north central Oklahoma (Sims and Dwyer 1965). Although blue grama increased with increasing grazing pressure, the composition of this species was erratic at heavier grazing intensities. However, buffalograss (*Buchloë dactyloides*), however, continued to increase on the more heavily grazed rangeland. Kelting (1954) found that moderate grazing favored little bluestem and that moderately grazed central Oklahoma tallgrass prairie had a larger number of species and greater production of living material than nearby ungrazed prairie.

Herbicides have been used on rangelands since the 1940s. The phenoxy herbicides, particularly 2,4-D, are effective in controlling sand sagebrush (*Artemesia filifolia*) and an array of broadleaf species in the Southern Plains (McIlvain and Savage 1949). Periodic spraying does not eliminate all forbs, but their density is less on the sprayed compared to the nonsprayed areas.

For this discussion, we assume that vegetation is subject to continual change in response to annual and seasonal climate dynamics as well as to the presence or absence of large herbivores. The objective of this study was to determine vegetation responses to cattle grazing in sandhills mixed-prairie pastures of the Southern Plains as compared to adjacent areas where cattle were excluded for 50 years.

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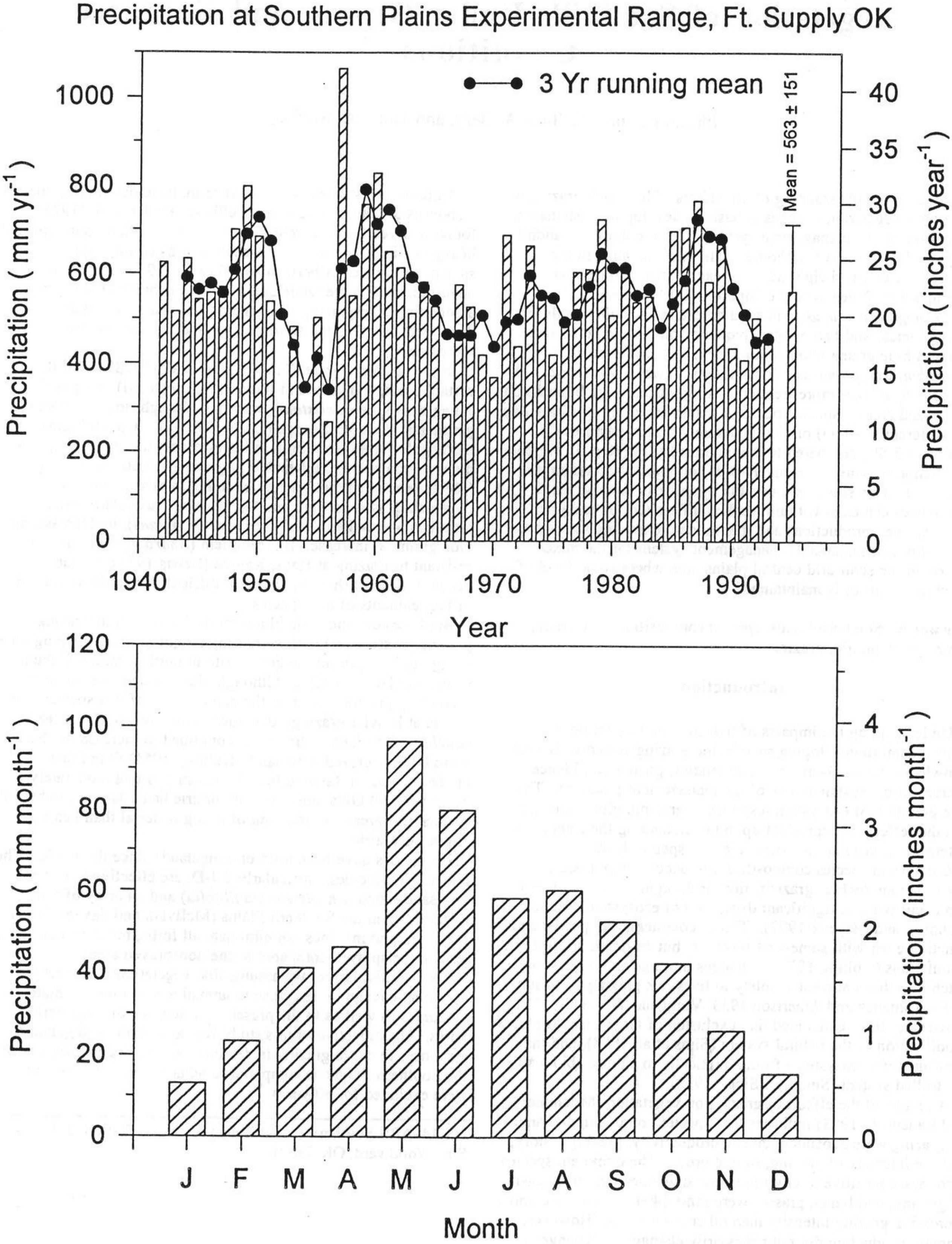

FIG. 1. Annual and monthly average precipitation at the Southern Plains Experimental Range, Ft. Supply, OK between 1942 and 1993.

Materials and Methods

The Study Site

This study was on the USDA Southern Plains Experimental Range (SPER) 2 km north of Fort Supply in northwestern Oklahoma. The SPER includes 1200 ha of native sandhill rangeland that in 1936 was "observed to be in extremely poor condition as a result of severe drought, intense heat and close grazing" (D. A. Savage, 1941 file report, Southern Plains Range Research Station, Woodward, OK). In 1941, experimental pastures (20 to 80 ha) and associated livestock exclosures (0.4 to 4 ha) were established prior to initiation of rotation grazing (McIlvain and Savage, 1951) and cattle stocking-rate studies (McIlvain and Shoop, unpublished manuscript, Southern Plains Range Research Station, Woodward, OK).

The native vegetation is sand sagebrush-bluestem prairie (Küchler 1964). However, because of a history of heavy domestic livestock grazing (beginning in the 1880s) sand sagebrush - mixed prairie is usually a more appropriate description (Berg 1994). The topography is rolling sandhills with undefined drainage patterns. Pratt soils (sandy, mixed thermic Psammentic Haplustalfs) are on lower slopes and more level areas, and Tivoli soils (mixed, thermic Typic Ustipsamments) are on the upper slopes. The 50-year mean annual precipitation is 563 mm (Figure 1). The annual precipitation pattern is unimodal with a peak in May (Figure 1). The frost-free period is generally from mid April until late October.

Sand sagebrush has been nearly eliminated in some of the experimental pastures by herbicide spraying (primarily 2,4-D) that began in 1946 (McIlvain and Savage 1949). Sagebrush also has been nearly eliminated in portions of some of the exclosures as well, even though spraying on a variable schedule of every 3 to 7 years was limited to the grazed pastures. Eight locations were selected for this study that were: 1) on Pratt loamy sand soils, 2) void or nearly void of sand sagebrush, and 3) on uniform topography within a sampling area of 20 x 100 m. Two sampling areas were defined at each of the eight locations, one was within an exclosure and the other was on an adjacent grazed area in the surrounding pasture. To avoid sampling next to the fence where cattle may have concentrated grazing and traveling, the paired sampling areas were separated by a 10 m wide strip on the pasture side of the exclosure fence.

The exclosures were ungrazed by livestock from 1941 until vegetation was sampled in 1993. The eight pastures associated with the exclosures generally had been grazed under 'moderate' stocking of 3.5 ha steer^{-1} year^{-1} or 7 ha cow-calf pair^{-1} year^{-1} since 1961. Moderate, year-long stocking is defined as 50% use of the current year's forage production by fall (McIlvain and Shoop 1961). From 1942 to 1961, two pastures were grazed at a heavy stocking (2.6 ha steer^{-1} yr^{-1})rate. In addition, residue within one exclosure was burned accidently in 1943, one half of one exclosure was burned intentionally in May 1951, and one exclosure was burned accidently in 1959.

Vegetation Sampling

Pasture sampling areas were fenced in March 1993 to exclude livestock. Vegetation frequency and biomass were sampled during the last week of July 1993. Within each 20 x 100 m sampling area the location of 20 sampling stations was assigned randomly. If a sample station fell within the canopy of a sand sagebrush plant, the station was voided and another station used.

Frequency of plants rooted within a 0.1 m^2 (square) quadrat placed on each sampling station was recorded. Frequencies were also recorded on four additional quadrats 1.5 m in each cardinal direction from the original station for a total of five quadrats per station. This gave frequency on 100, 0.1 m^2 quadrats per sample area. Biomass by species or classes of species was clipped near ground level at each sampling station within a 0.30 x 1.67-m quadrat and dried at 57 °C until a constant weight was achieved.

Vegetation biomass data were analyzed by analysis of variance using GLM of SAS (1989). The randomized complete block design used the eight sampling sites as blocks. Species frequency was analyzed using the Chi square test.

Results

A total of 37 species was encountered within the sampled areas on the ungrazed exclosures and moderately grazed pastures. This included 18 grasses, 16 of which were perennials, and 19 forbs, of which 8 were perennials and 11 were annuals (Table 1). Only 3 species, sand and little bluestems and western ragweed, occurred on both the grazed and ungrazed treatments at all eight locations. Thirteen species (7 perennial grasses, 3 perennial forbs, and 3 annual forbs) occurred at all eight locations.

Table 1. List of Plants found in 1993 Exclosure and Pasture Frequency Sampling at the Southern Plains Experimental Range near Ft. Supply, Oklahoma.

Common Name	Scientific Name from 'Flora of Great Plains' (1986)
Perennial Grasses	
Big sandreed	Calamovilfa gigantea
Blue grama	Bouteloua gracilis
Canada wild rye	Elymus canadensis
Indian grass	Sorghastrum nutans
Little bluestem	Andropogon scoparius
Rough dropseed	Sporobolus asper
Sand bluestem	Andropogon hallii
Sand dropseed	Sporobolus cryptandrus
Sand lovegrass	Eragrostis trichodes
Sand paspalum	Paspalum setaceum var stramineum
Sand sedge	Cyperus schweinitzii
Scribner dichanthelium	Dichanthelium oligosanthes var. scribnerianum
Sideoats grama	Bouteloua curtipendula
Switchgrass	Panicum virgatum
Texas bluegrass	Poa arachnifera
Windmill grass	Chloris verticillata
Annual Grasses	
Brome	Bromus spp.
Sandbur	Cenchrus incertus
Perennial Forbs	
Eastern prickly pear	Opuntia humifusa
Ground cherry	Physalis longifolia
Heath aster	Aster ericoides
Plains milkweed	Asclepias pumila
Silverleaf nightshade	Solanum elaeagnifolium
Spiderwort	Tradescantia occidentalis
Stickleaf	Mentzelia nuda
Western ragweed	Ambrosia psilostachya
Annual Forbs	
Annual eriogonum	Eriogonum annum
Camphorweed	Heterotheca latifolia
Horse-weed	Conyza canadensis
Indian blanket flower	Gaillardia pulchella
Lamb's quarters	Chenopodium album
Plains sunflower	Helianthus petiolaris
Rough pigweed	Amaranthus retroflexus
Russian thistle	Salsola iberica
Texas croton	Croton texensis
Western wild lettuce	Lactuca ludoviciana
Woolly plantain	Plantago patagonica (=P. purshii)

Species change

Twenty of the seven species encountered had significantly different ($P<0.05$) frequencies (Table 2) on the grazed and ungrazed treatments. Some of these changes in frequency were relatively large (Figure 2). For example, blue grama frequency was 3% on the ungrazed areas compared to 34% on the grazed areas. Frequencies of sand dropseed were 1 and 11% on the ungrazed and grazed treatments, respectively. In contrast, the frequency of little bluestem was 46% on the ungrazed areas compared to 24% under moderate grazing. A similar change also occurred with Texas bluegrass (*Poa arachnifera*). However, sand bluestem, a dominant (43% frequency) on the ungrazed areas, was also a dominant on the grazed pastures (37% frequency).

Table 2. Frequency within 0.1 m^2 quadrat of perennial and annual grasses and forbs and the Chi-Square probability of differences between moderately grazed pastures and ungrazed exclosures on the Southern Plains Experimental Range near Ft. Supply, Oklahoma in summer, 1993.

Species	Ungrazed	Grazed	Chi-Square Prob.
Perennial Grasses	--------------%-----------		
Big sandreed	0.1	1.9	0.000
Blue grama	2.8	34.5	0.000
Canada wild rye	4.6	2.3	0.009
Indian grass	0.3	0.0	0.157
Little bluestem	45.6	23.5	0.000
Rough dropseed	0.8	2.5	0.006
Sand bluestem	42.6	37.3	0.028
Sand dropseed	0.8	10.6	0.000
Sand lovegrass	3.6	1.5	0.007
Sand paspalum	0.8	6.9	0.000
Sand sedge	2.0	2.9	0.256
Scribner dichanthe	3.8	4.4	0.527
Sideoats grama	4.8	3.3	0.126
Switchgrass	3.4	5.0	0.105
Texas bluegrass	41.9	29.0	0.000
Windmill grass	0.4	0.9	0.204
Annual Grasses			
Bromus spp.	8.0	17.3	0.000
Sandbur	0.1	6.9	0.000
Perennial Forbs			
Eastern prickly pear	0.0	0.4	0.083
Ground cherry	0.0	0.3	0.157
Heath aster	0.4	0.0	0.083
Plains milkweed	0.1	0.4	0.317
Silverleaf nightshade	6.9	0.5	0.000
Spiderwort	18.9	4.6	0.000
Stickleaf	2.5	1.9	0.393
Western ragweed	35.4	75.0	0.000
Annual Forbs			
Annual eriogonum	7.8	13.8	0.000
Camphorweed	17.4	35.8	0.000
Horse-weed	2.3	1.3	0.127
Indian blanket flower	0.3	0.5	0.413
Lamb's quarters	1.4	1.8	0.545
Plains sunflower	5.0	0.0	0.000
Rough pigweed	0.3	0.1	0.563
Russian thistle	0.4	0.0	0.083
Texas croton	0.0	1.0	0.005
Western wild lettuce	0.3	0.1	0.563
Woolly plantain	3.6	16.0	0.000

Spiderwort (*Tradescantia occidentalis*) decreased ($P<0.05$) under grazing, whereas western ragweed increased dramatically ($P<0.05$) with grazing. Perennial forbs such as stickleaf (*Mentzelia nuda*), heath aster (*Aster ericoides*), ground cherry (*Physalis longifolia*), plains milkweed (*Asclepias pumila*), and eastern prickly pear (*Opuntia humifusa*) were not different ($P>0.05$) on the two treatments. Herbicide spraying in previous years could have had some direct influence on the frequency of forbs, both annual and perennial. It also could have had an indirect effect on grasses in the grazed areas by reducing competition from forbs.

The two annual grasses, annual brome (*Bromus* sp.) and sandbur (*Cenchus incertus*), had higher ($P<0.001$) frequencies on the grazed compared to the ungrazed regime. Annual forbs with a lower ($P<0.05$) frequency on the grazed areas were plains sunflower (*Helianthus petiolaris*), horseweed (*Conyza canadensis*), and Russian thistle (*Salsola iberica*). Annual forbs increasing ($P<0.05$) in the grazed pastures were Texas croton, annual eriogonum (*Erigonum annuum*), woolly plantain (*Plantago patagonica*), and camphorweed (*Heterotheca latifolia*).

Richness

Species richness, the number of plant species encountered within frequency quadrats on each treatment sampling area, was not different ($P>0.05$) between moderately grazed pastures and ungrazed exclosures (Table 3). The average for the grazed pastures was 21 species compared to 18 within ungrazed exclosures. Within quadrats sampled, the number of species ranged from 15 to 25 across the eight moderately grazed pastures, compared to 14 to 22 in the ungrazed exclosures. Indiangrass was the only perennial grass that occurred in the ungrazed but was not observed in the grazed areas. Of the perennial forbs, heath aster occurred only in the ungrazed and ground cherry only in the grazed treatment. Plains sunflower was the only annual forb that occurred only in the ungrazed treatments, whereas Texas croton (*Croton texensis*) was the only annual forb found only in the grazed treatment.

Table 3. Species richness (number of species of plants found within 100 0.1 m^2 quadrats) in moderately grazed pastures and ungrazed exclosures on the Southern Plains Experimental Range in summer, 1993.

Location	Moderately grazed	Ungrazed
19N	20	20
19S	23	18
21N	15	18
22	22	14
23ab	20	17
29	25	22
34ab	22	21
Average ± s.e.	21±3	18±2

Herbage production

Herbage production averaged near 2000 kg ha^{-1} and was similar on grazed and ungrazed mixed grass prairie (Table 4). However, the production by important species was quite different. Those species or species groups with less ($P<0.05$) production in the grazed compared to the ungrazed treatment were little bluestem, sand bluestem, and total grasses. Production was greater under moderate grazing for annual forbs ($P<0.02$), perennial forbs ($P<0.01$), and total forbs ($P<0.01$).

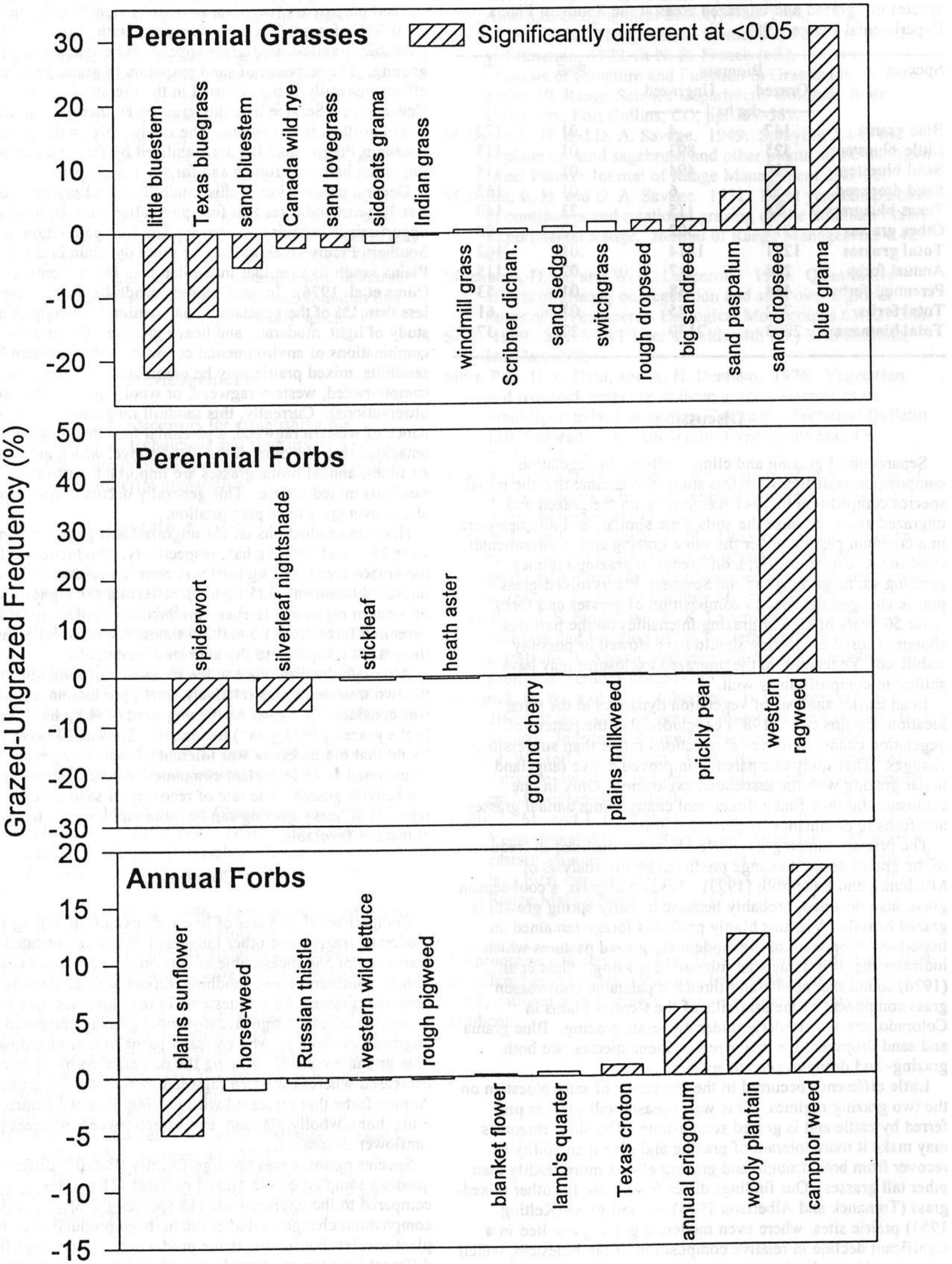

FIG. 2. The difference in frequencies between grazed and ungrazed mixed-prairie species of perennial grasses, perennial forbs, and annual forbs at the Southern Plains Experimental Range, Ft. Supply, OK after 50 years of treatment.

Table 4. Herbage biomass by important species and classes of species in grazed and ungrazed areas at the Southern Plains Experimental Range, 1993.

Species	Biomass Grazed	Biomass Ungrazed	P>F	CV
	kg ha^{-1}	kg ha^{-1}		
Blue grama	147	4	.01	172
Little bluestem	325	893	.01	115
Sand bluestem	299	494	.01	118
Sand dropseed	53	6	.01	162
Texas bluegrass	88	115	.23	140
Other grasses	319	302	.72	93
Total grasses	1231	1814	.01	162
Annual forbs	288	187	.02	115
Perennial forbs	484	138	.01	53
Total forbs	772	325	.01	61
Total biomass	2003	2139	.27	37

Discussion

Separation of grazing and climate effects on vegetation composition is difficult. In this study, we assume that the initial species composition in 1941 was similar on the grazed and ungrazed areas, because the soils were similar, and all sites were in a common pasture under the same grazing and environmental conditions. Consequently, a difference in grazing regimes (grazing vs. no grazing) on the Southern Plains mixed-grass prairie changed the species composition of grasses and forbs. After 50 years of similar grazing intensities on the pastures, changes caused by grazing should have slowed or possibly stabilized. Vegetation in the ungrazed exclosures may have shifted in composition as well.

In an earlier analysis of vegetation dynamics at the same location, Collins et al. (1987) concluded that the pattern of vegetation change reflected fluctuations rather than successional changes. That study compared unimproved native rangeland under grazing with the associated exclosures. Only in one exclosure did they find a directional change from annual grasses and forbs to dominance by perennial grasses.

The primary bunch grass, little bluestem, declined in frequency in the grazed areas, a change predicted by the analysis of Milchunas and Lauenroth (1993). Texas bluegrass, a cool-season grass, also declined, probably because its early spring growth is grazed heavily. Yet, this highly preferred forage remained an important component of the moderately grazed pastures which indicates that it is somewhat tolerant to grazing. Sims et al. (1976) found that needle-and-thread, a palatable cool-season grass component of the sandhills of the Central Plains in Colorado, reacted similarly under moderate grazing. Blue grama and sand dropseed, the major replacement species, are both grazing- and drought-tolerant species.

Little difference occurred in the frequency of sand bluestem on the two grazing regimes. This warm-season tall grass is preferred by cattle and is grazed season-long. The short rhizomes may make it more tolerant of grazing and give it an ability to recover from both drought and grazing effects more readily than other tall grasses. Our findings differ from those for other mixed-grass (Tomanek and Albertson 1953) and tall-grass (Kelting 1954) prairie sites, where even moderate grazing resulted in a significant decline in relative composition of big bluestem, which some consider to be the same species as sand bluestem. Thus, differences may exist between sand and big bluestems in response to grazing. Also, selection of the moderate grazing level at the SPER was based partly on the conservation of sand bluestem.

Sand paspalum (*Paspalum setaceum*) significantly increased ($P<0.0001$) from 0.8 to 6.9% frequency with grazing. This highly palatable, fragile-leafed grass appears to be tolerant of moderate grazing. The response of sand paspalum to grazing and climate effects generally is not reported in the literature. The Soil Conservation Service lists this grass as an increaser on the Dune site in northwest Oklahoma. The sandy soils on the dunes of the Southern Plains sandhills are stabilized by this grass, making it important both as a forage and for soil conservation.

General observation of this sandhills mixed prairie over the last 30 years indicates that forb populations are dynamic and opportunistic in their occurrence. The forb population in the Southern Plains sandhills may be more dynamic in the Southern Plains sandhills than that in similar sites in the Central Plains (Sims et al. 1976). In the Colorado sandhills, forbs comprised less than 1% of the vegetation composition by weight in a 15-year study of light, moderate, and heavy grazing. Under a variety of combinations of environmental conditions, the Southern Plains, sandhills, mixed prairie may be dominated by horsemint, camphorweed, western ragweed, or woolly plantain (personal observations). Currently, this sandhill rangeland has an abundance of western ragweed, a perennial forb that may be more tenacious than the other forbs listed above, which are annuals. At times, annual bromegrasses are important constituents of the sandhills mixed prairie. This generally occurs during years of above-average winter precipitation.

Herbage productions on the ungrazed and grazed treatments were 2139 and 2003 kg ha^{-1}, respectively. Production of forbs on the grazed areas (772 kg ha^{-1}) was over twice that found on the ungrazed treatment (325 kg ha^{-1}), reflecting the higher frequency of western ragweed. Herbage productions by the annual and perennial forbs were 1.5 and 3.5 times, respectively, greater on the grazed compared to the ungrazed treatments.

Although the difference in the frequency of sand bluestem on the two treatments was relatively small, production of biomass was considerably higher on the ungrazed (494 kg ha^{-1}) compared to the grazed (299 kg ha^{-1}) treatments. Sims and Dwyer (1965) found that big bluestem was tolerant of moderate grazing and that it remained as an important component of the tallgrass prairie if not heavily grazed. The rate of recovery of sand bluestem after removal of heavy grazing can be quite rapid, e.g., 3 to 5 years, if climate is favorable.

Conclusions

Comparison of 50 years of livestock exclusion to long-term moderate grazing and other rangeland practices indicated that management had measurable effects on the vegetation composition of Southern Plains, sandhills, mixed prairie. Among perennial grasses, little bluestem, Texas bluegrass, and sand bluestem decreased significantly under grazing compared to the ungrazed exclosures, whereas sand paspalum, sand dropseed, and blue grama increased. Among the perennial forbs, spiderwort decreased whereas western ragweed increased with grazing. Annual forbs that increased with grazing included annual eriogonum, woolly plantain, and camphorweed, whereas plains sunflower decreased.

Species richness was not significantly ($P>0.05$) different in quadrats sampled on the grazed pastures (21 species ± 3 SE) compared to the ungrazed site (18 species ± 2 SE). Species composition changes did alter the herbage production among plant species, but total herbage production was not significantly different between moderately grazed and ungrazed grassland. Perennial grases were replaced by forbs under moderate grazing.

The shift from production of perennial grasses to annual and perennial forbs protects the soils under this mixed-grass prairie from wind and water erosion. Earlier studies show that an increase in blue grama with moderate grazing pressure results in increased basal ground cover. Indicators of rangeland stability, particularly those related to soil cover and stability, indicate that the productivity of this rangeland site is being protected, while yielding a reasonable level of production. This study supports the hypothesis that species changes can occur without marked alteration in ecosystem function, i.e. herbage production, and that moderate grazing is a sustainable management system. Compared to the exclosures, the grazed areas had a marked shift from species used by cattle to species not as readily grazed by cattle. On the other hand, an exclosure is such an artificial situation that it is perhaps not the best standard of comparison. These findings indicate that herbage production can be sustained with moderate grazing within the climate and weather conditions found in this study area, and where control of dominant woody species is practical.

Acknowledgements

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Literature Cited

Albertson, F. W., and J. E. Weaver. 1946. Reduction of ungrazed mixed prairie to short grass as a result of drought. Ecological Monographs 16:449-463.

Berg, W. A. 1994. Sand sagebrush - mixed prairie. pp. 99. *In* T. N. Shiflet (ed.) Rangeland Cover Types of the United States. Society for Range Management, Denver, CO.

Branson, F. A. 1985. Vegetation changes on western rangeland. Range Monograph No. 2, Society for Range Management, Denver, CO, 76 pp.

Collins, S. L., J. A. Bradford and P. L. Sims. 1987. Succession and fluctuation in *Artemisia* dominated grassland. Vegetatio 73:89-99.

Coupland, R. T. 1992. Mixed prairie. Chapter 10, pp. 151-182. IN: Coupland, R. T. (Ed.). 1992. Natural Grasslands, Introduction and Western Hemisphere, Ecosystems of the World 8A, 469 pp. Elsevier Science Publications, New York.

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

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1-23.

Hyder, D. N., R. E. Bemment, E. E. Remmenga, and D. F. Hervey. 1975. Ecological responses of native plants and guidelines to management of shortgrass range. Technical Bulletin. Number 1503, USDA, Agricultural Research Service, Washington, D.C. 87 pp.

Johnson, H. B., and H. S. Mayeux. 1992. Viewpoint: a view on species additions and deletions and the balance of nature. Journal of Range Management 45:322-333.

Kelting, R. W. 1954. Effects of moderate grazing on the composition and plant production of a native tall-grass prairie in central Oklahoma. Ecology 35:200-207.

Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Special Publication 36, American Geographical Society, New York, 116 pp.

Lewis, J. K. 1971. The grassland biome: a systhesis of structure and function, 1970. *In* N. R. French (ed.), Preliminary Analysis of Structure and Function in Grasslands. Science Series 10, Range Science Department. Colorado State University, Fort Collins, CO, pp. 317-387.

McIlvain, E. H. and D. A. Savage. 1949. Spraying 2,4-D by airplane on sand sagebrush and other plants of the Southern Great Plains. Journal of Range Management 2:43-52.

McIlvain, E. H. and D. A. Savage. 1951. Eight year comparisons of continuous and rotational grazing on the Southern Plains Experimental Range. Journal of Range Management 4:42-47.

Milchucas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327-366.

SAS. 1989. SAS/STAT User's Guide (4th Ed.) SAS Institute, Inc. Cary, NC.

Sims, P.L., B. E. Dahl, and A. H. Denham. 1976. Vegetation and livestock response at three grazing intensities on sandhill rangeland in eastern Colorado. Technical Bulletin 130, Colorado State University Experiment Sta., Ft. Collins, 48 pp.

Sims, P. L., and D. D. Dwyer. 1965. Pattern of retrogression of native vegetation in north central Oklahoma. Journal of Range Management 18:20-25.

Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands: III. Net primary production, turnover and efficiencies of energy capture and water use. Journal of Ecology 66:573-597.

Sims, P. L., J. S. Singh, and W. K. Lauenroth. 1978. The structure and function of ten western North American grasslands: I. Abiotic and vegetational characteristics. Journal of Ecology 66:251-285.

Tomanek, G. W., and F. W. Albertson. 1953. Some effects of different intensities of grazing on mixed prairies near Hays, Kansas. Journal of Range Management 6:299-306.

Voigt, J. W., and J. E. Weaver. 1951. Range condition classes of native midwestern pasture: an ecological analysis. Ecological Monographs 21:39-60.

White, L. M., and J. J. Newbauer III, and R. J. Wight. 1978. Vegetational differences on native range during 38 years in eastern Montana. pp. 260-262. *In* D. Hyder (ed.) Proceedings First International Rangeland Congress, Society for Range Management, Denver, CO.

Wetlands May Change Tallgrass Prairie from a Sink to a Source for Atmospheric Methane

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Abstract. The belief that tallgrass prairie is a small but measurable sink for atmospheric methane (CH4, a greenhouse gas) has not considered the role of wetlands that tend to be strong sources of atmospheric CH4. We measured CH4 emission from cattail (*Typha latifolia*) dominated marshes to the atmosphere in northeastern Kansas, focusing on the flow of sediment-derived CH4 into, through, and out of the plant to the atmosphere. Emission rates were negligible at night, but rates were 0.1 to 0.5 ¦mol m-2 [leaf] s-1 from noon to sunset, with maximum rates of 1.7 ¦mol m-2 [leaf] s-1 at midday. The emission rate per unit of ground area was as high as 1000 mg CH4 m-2 d-1, which is a relatively high rate for wetlands. Assuming wetlands cover just 1% of the prairie landscape, CH4 emission from the wetland is large enough to offset CH4 consumption in the uplands. The results show that even minor components of landscapes are important in local and regional budgets for atmospheric CH4.

Key words: atmospheric methane, cattail, climatic change, greenhouse gas, Kansas, prairie wetland, *Typha latifolia*

Introduction

Prairie wetlands have important roles in determining water quality and water quantity, as waterfowl habitat, and as sites of biodiversity (cf., Van der Valk 1989). The persistence of these wetlands is threatened by human activities, including drought induced by projected climatic change (Poiani and Johnson 1993, Larson 1994). In this study, we address a possible role of prairie wetlands as agents of climatic change by emitting more CH4 (a +greenhouse+ gas) to the atmosphere than is consumed by upland soil. Methane is an odorless, colorless gas that plays a fundamental role in the chemistry and radiation budget of the earth+s atmosphere (Ramanathan et al. 1985). Currently, atmospheric CH4 accounts for a significant portion of the earth+s greenhouse effect, and the changing atmospheric concentration of CH4 will have a profound effect on the projected climatic change (Prinn 1994). Atmospheric CH4 comes entirely from the earth+s surface. The major sources include microbial production of CH4 anaerobically (i.e., in the absence of oxygen) in natural and constructed wetlands, in landfills, and in ruminant animals, as well as the emission of natural gas to the atmosphere (Crutzen 1991). The largest sink is chemical oxidation in the atmosphere (Crutzen 1991); however, several studies have found a small but significant sink for atmospheric CH4 in well-drained soil containing aerobic CH4-oxidizing bacteria (cf., King 1992, Ojima et al. 1993, Dorr et al., 1993).

In a recent study, Tate and Striegl (1993) found consumption of atmospheric CH4 by soil in tallgrass prairie, which continued even after the land was converted to agriculture. Given the prominence of grasslands on the earth+s surface, especially in North America, the authors speculated that tallgrass prairie and associated agricultural land could play an important role in a regional budget for atmospheric CH4. This is an important consideration as countries work towards limiting their emissions of greenhouse gases to the atmosphere (Houghton et al. 1992). However, the study by Tate and Striegl (1993) did not consider the diversity of land use across the prairie landscape, including wetlands as sources of atmospheric CH4 that might offset consumption by soil in the uplands.

We specifically studied wetlands dominated by the emergent macrophyte *Typha latifolia* because (i) it occurs widely across the prairie region (McNaughton 1966) and, in particular, (ii) it facilitates CH4 emission to the atmosphere by serving as a conduit for CH4 transport from wetland sediment to the atmosphere (Sebacher et al. 1985).

Methods

Sampling was done at two sites in northeastern Kansas. One small wetland, covering about 300 m2, occurred downstream from a spring on the Konza Prairie Natural Area near Manhattan, Kansas (39o11.0+N, 96o34.5+W) and was sampled in July 1992 and again in August 1993. The second site was a larger wetland, covering about 0.1 ha, located at the inlet end of Pottawatomie #2 reservoir also near Manhattan and was sampled in July 1994. Each site had a monospecific stand of *T. latifolia* established on a silty-clay sediment.

There is compelling evidence that CH4 produced microbially in wetland sediments can flow into aquatic emergents such as *T. latifolia* and then escape to the atmosphere through pores or stomatal openings on leaf surfaces (Knapp and Yavitt 1992). Therefore, we estimated rates of CH4 emission directly from *T. latifolia* as well as the CH4 diffusing directly from the sediment to the atmosphere.

At each site, CH4 emission from *T. latifolia* was measured periodically during the day and at ambient temperature, humidity, and sunlight. We studied three to nine shoots at each site, and separate measurements were made on 6-10 cm2 parts of two leaves per shoot. *Typha latifolia* leaves grow as high as 2 m, although we consistently sampled the upper 1/3 of the canopy. The emission estimate was made with a field-portable, closed flow system (LI-COR model 6200, Licor Inc., Lincoln, NE) and a 1/4 l plexiglass cuvette. Leaves were sealed into the cuvette, and the emission rate was measured during a 3-min enclosure time by taking 10-ml gas samples with plastic syringes (i) just before closing the cuvette, thus sampling ambient air at the same place in the plant canopy where the cuvette was placed and (ii) from the cuvette headspace (405 ml total volume) 1, 2, and 3 min after closure. The syringes served as storage vessels until gas analysis within 72 h of collection. While in the field, we filled several syringes with CH4 standards of known concentration and analyzed them along with the *T. latifolia* samples to correct for leakage from the sample syringes. Humidity within the cuvette was maintained close to the ambient level by directing flow through a desiccant in the LI-COR system. Leaf temperature was not regulated but remained within 2ÑC of ambient during the relatively short incubation period. The leaf was removed from the cuvette following the emission estimate and reinserted for subsequent measurements.

Following each individual gas-exchange measurement, we collected separate <5-ml gas samples from within the part of the leaf enclosed by the cuvette using plastic syringes and a 25 gauge needle (about 16 mm long). Leaves typically have an air-filled volume of 450 cm3 (cf., Tornbjerg et al. 1994); hence, our gas sample was <1% of the total volume. Additional samples taken from plant bases below the waterline collected air and no water, suggesting that ambient air did not mix with samples collected from emergent leaves.

We also sampled gases dissolved in sediment pore waters (n = 3 per site at 1 and 7.5 cm depth). Dissolved gases were extracted from the water sample by shaking it vigorously for 2 min. The total amount of dissolved CH4 (C in ¦l liter-1) in the water sample was calculated using transfer equations given by Flett et al. (1976):

$$C = x\,(1 + {}^{\circ}Vw/Vg)$$

where x is the mixing ratio in the gas phase (ppmv = ¦l liter-1), ° is the temperature-dependent Bunsen adsorption coefficient (cf., Yamamoto et al. 1976), Vw is the volume of the water extracted, and Vg is the volume of the gas phase. We express the final CH4 concentration as a partial pressure (i.e., 1 ¦l liter-1 = 30 ¦atm pCH4 at 19ÑC) to compare directly to CH4 concentration in ambient air and within *T. latifolia* plants. Sediment temperatures were measured with a thermistor.

Methane in air samples was analyzed with a gas chromatograph (Perkin Elmer, Inc., model Sigma 3B) equipped with a flame ionization detector and a 3-m Poropak-Q (80/100 mesh) column. We quantified CH4 concentrations by comparing peak areas for samples and several standards (1.09 to 10,300 ¦l liter-1 CH4 in N2; Scott Specialty Gases, Plumsteadville PA), which bracketed every 5-10 samples. Analytical precision was <0.2% for the lowest standard and was always within 2%. With this system, we could measure a minimum rate of CH4 emission of 0.01 ¦mol m-2 [leaf] s-1.

Results

During the day, the mean rate of CH4 emission was 0.25 ¦mol m-2 [leaf] s-1. Individual estimates ranged from detection limit to a high rate of 1.7 ¦mol m-2 [leaf] s-1. Figure 1 shows that the mean emission rate of 0.40 ¦mol m-2 [leaf] s-1 at the Pottawatomie site was significantly higher ($p < .05$) mean emission rate than the mean rate of 0.08 ¦mol m-2 [leaf] s-1 at Konza. Diurnal measurements of CH4 emission revealed maximum values from 1000 h to about 1400 h, with lower values in the early morning and later afternoon (Fig. 1).

At the Konza site, we measured CH4 emission from *T. latifolia* to the atmosphere on two dates during the growing season. The mean emission rate during the day was somewhat higher in July 1992 (0.25 ¦mol m-2 [leaf] s-1) than in August 1993 (0.08 ¦mol m-2 [leaf] s-1).

Methane concentrations within *T. latifolia* plants (Table 1) were always greater than the atmospheric concentration of about 1.7 ¦l liter-1, indicating a leaf-to-air gradient for CH4. Likewise, CH4 concentrations in sediment pore waters were relatively high. The mean values of pCH4 at the sediment/water interface were 23,000 ¦atm at the Konza site and 181,000 ¦atm the Pottawatomie site. Within the sediment (7.5 cm depth), the pore water CH4 was similar at both sites (ca., 200,000 ¦atm).

Table 1. Mean concentrations of CH4 in ambient air and in *Typha latifolia* plants (¦l liter-1) and pCH4 in sediment pore water (¦atm) of two *Typha*-dominated wetlands in Kansas.

	Konza		Pottawatomie
Location	July1992	August 1993	July 1994
Ambient air	1.72	1.77	1.77
Typha latifloia			
leaves	2.84	2.93	3.63
stem below waterline	150.0	191.0	234.0
Sediment			
1 cm depth	18,000	29,000	181,000
7.5 cm depth	190,000	202,000	204,000

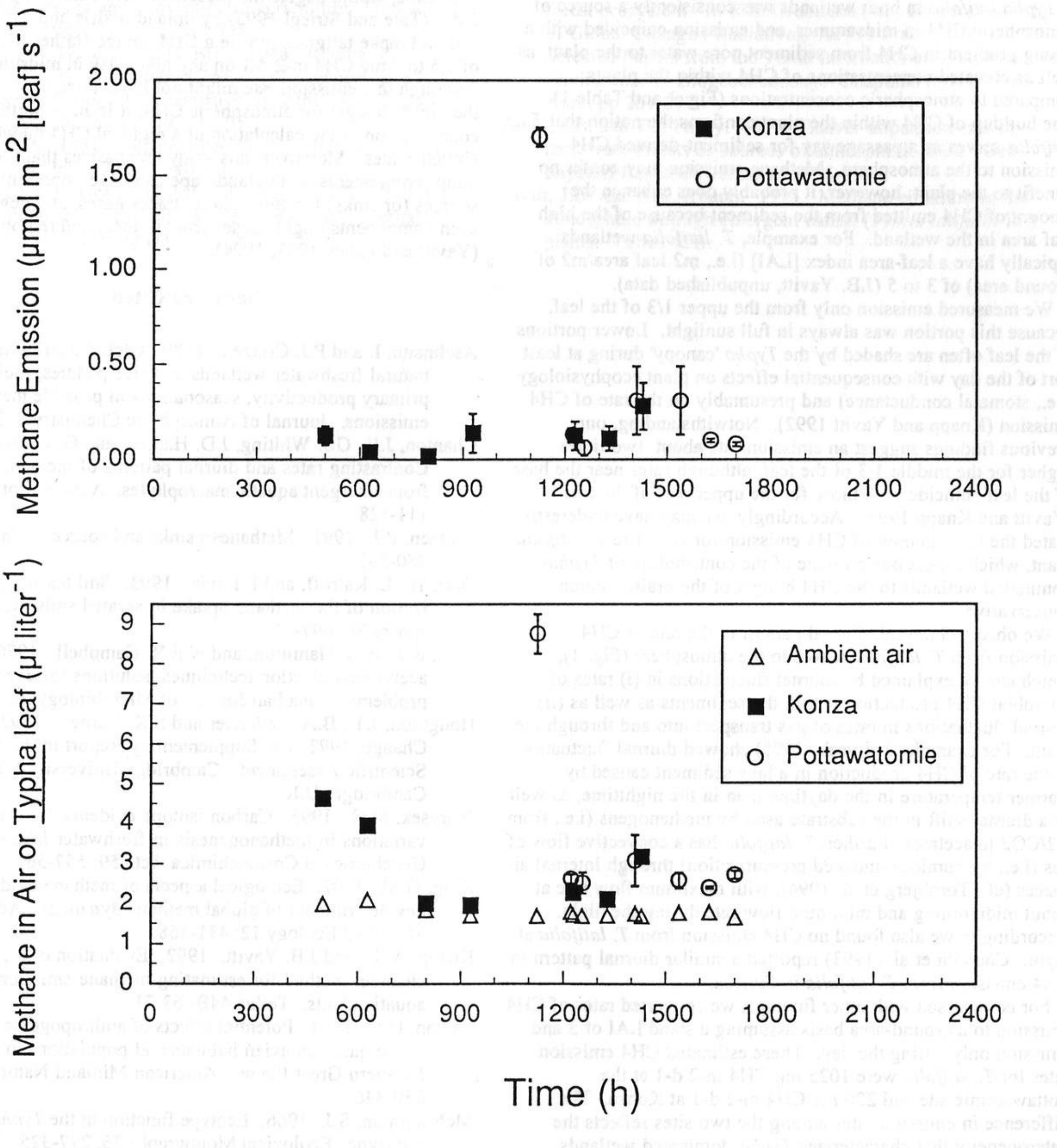

FIG. 1. Diurnal pattern of CH4 emission to the atmosphere (top panel) and CH4 concentrations in ambient air and in *Typha latifolia* leaves (bottom panel) for two sites in northeastern Kansas.

Discussion

Typha latifolia in both wetlands was consistently a source of atmospheric CH4 in midsummer, and emission coincided with a strong gradient in CH4 from sediment pore water to the plant, as well as elevated concentrations of CH4 within the plants compared to atmospheric concentrations (Fig. 1 and Table 1). The buildup of CH4 within the plant confirms the notion that *T. latifolia* serves as a passageway for sediment-derived CH4 emission to the atmosphere. Methane emission may confer no benefit to the plant; however, it probably does enhance the amount of CH4 emitted from the sediment because of the high leaf area in the wetland. For example, *T. latifolia* wetlands typically have a leaf-area index [LAI] (i.e., m2 leaf area/m2 of ground area) of 3 to 5 (J.B. Yavitt, unpublished data).

We measured emission only from the upper 1/3 of the leaf, because this portion was always in full sunlight. Lower portions of the leaf often are shaded by the *Typha* 'canopy' during at least part of the day with consequential effects on plant ecophysiology (i.e., stomatal conductance) and presumably on the rate of CH4 emission (Knapp and Yavitt 1992). Notwithstanding, our previous findings suggest an emission rate about two times higher for the middle 1/3 of the leaf, although rates near the base of the leaf coincide with those for the upper part of the leaf (Yavitt and Knapp 1995). Accordingly, we may have underestimated the total amount of CH4 emission for an entire *T. latifolia* plant, which makes our estimate of the contribution of *Typha*-dominated wetlands to the CH4 budget of the prairie region conservative.

We observed a weak diurnal pattern in the rate of CH4 emission from *T. latifolia* leaves to the atmosphere (Fig. 1), which can be explained by diurnal fluctuations in (i) rates of microbial CH4 production within the sediments as well as (ii) diurnal fluctuations in rates of gas transport into and through the plant. For example, Jedrysek (1995) showed diurnal fluctuation in the rate of CH4 production in a lake sediment caused by warmer temperature in the daytime than in the nighttime, as well as a diurnal shift in the substrate used by methanogens (i.e., from H2/CO2 to acetate). Further, *T. latifolia* has a convective flow of gas (i.e., by humidity-induced pressurization) through internal air spaces (cf., Tornbjerg et al. 1994), with maximum flow rate at about midmorning and minimum flow rate during the night. Accordingly, we also found no CH4 emission from *T. latifolia* at night. Chanton et al. (1993) reported a similar diurnal pattern in CH4 emission from *T. latifolia* in Florida.

For comparison with other findings, we converted rates of CH4 emission to a ground-area basis assuming a stand LAI of 3 and emission only during the day. These estimated CH4 emission rates for *T. latifolia* were 1025 mg CH4 m-2 d-1 at the Pottawatomie site and 220 mg CH4 m-2 d-1 at Konza. The difference in emission rates among the two sites reflects the heterogeneity that characterizes *Typha*-dominated wetlands across the prairie landscape. For example, we sampled the Pottawatomie site because it had more organic matter in the sediment than the Konza site to fuel higher rates of microbial CH4 production (i.e., higher pore water CH4 concentration) and the higher emission rates.

The highest values confirm the notion that marshes dominated by *T. latifolia* are extraordinary sources of CH4. For example, the global mean rate for CH4 emission from marshes dominated by aquatic emergents is 238 mg CH4 m-2 d-1, as summarized by Aselmann and Crutzen (1989). Chanton et al. (1993) reported emission rates of 400 to 1500 mg CH4 m-2 d-1 for a *T. latifolia* wetland in Florida.

To further put these values into perspective, the CH4 emitted from prairie wetlands, assuming they covered just 1% of the landscape, would negate the presumed CH4 sink of 1 mg CH4 m-2 d-1 (Tate and Striegl 1993) by upland prairie and agricultural soil and make tallgrass prairie a CH4 source (rather than a sink) of 1.5 to 7 mg CH4 m-2 d-1 on any given day in midsummer. Although this emission rate might not have much of an impact on the global budget for atmospheric CH4, it is an important consideration in the calculation of a regional CH4 budget for the United States. Moreover, this study emphasizes that seemingly minor components on the landscape can have important roles as sources (or sinks) for atmospheric traces gases, and neglecting such components might cause errors in local and regional budgets (Yavitt and Fahey 1993, 1994).

Literature Cited

Aselmann, I. and P.J. Crutzen. 1989. Global distribution of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. Journal of Atmospheric Chemistry 8: 307-358.

Chanton, J.P., G.J. Whiting, J.D. Happell and G. Gerard. 1993. Contrasting rates and diurnal patterns of methane emission from emergent aquatic macrophytes. Aquatic Botany 46: 111-128.

Crutzen, P.J. 1991. Methane+s sinks and sources. Nature 350, 380-381.

Dorr, H., L. Katruff, and I. Levin. 1993. Soil texture parameterization of the methane uptake in aerated soils. Chemosphere 26: 697-713.

Flett, R.J., R.D. Hamilton, and N.E.R. Campbell. 1976. Aquatic acetylene-reduction techniques: solutions to several problems. Canadian Journal of Microbiology 22: 43-51.

Houghton, J.T., B.A. Callander and S.K. Varney. 1992. Climate Change, 1992, The Supplementary Report to the IPCC Scientific Assessment. Cambridge University Press, Cambridge, U.K.

Jedrysek, M.O. 1995. Carbon isotope evidence for diurnal variations in methanogenesis in freshwater lake sediments. Geochimica et Cosmochimica Acta 59: 557-561.

King, G.M. 1992. Ecological aspects of methane oxidation, a key determinant of global methane dynamics. Advances in Microbial Ecology 12: 431-468.

Knapp, A.K., and J.B. Yavitt. 1992. Evaluation of a closed-chamber method for estimating methane emissions from aquatic plants. Tellus 44B: 63-71.

Larson, D.L. 1994. Potential effects of anthropogenic greenhouse gases on avian habitats and populations in the Northern Great Plains. American Midland Naturalist 131: 330-346.

McNaughton, S.J. 1966. Ecotype function in the *Typha* community-type. Ecological Monographs 36: 297-325.

Ojima, D.S., D.W. Valentine, A.R. Moiser, W.J. Parton, and D.S. Schimel. 1993. Effect of land use change on methane oxidation in temperate forest and grassland soils. Chemosphere 26: 675-685.

Poiani, K.A. and W.C. Johnson. 1993. Potential effects of climate change on a semi-permanent prairie wetland. Climatic Change 24: 213-232.

Prinn, R.G. 1994. The interactive atmosphere: global atmospheric-biospheric chemistry. Ambio 23, 50-61.

Ramanathan, V., R.J. Cicerone, H.B. Singh, and J.T. Kieht. 1985. Trace gas trends and their potential role in climate change. Journal of Geophysical Research 90: 5547-5566.

Sebacher, D.I., R.C. Harriss, and K.B. Bartlett. 1985. Methane emissions to the atmosphere through aquatic plants. Journal of Environmental Quality 14: 40-46.

Tate, C.M. and R.G. Striegl. 1993. Methane consumption and carbon dioxide emission in tallgrass prairie: effects of biomass burning and conversion to agriculture. Global Biogeochemical Cycles 7: 735-748.

Tornbjerg, T., M. Bendix, and H. Brix. 1994. Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L. 2. Convective throughflow pathways and ecological significance. Aquatic Botany 49: 91-105.

Van der Valk, A. 1989. Northern Prairie Wetlands. Iowa State University Press, Ames. +400 pp.

Yamamoto, S., J.B. Alcauskas, and T.F. Crozier. 1976. Solubility of methane in distilled water and seawater. Journal of Chemical Engineering Data 21: 78-80.

Yavitt, J.B. and T.J. Fahey. 1993. Production of methane and nitrous oxide by organic soils within a northern hardwood forest ecosystem. *In* R.S. Oremland (ed.) Biogeochemistry of Global Change : Radiatively Active Trace Gases: Selected Papers from the Tenth International Symposium on Environmental Biogeochemistry. Chapman & Hall, New York, pp 261-277.

Yavitt, J.B. and T.J. Fahey. 1994. Beaver impoundments in temperate forests as sources of atmospheric CO2. Geophysical Research Letters 21: 995-998.

Yavitt, J.B. and A.K. Knapp. 1995. Methane emission to the atmosphere through emergent cattail (*Typha latifolia* L.) plants. Tellus 47B.

Observing Spatial Structure in the Flint Hills using AVHRR Biweekly Composites of Maximum NDVI

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Abstract. The Advanced Very High Resolution Radiometer (AVHRR) offers twice-daily coverage with coarse spatial resolution (1 km pixels). The Normalized Difference Vegetation Index (NDVI), which indicates the degree of green vegetation present within a pixel, can be calculated from the red and near-infrared bands of AVHRR. The EROS Data Center of the U.S. Geological Survey produces a standard dataset on CD-ROM of the biweekly composites of maximum NDVI for the conterminous United States. We extracted from each of the 21 images in the 1991 dataset a 39,633 pixel area corresponding to the Flint Hills, the largest extant region of tallgrass prairie. We measured the temporal dynamics of spatial structure in the image series using lacunarity analysis and scale of fluctuation analysis. Our results capture phenological differences across the Flint Hills and illustrate the importance of measuring the spatial as well as the spectral characteristics of remotely sensed imagery.

Key words: AVHRR, NDVI, spatio-temporal variability, lacunarity, scale of fluctuation, correlation length, tallgrass prairie, Flint Hills, Kansas, Oklahoma

Introduction

Concerns about global change, biodiversity, and ecosystem management have increased attention to the characterization of ecological dynamics across regional landscapes (Turner 1989; Groffman and Likens 1994). A principal difficulty in spatially explicit ecological investigations lies in the knotty problem of rescaling the heterogeneity of processes and patterns found in natural landscapes (Milne 1991). Seldom do either functional representations of nonlinear processes (King et al. 1991) or statistical moments of distributions of spatial patterns (Openshaw and Taylor 1981; Arbia 1989) retain essential characteristics under rescaling operations. Yet there is a strong tendency in ecology to extrapolate findings using the principle of similitude (Iverson et al. 1994). For example, Konza Prairie Research Natural Area (KPRNA), 3700 ha of native tallgrass prairie in northeast Kansas, is intensively studied as representative of the tallgrass prairie ecosystem (Franklin et al. 1990). However, it amounts to only about 0.25% of the area in the Flint Hills, the largest extant expanse of tallgrass prairie. Thus arises the question: how can general ecological findings gleaned at finer scales (spatial, temporal, structural, functional) be rescaled usefully to coarser scales?

Ecological hierarchy theory (O'Neill et al. 1986) notes that lower frequency fluctuations occur at coarser spatio-temporal scales and that the higher frequency fluctuations occuring at finer spatio-temporal scales are constrained by those lower frequency dynamics. In other words, everything ecological (whether process or pattern) is dynamic, but relative disparities in rates of change allow some things to be viewed as the background against which higher-frequency dynamics unfold. Landscape-level remote sensing studies at KPRNA have demonstrated that surrogate measures of canopy phenology are modulated by spatio-temporal forcings of higher frequency (precipitation and grazing) and lower frequency (fire, drought, topography) (Briggs and Nellis 1991; Henebry 1993; Henebry and Su 1993). We expect that several of these factors will be relevant throughout the Flint Hills, but we also expect other factors, such as temperature, to gain explanatory power at the regional scale (Reed et al. 1994).

Scaling up from watershed to regional observations also requires a conceptual shift. At a spatial resolution of 30 m, the canopy is still meaningful as a resolvable scene object; thus, the phenology of the canopy can be observed. At a spatial resolution of 1 km, however, landscape details typically are too blurred to enable canopies is to be well-resolved; thus, we introduce the concept of phenology of the land surface. Implicit to this concept is the assumption of a significant degree of spectral mixing from different land covers. This is not a traditional phenology associated with specific events in a plant's life history; rather, land surface phenology describes the seasonality of reflectance characteristics that are associated with stages of vegetation development (cf. Reed et al. 1994). Mapping Normalized Difference Vegetation Index (NDVI) values back to green biomass, for instance, can be a dubious endeavor (Turner et al. 1992). At this juncture, we need instead to address directly the phenomenology of NDVI and other spectral vegetation indices because these are the only kind of data available at the synoptic, regional level.

Before we seek out the principal processes controlling land surface phenology across the region, we must find appropriate ways to summarize the spatio-temporal complexity of the data. What we describe here is a preliminary investigation of the spatio-temporal variation in reflectance across the entire Flint Hills over a single year. We wish to test the utility of time series of spatial metrics in expressing regional dynamics. Specifically, we assess lacunarity, which is a multiscale index of spatial heterogeneity in binary imagery, and the scale of fluctuation, which is an estimate of correlation length in interval-scaled imagery.

Vanmarcke (1983) developed an approach for characterizing "distributed disordered systems" which is amenable to remote sensing applications. He defined the scale of fluctuation (SOF) of an underlying spatial stochastic process as the parameter that controls the behavior of the process under extended local averaging. Spatial variation is analyzed through averages along transects or across areas. The 1-D SOF is the correlation length: the distance on average required to obtain samples that are statistically independent. Pixels within the correlation length exhibit positive spatial autocorrelation, i.e., their residual variance is less than that expected at random. A longer correlation length implies a more homogeneous landscape; it is effectively an estimate of patch size. Details of the algorithm and implementations for imagery were discussed in Henebry (1993).

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Lacunarity describes the complex intermingling of the shape and distribution of gaps within an image: a highly *lacunar* image exhibits gaps distributed across a broad range of sizes (Mandelbrot, 1983). Lacunarity is an aspect of fractal geometry: lacunarity (L) is the multiplicative prefactor in the general power-law formula of which the fractal dimension is the exponent, $F(x)=Lx^{(D-E)}$. As a measure of spatial heterogeneity, lacunarity quantifies the deviation of a geometric object (e.g., shape, pattern, fractal) from translational invariance and, thus, is well-suited to analysis of natural scenes. Simply stated, lacunarity is sensitive to clumping. Plotnick et al. (1993) discussed details of the algorithm and its applicability to landscape ecology. Implementations for quantitative image analysis were presented in Henebry and Batista (1994), Kux and Henebry (1994a,b), and Henebry and Kux (1995). Seasonal changes in the spatial arrangement of reflectance across land surfaces translates into changes in lacunarity; thus, lacunarity can characterize natural spatio-temporal variability as well as detect change.

We applied these spatial measures to a standard dataset readily available on CD-ROM, the 1991 AVHRR (Advanced Very High Resolution Radiometer) biweekly composites for the conterminous United States (USGS-EDC 1991).

Methods

The 1991 AVHRR biweekly composites produced by the EROS Data Center of the United States Geological Survey is composed of 21 separate 14-day maximum NDVI composites (Table 1) that were generated from nearly 500 NOAA-11 images (USGS-EDC 1991). In addition to 17 biweekly composites that encompass the growing season (March 1, 1991 to October 22, 1991), the months of January, February, November, and December are each represented by a single biweekly composite. The daily observations in the dataset had been calibrated to reflectance, scaled to byte data, and geometrically registered to the Lambert Azimuthal Equal Area map projection. The NDVI, computed from AVHRR bands 1 and 2, had been scaled for byte representation in the range of 0-200, with computed NDVI values of -1.0, 0, and 1.0 being mapped to 0, 100, and 200, respectively. (Subsequent analyses used the byte format, but the results were converted back into the unit interval format for presentation.) NDVI values less than zero indicate clouds, snow, water, and other nonvegetated surfaces, values greater than zero indicate surfaces with vegetated cover.

The boundaries of the Flint Hills were identified visually using a seasonal NDVI composite. An irregular shape of 39,633 pixels then was digitized onscreen and embedded within a rectangular mask of 399 lines with 130 samples per line to extract a consistent region from each 13 Mb composite image of the conterminous US. Two measures of spatial structure, scale of fluctuation and lacunarity, were calculated for each of the resulting 21 NDVI images of the Flint Hills.

Table 1: Biweekly composite periods for 1991

Period	Date of coverage	Day of year
1	01/04 - 01/17	004 - 017
2	02/01 - 02/13	032 - 045
3	03/01 - 03/14	060 - 073
4	03/15 - 03/28	074 - 087
5	03/29 - 04/11	088 - 101
6	04/12 - 04/25	102 - 115
7	04/26 - 05/09	116 - 129
8	05/10 - 05/23	130 - 143
9	05/24 - 06/06	144 - 157
10	06/07 - 06/20	158 - 171
11	06/21 - 07/04	172 - 185
12	07/05 - 07/18	186 - 199
13	07/19 - 08/01	200 - 213
14	08/02 - 08/15	214 - 227
15	08/16 - 08/29	228 - 241
16	08/30 - 09/12	242 - 255
17	09/13 - 09/26	256 - 269
18	09/27 - 10/10	270 - 283
19	10/11 - 10/24	284 - 297
20	11/08 - 11/21	312 - 325
21	12/06 - 12/19	340 - 353

Correlation length was estimated in each NDVI image using a random-walk transect resampling technique (Henebry 1993). Each transect was constructed from a random starting point and each next step was selected randomly with equal probability from among the eight nearest neighbors or remaining in place (viz., 1/9). Transects sampled only the image data; steps into the background matrix were forbidden. The length of each transect was 2593 pixels or 6.5% of the image data. Correlation length was estimated using successive local averaging with a maximum possible smoothing window of 255 and a convergence criterion of 2.5% between successive averagings. The sampling distribution of correlation length resulting from 100 transects was characterized by mean; standard deviation; skewness; and several percentiles (5, 25, 50, 75, 95), from which the coefficient of variation and interquartile range could be calculated.

The lacunarity index described by Plotnick et al. (1993) is defined only for binary data. Interval-scaled NDVI images can be analyzed by deriving a series of binary images based on quantiles of the image histogram (Henebry and Kux 1995). Here we constructed six binary images from each NDVI image corresponding to the following percentile intervals of the histogram: <5, 5-25, 25-50, 50-75, 75-95, >95. For example, pixels having NDVI values greater than the 95th percentile are mapped to white and remaining pixels are mapped to black. The resulting binary image illustrates the spatial distribution of the areas within the Flint Hills that have very high NDVI. This approach defines the percentile intervals relative to each image date, thus enabling an adaptive partitioning of the histogram as it changes during the growing season. Lacunarity was estimated in each of six binary images for each composite date using the complete sampling technique outlined in Plotnick et al. (1993) and a range of square windows that measured from one to 63 pixels on a side.

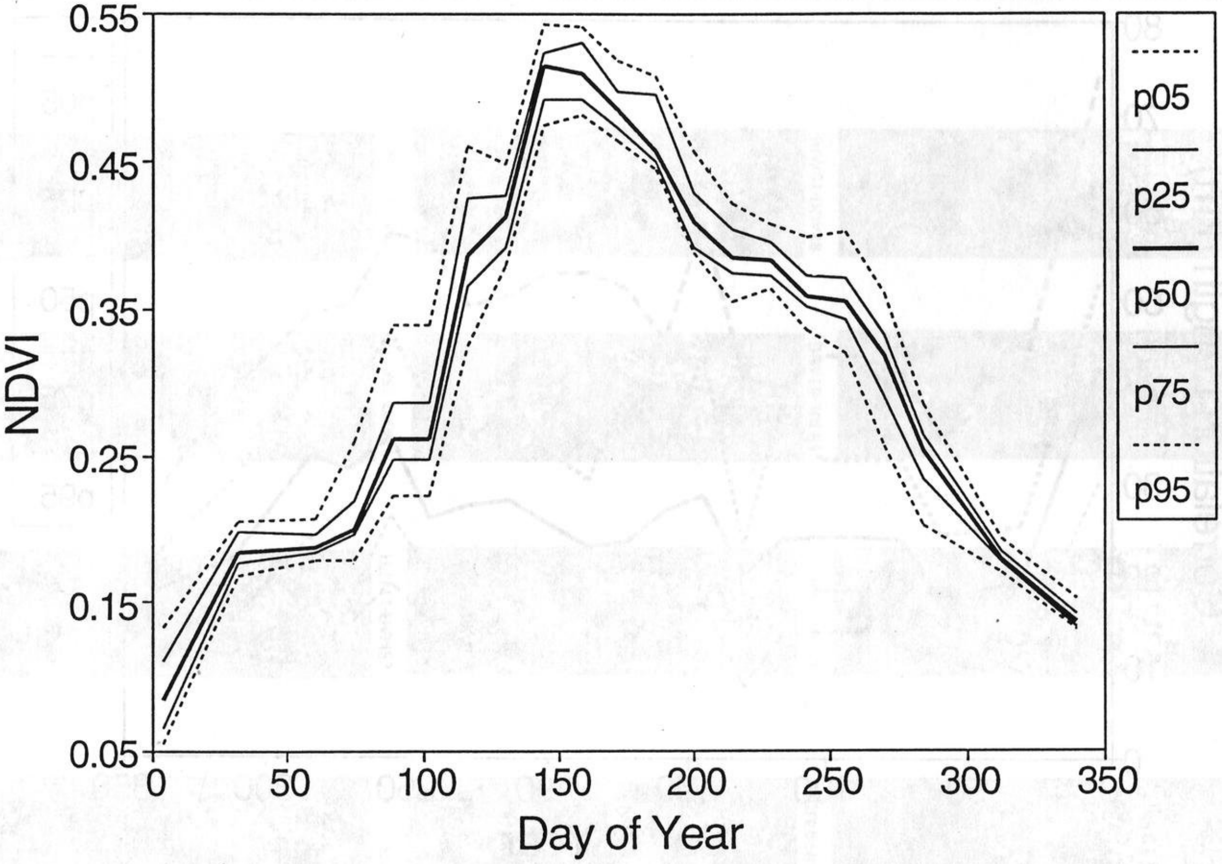

FIG. 1. Normalized Difference Vegetation Index (NDVI) of the Flint Hills during 1991. Median estimate is bracketed by other percentiles of the sampling distribution.

Results

The histogram time series of NDVI in the Flint Hills is illustrated in Figure 1. The seasonality of surface reflectance is clearly evident. The regional variability of NDVI at each date is captured by the percentiles bracketing the median value, e.g., the empirical 90% confidence interval is the area between the dashed lines. Note the pattern of a rapid increase in NDVI soon after day 100 (mid-April), a peak before day 150 (late May), the relatively swift decline in NDVI until a later season phase from about day 225 to day 275 (mid-August to early October). Typically, the peak occurs slightly later and the subsequent decline is more gradual; however, precipitation was below normal during June and July of 1991.

The correlation length time series presented in Figure 2 show no significant seasonality and much variation in the sampling distribution at each date. The median estimate of correlation length is about 25 km, which may result directly or indirectly from climatic factors. Direct effects may include common vegetation responses to precipitation gradients or common storm paths; indirect effects may include land management responses to seasonal temperature gradients and artifactual patchiness from the compositing process.

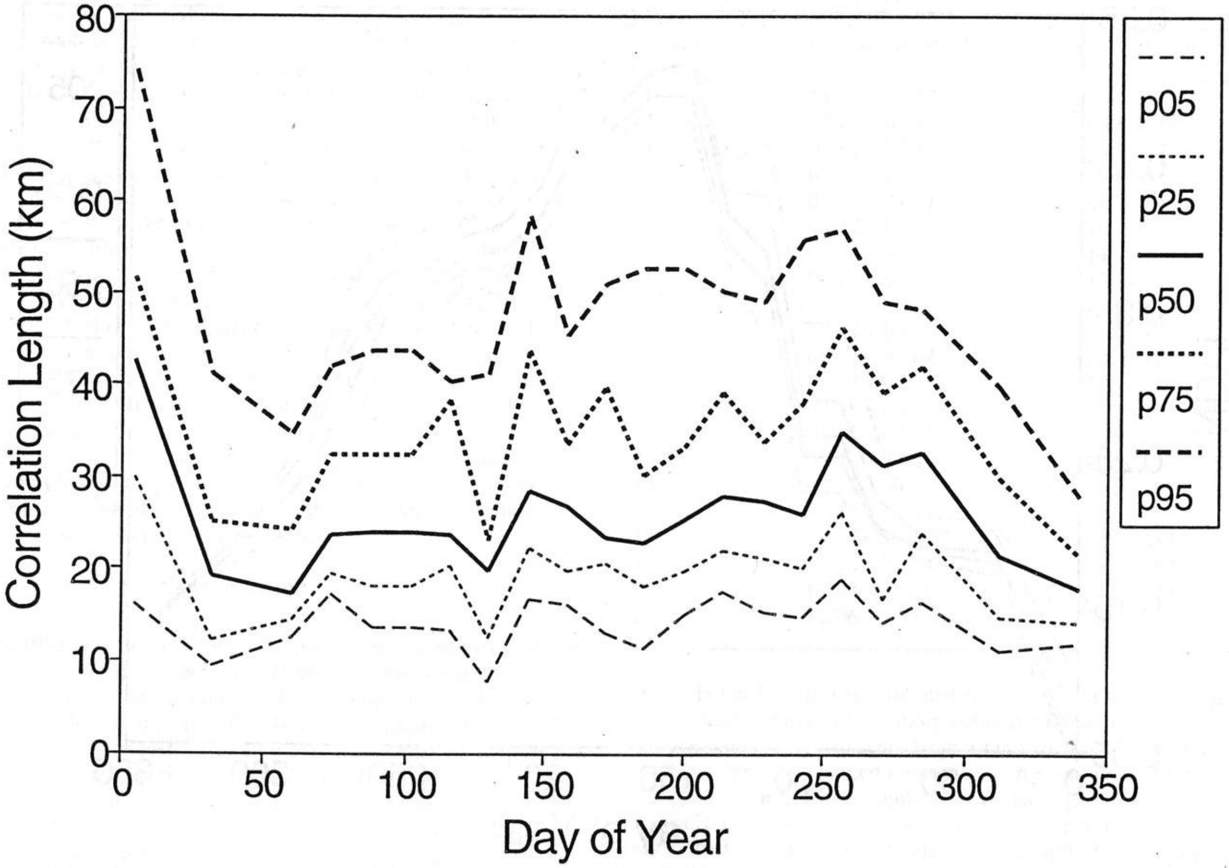

FIG. 2. Correlation length in NDVI images of the Flint Hills during 1991. Median estimate is bracketed by other percentiles of the sampling distribution.

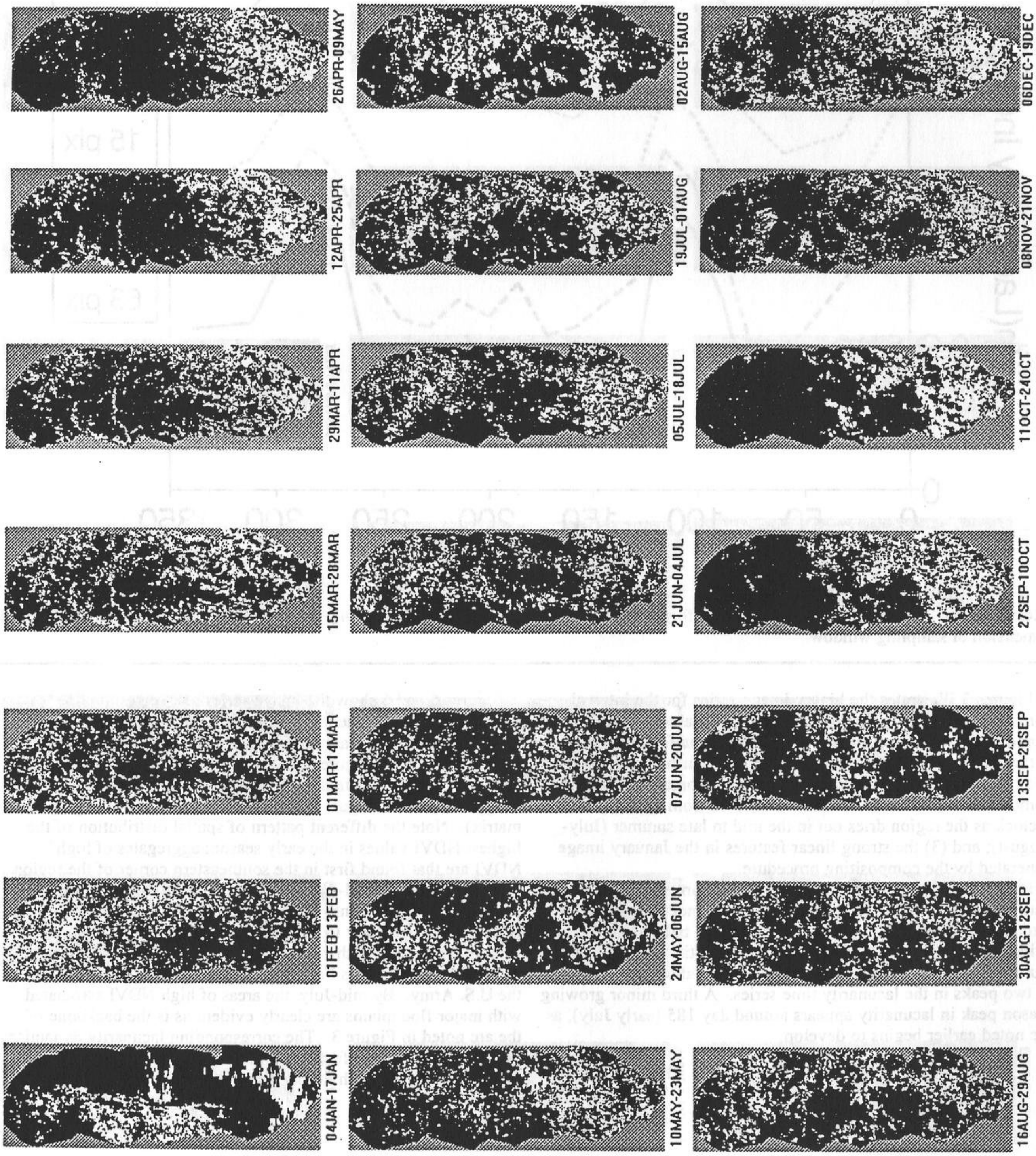

FIG. 3. Binary images formed from NDVI values in the 75th to 95th percentiles.

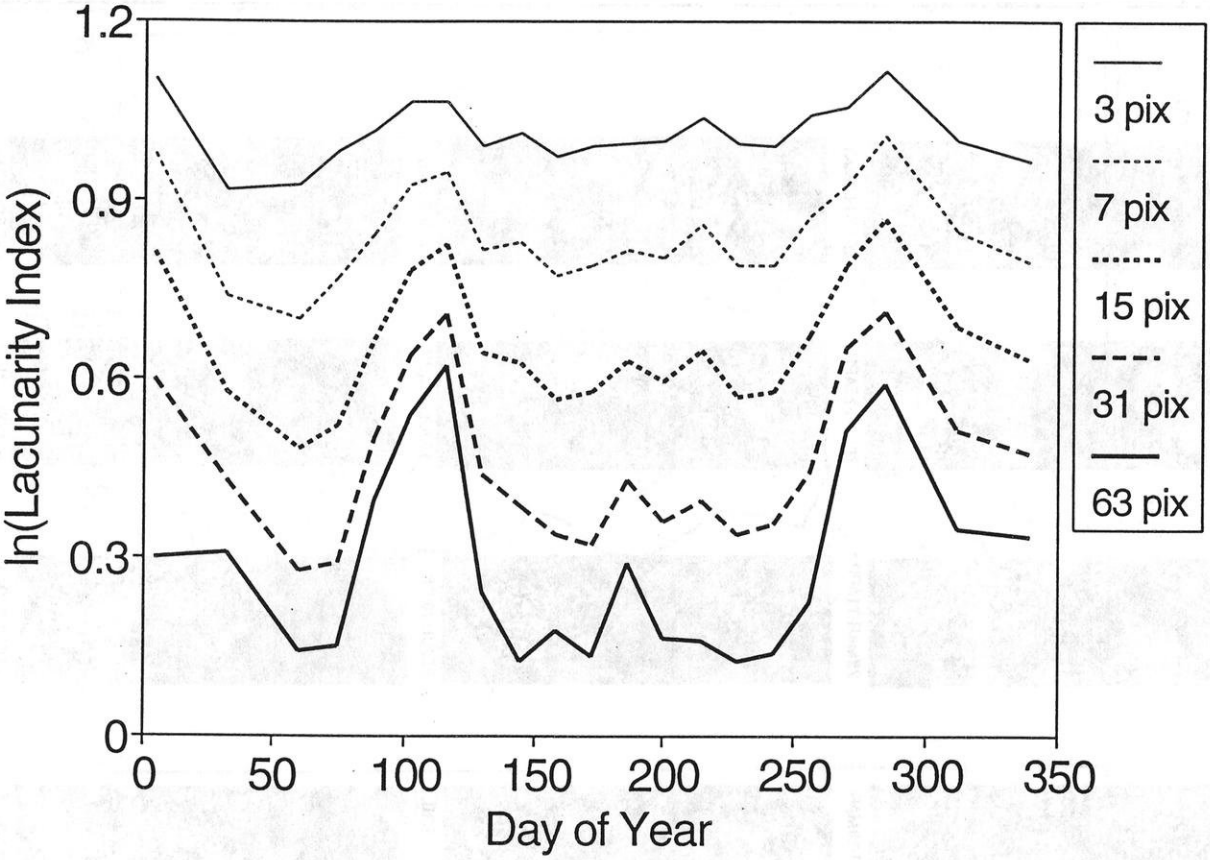

FIG. 4. Lacunarity indices for binary images formed from NDVI values in the 75th to 95th percentiles as a function of day of year and dimension of sampling window.

Figures 3 illustrates the binary image series for the interval containing the 75th to 95th percentile NDVI values. Amidst the spatio-temporal complexity of the data, note the following patterns: (1) definite north-south anisotropy during early (April) and late (October) growing season; (2) development of an arc of comparable NDVI values running clockwise from 12 o'clock to 7 o'clock as the region dries out in the mid to late summer (July-August); and (3) the strong linear features in the January image generated by the compositing procedure.

Figure 4 shows the lacunarity time series corresponding to the data in Figure 3. Note how lacunarity is dependent upon window size and how the seasonality of spatial pattern becomes more evident as larger window sizes are used for estimation. The clumping evident in the image series in April and October appear as two peaks in the lacunarity time series. A third minor growing season peak in lacunarity appears around day 185 (early July), as arc noted earlier begins to develop.

Figures 5 and 6 show the image series and corresponding lacunarity series for the highest 5% of NDVI values. Note that only 5% of the pixels are turned on in this image series as opposed to 20% in Figure 3. Again, temporal compositing leads in January to significant clumping (the density of which is exaggerated in this figure by the lower resolution of the graphical matrix). Note the different pattern of spatial distribution of the highest NDVI values in the early season: aggregates of high NDVI are that found first in the southeastern corner of the region during March into mid-April, shift to the southern tip of the Flint Hills from mid-April into May. Note the diagonal line of high NDVI during late May to early July extending from the north central area to the northwest corner of the region; the northwest extremity of this line is Fort Riley, a 41,000 ha training site for the U.S. Army. By mid-July, the areas of high NDVI associated with major floodplains are clearly evident as is the backbone of the arc noted in Figure 3. The corresponding lacunarity dynamics capture some of these features; specifically, the concentrations of high NDVI in the south during April and October and the January compositing effect.

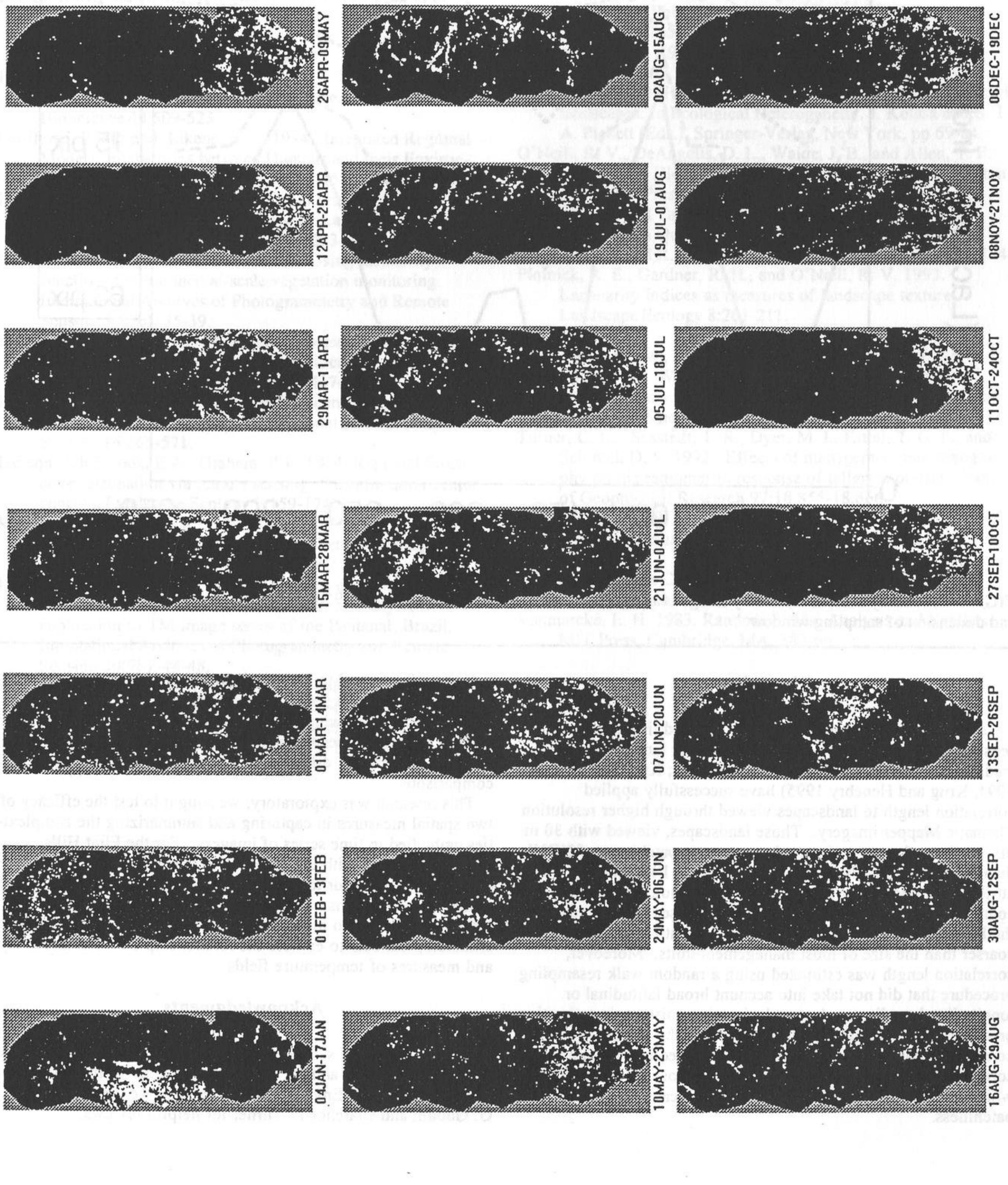

FIG. 5. Binary images formed from NDVI values greater than the 95th percentile.

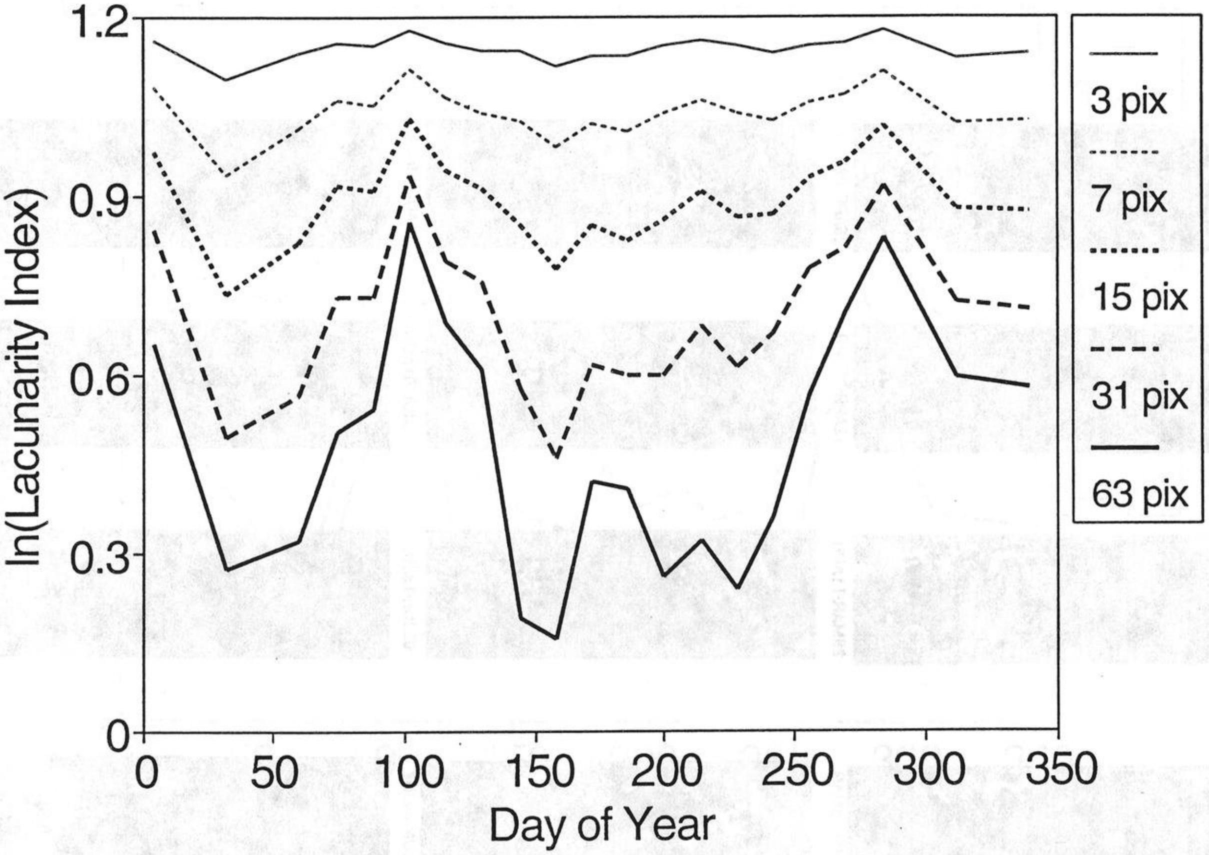

FIG. 6. Lacunarity indices for binary images formed from NDVI values greater than the 95th percentile as a function of day of year and dimension of sampling window.

Discussion

To our surprise, correlation length exhibited little temporal sensitivity to an obviously complex, changing landscape. Prior studies (Henebry 1993; Henebry and Su 1993; Krug and Henebry 1994, Krug and Henebry 1995) have successfully applied correlation length to landscapes viewed through higher resolution Thematic Mapper imagery. Those landscapes, viewed with 30 m pixels, showed stronger internal structure or patchiness of NDVI than did the Flint Hills when viewed through 1 km pixels. We attribute the poor performance of the correlation length to the combination of the broad similarity of land use and land cover in the Flint Hills and the blurring effect of a spatial resolution coarser than the size of most management units. Moreover, correlation length was estimated using a random walk resampling procedure that did not take into account broad latitudinal or longitudintal gradients. A reanalysis using anisotropic estimation procedure might yield better information on the seasonality of correlation length. On the other hand, the median estimate for correlation length in the image series was about 25 km, a scale at which the lacunarity index revealed a significant seasonality in patchiness.

Lacunarity proved to be sensitive to both spatial and temporal patterns in the image series. The ability of lacunarity to respond to early and late growing season clumping in the southern extent of the Flint Hills poses the possibility of calibrating lacunarity to regional temperature differences to facilitate interannual comparisons.

This research was exploratory; we sought to test the efficacy of two spatial measures in capturing and summarizing the complexities embodied in time series of imagery. For the Flint Hills landscape viewed with the AVHRR sensor, lacunarity analysis appears to be superior to scale of fluctuation analysis for eliciting sensitive comparisons. Our next task will be to extend the lacunarity analysis to multiple years and to gather the appropriate climatological data to explore the relationship between lacunarity and measures of temperature fields.

Acknowledgments

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Literature Cited

Arbia, G. 1989. Spatial Data Configuration in Statistical Analysis of Regional Economic and Related Problems. Kluwer, Boston. 256 pp.

Briggs, J. M., and Nellis, M. D. 1991. Seasonal variation of heterogeneity in the tallgrass prairie: a quantitative measure using remote sensing. Photogrammetric Engineering and Remote Sensing 57:407-411.

Franklin, J., Bledsoe, C. S., and Callahan, J. T. 1990. Contributions of the Long-Term Ecological Research program. BioScience 40:509-523.

Groffman, P. M., and Likens, G.E. 1994. Integrated Regional Models: Interactions between Humans and their Environment. Chapman & Hall, New York. 157 pp.

Henebry, G.M. 1993. Detecting change in grasslands using measures of spatial dependence with Landsat TM data. Remote Sensing of Environment 46:223-234.

Henebry, G.M. and Batista, G. T. 1994. Using lacunarity functions for continental-scale vegetation monitoring. International Archives of Photogrammetry and Remote Sensing 30(7b): 35-39.

Henebry, G.M. and Su, H. 1993. Using landscape trajectories to assess the effects of radiometric rectification. International Journal of Remote Sensing 14(12):2417-2423.

Henebry, G.M., and Kux, H.J.H. 1995. Lacunarity as a texture measure for SAR imagery. International Journal of Remote Sensing 16:565-571.

Iverson, L.R., Cook, E.A., Graham, R.L. 1994. Regional forest cover estimation via remote sensing: the calibration center concept. Landscape Ecology 9:159-174.

King, A.W., Johnson, A.R., and O'Neill, R.V. 1991. Transmutation and functional representation of heterogeneous landscapes. Landscape Ecology 5:239-253.

Krug, T. and Henebry, G.M. 1994. Temporal dynamics of correlation length in a disturbance driven ecosystem: application to TM image series of the Pantanal, Brazil. International Archives of Photogrammetry and Remote Sensing 30(7b): 44-48.

Krug, T. and Henebry, G.M. 1995. Seasonality of reflectance in the southern Pantanal of Brazil: spatio-temporal landscape segmentation using correlation length and lacunarity of NDVI images. Digest of IGARSS '95. IEEE, Piscataway, NJ. pp 1538-1541.

Kux, H.J.H. and Henebry, G.M. 1994a. Multi-scale texture in SAR imagery: landscape dynamics of the Pantanal, Brazil. Digest of IGARSS '94. IEEE, Piscataway, NJ. pp. 1359-1364.

Kux, H.J.H. and Henebry, G.M. 1994b. Evaluating anisotropy in SAR imagery using lacunarity functions. International Archives of Photogrammetry and Remote Sensing 30(7a):141-145.

Mandelbrot, B.B. 1983. The Fractal Geometry of Nature, Freeman, New York.

Milne, B. T. 1991. Heterogeneity as a multiscale characteristic of landscapes. In Ecological Heterogeneity. J. Kolasa and S. T. A. Pickett (Eds.), Springer-Verlag, New York, pp 69-84.

O'Neill, R. V., DeAngelis, D. L., Waide, J. B., and Allen, T. F. H. 1986. A Hierarchical Concept of Ecosystems, Princeton University Press, Princeton, NJ, 253 pp.

Openshaw, S. and Taylor. P. J. 1981. The modifiable unit area problem. In Quantiative Geography: a British view. N. Wrigley and R.J. Bennett (Eds.), Pion, London, pp 127-144.

Plotnick, R. E., Gardner, R. H., and O'Neill, R. V. 1993. Lacunarity indices as measures of landscape texture. Landscape Ecology 8:201-211.

Reed, B. C., Brown, J. F., VanderZee, D., Loveland, T. R., Merchant, J. W., and Ohlen, D. O. 1994. Measuring phenological variability from satellite imagery. Journal of Vegetation Science 5:703-714.

Turner, C. L., Seastedt, T. R., Dyer, M. I., Kittel, T. G. F., and Schimel, D. S. 1992. Effects of management and topography on the radiometric response of tallgrass prairie. Journal of Geophysical Research 97:18,855-18,866.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20:171-197.

USGS-EROS Data Center. 1991. Conterminous U.S. AVHRR Biweekly Composites, CDRM 615500, 6 volumes.

Vanmarcke, E. H. 1983. Random Fields: Analysis and Synthesis, MIT Press, Cambridge, MA, 382 pp.

Isotopic Evidence for the Replacement of Prairie by Forest in the Loess Hills of Eastern South Dakota

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Abstract. Newton Hills State Park in extreme eastern South Dakota contains forest and native prairie elements at the northern edge of the loess hills. The park contains relict native prairie communities on ridgetops and south facing slopes, elements of simplified eastern deciduous forest in valley bottoms and sides, and *Rhus glabra* (sumac) and *Quercus macrocarpa* (bur oak) communities between these two extremes. Prairie vegetation at this latitude yields carbon isotope ($\delta^{13}C$) values near -15‰, whereas forest vegetation is substantially more depleted in ^{13}C, yielding values near -27‰. The $\delta^{13}C$ values persist as the vegetation is incorporated into the soil organic matter (SOM), providing a signal to infer past community composition. A series of transects spanning a spectrum of community types from prairie relicts to upland deciduous systems was sampled and analyzed for their vegetation and SOM carbon isotope ratios. SOM $\delta^{13}C$ values at Newton Hills decreased from prairie relicts, which approached -17‰, to adjoining sumac communities types at close to -20‰, to oak savanna community types at -22‰, to upland deciduous community types near -25‰. This trend of decreasing $\delta^{13}C$ values from prairie relicts to upland deciduous communities and the increasingly positive values with depth confirm the succession from prairie to forest taking place in this preserve. The results suggest that the presettlement forest was restricted to valley bottoms and that the cessation of fires following European settlement has allowed forest to expand into the few remaining prairie sites, where the SOM already shows the isotopic impact from adjacent forest litter.

Key words: ^{13}C, carbon isotope, soil organic matter, succession, fire, prairie, loess, savanna, Holocene, decomposition, fractionation

Introduction

Carbon isotope analysis of soil organic matter (SOM) is a potentially important tool for detecting past vegetation changes and supplementing traditional approaches (White et al. 1969) based on soil morphology and chemistry. The technique is based on the assumption that, as plant material decomposes and becomes SOM, it retains the carbon isotope value ($\delta^{13}C$) of the vegetation from which it was derived (Balesdent et al. 1988), effectively recording the isotopic signature of past plant types in the soil. For example, SOM derived from a forest, usually exclusively C_3 species, and SOM derived from C_4 prairie species should produce $\delta^{13}C$ values that can be used to quantify vegetation changes (Martin et al. 1990, Balesdent et al. 1987, Volkoff and Cerri 1987, Schwartz et al. 1986, Dzurec et al. 1985). Because the SOM exists in fractions that vary from labile to very recalcitrant (Parton et al. 1987, Cambardella, 1993, Cambardella and Elliot 1994), a quantitative analysis of community changes can be reconstructed through time, either as C_3 and C_4 composition changes (Nordt et al. 1994) or as woody growth forms replace grasslands (e.g., Steuter et al. 1990, Tieszen and Archer 1990, McPherson et al. 1993).

Forest systems usually are composed entirely of vegetation utilizing the C_3 pathway and, therefore, are relatively depleted in ^{13}C, usually yielding a $\delta^{13}C$ value between -26‰ and -28‰ (Tieszen 1991, Cerling et al. 1989), although reassimilation of respired CO_2 can result in still more negative values (Schleser and Jayasekara 1985, Lobo Sternberg et al. 1989). On the other hand, prairies consist of assemblages of C_4 and C_3 grasses, C_4 and C_3 sedges, C_3 forbs, and a few shrubs. The C_4 plants are relatively enriched in ^{13}C, yielding $\delta^{13}C$ values between -12‰ and -14‰ (Tieszen 1991, Cerling et al. 1989). However, important genetic and environmental factors determine quantifiable variations in isotopic composition (Ehleringer and Monson, 1993). The abundance of the photosynthetic types also varies locally as functions of topography, water availability, soil nutrients (Novacek et al. 1985, Barnes et al. 1983, Tieszen and Steuter 1991), and perhaps grazing pressure. At a regional level, the abundance of C_4 species is determined largely by temperature (Tieszen et al. 1979, Tieszen et al. unpublished, Cavagnaro 1988, Terri and Stowe 1976). Consequently, substantial differences in isotopic values exist among Great Plains systems, as reviewed by Tieszen (1994).

The dominant community type of most of the Great Plains immediately prior to European settlement was native prairie (Grimm 1983). The Tallgrass prairie occupied an estimated 575,000 km (Kuchler 1964) and bordered the eastern deciduous forest elements or oak savanna systems (Abrams 1986). Presumably, frequent fires prevented the expansion of even opportunistic tree species (see Anderson, 1990). In the presettlement prairie, forested land persisted only near bodies of water or in association with steep terrain (Grimm 1984), where fire frequency apparently was reduced. Occasionally, topography served as an especially effective firebreak, and large areas of forest could develop. However, this once widespread original prairie has now been cultivated or is used as grazing land. Remnants do remain in sizable areas unfit for modern agriculture, as, for example, Konza Prairie Research Natural Area and Tallgrass Prairie Preserve, or as more localized relicts in areas of rough topography or too small and inaccessible to be farmed. Even the Konza (Knight et al. 1994) and Tallgrass (Tieszen, 1995, pers. comm.) prairies, however, now show an expansion of forest systems into adjacent grasslands.

The isotopic reconstruction of past vegetation types is complicated by uncertainties of isotopic fractionation during the decomposition process. Some studies (Martin et al. 1990, Vitorello et al. 1989) have suggested that carbon isotope ratios become enriched with depth. Several explanations have been proposed for the enrichment process, ranging from isotopic fractionation during decomposition to an anthropogenic effect related to the depletion of atmospheric $^{13}CO_2$ because of large-scale fossil fuel combustion (Martin et al. 1990), deforestation, and agriculture. Because these recent carbon inputs are derived from C_3 plants, the atmospheric pool of $^{13}CO_2$ fixed by plants has become depleted, on the order of 1.5‰ (Marino and McElroy, 1991, Friedli et al. 1986, Tieszen and Fagre 1993). As more modern vegetation fixes this depleted $^{13}CO_2$, the older SOM would appear relatively enriched, as shown by von Fischer and Tieszen (1995) in rainforests. These changes in soil ä^{13}C values that are independent of plant community change pose difficulties in reconstructing past vegetation types and must be better understood. In this study, we use the ä^{13}C signal in SOM to establish vegetation changes in one of these forest-prairie systems, the loess and loess-capped hills near the Big Sioux River of eastern South Dakota.

Loess hill communities represent a dynamic system that may change to forest or prairie, depending upon local conditions. The climate and soils of the area are capable of supporting either type of ecosystem (Novacek et al. 1985). Thus, in the absence of fires, tree species often expand into prairie areas (Heineman 1982, Rogers 1972), a progression noted at loess hill sites using aerial photography and vegetation analysis (Heineman 1982). The progression generally begins with encroachment of sumac onto prairie areas and a subsequent invasion by oak (Heineman 1982). The oaks, in turn, often are replaced by other climax species reminiscent of eastern deciduous forest (Abrams 1986, Shotola et al. 1992). This general pattern of successional progression in the northern loess hills is similar to Holocene changes documented in Minnesota from the pollen record (Clark 1990, Grimm 1984).

The forest and grassland character of Newton Hills State Park is similar to that of the northern loess hills as described by Mutel (1990) and was chosen as the location to quantify successional changes between forest and grassland communities at the eastern edge of the continuous prairie. The park encompasses over 600 acres of mainly forest vegetation, characterized by Hanson and Hazlett (1971) as a relatively simple upland deciduous system containing primarily species such as *Tilia americana* (basswood), *Ulmus americana* (elm), and *Juglans nigra* (black walnut). The prairie relicts are populated primarily by the grass species *Andropogon gerardii* (big bluestem), *Andropogon scoparius* (little bluestem), *Sorghastrum nutans* (Indian grass), *Bouteloua curtipendula* (side oats grama), and *Poa pratensis* (Kentucky bluegrass). Intermediate communities, including *Quercus macrocarpa* savanna and *Rhus glabra* shrubs, exist between these two successional extremes. We defined a series of transects traversing community types ranging from upland deciduous forest to prairie relict and extracted vegetation samples and soil cores for isotopic analysis. We document past shifts in community types throughout the park, and focus on the presumed succession from prairie to forest that has occurred as a result of fire suppression.

Materials and Methods

Site

The study was conducted in Newton Hills State Park in southeast South Dakota (Lincoln County, Township 97N, 49W, in Sections 11, 12, 13, & 14; 43° 13' N, 96° 35' W) immediately west of the Big Sioux River. Sargeant Creek bisects Newton Hills and runs into the Big Sioux River north of the park. Upland deciduous forest species occupy both sides of the creek bed, with adjacent hillsides covered in a mosaic of forest, savanna, and small prairie patches. Basswood and other eastern deciduous tree species populate the shadier, cooler, and moister north- and east-facing slopes. Conversely, the south- and west-facing slopes receive more solar radiation and are dominated by species tolerant to heat and lack of moisture (Hanson and Hazlett 1971). The oak savanna and prairie relicts are located primarily on these warm and dry slopes. The soil is derived from loess and consists of the Shindler-Renner complex (especially in the wooded areas) with 15 to 40% slopes. The profile for this soil type contains loam for approximately the first 46 cm and a clay loam thereafter (Driessen 1976). The highland portions of the park consist of the Egan type soil series with 3 to 6% slopes. This soil is composed of a silty clay loam and also originates from loess.

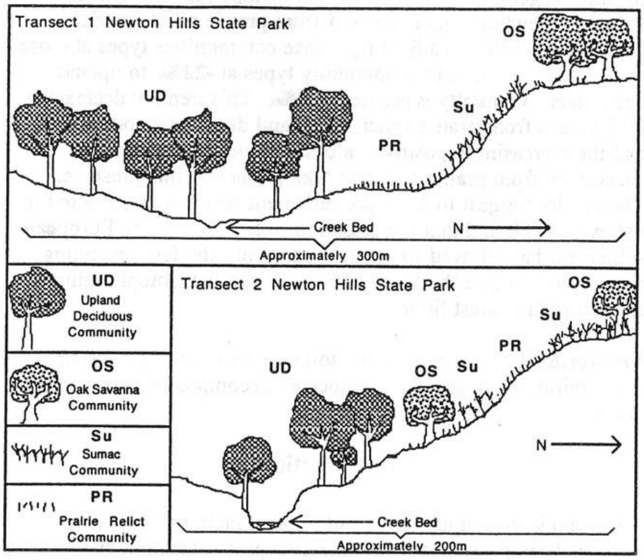

FIG. 1. Diagrammatic representations of the topographic positions of the two transects traversing the four communities sampled in this study.

Sample Sites

Two transects (Figure 1) were chosen to include four community types: prairie relict (PR), sumac (Su), oak savanna (OS), and upland deciduous (UD). The PR sites, characterized by native grasses and an absence of trees, were small (less than 1000 sq m) and distant from the nearest large prairie reserve (60 ha) located 37 km to the north. The PR portion of the first transect (1PR) extended from the toeslope on the south of a hillside, along the line between sections 13 and 14. The corresponding community type of the second transect (2PR) lay on the same south-facing hillside about 1 km to the east. The Su sites were identified by the presence of sumac. The Su site of the first transect (1Su) lay on a south-facing hillside; whereas the same community type of the second transect (2Su) was at the top of the hill above PR. The presence of bur oak, usually located on hillsides with fairly open canopies, characterized the OS sites. The OS portion of the first transect (1OS) occupied the hilltop directly above the PR and Su areas. The corresponding portion of the second transect (2OS) covered the bottom of the hill. The UD sites were identified by their "simplified eastern deciduous character" (Hanson and Hazlett 1971) containing species such as *U. americana, T. americana,* and *J. nigra.* The UD community types of both transects occupied both sides of the creek bed. The change in elevation between the hilltops and valley was only 30 m.

Field Procedure

Four quadrats (one m^2) were selected from each of the four community types along each transect to sample soil and herbaceous vegetation. Cover was measured for each species, and the point quarter method characterized the tree composition in the vicinity of each quadrat. We identified the closest tree in each quadrant by species, recorded the distance, and measured the breast height circumference (bhc). Litter (identifiable dead material) and O-layer (unidentifiable material in an advanced stage of decomposition) samples were taken to measure the organic inputs from various compartments into the SOM. Two soil cores were removed from each quadrat to a depth of 60 cm, pooled, and prepared for processing in the lab.

Vegetation was clipped from each of the PR and Su in late July of 1991, excluding the sumac "canopy." The clipped biomass was separated into live, dead, and litter; weighed; ground; and prepared for isotopic analysis. Leaves from common species in representative environments were collected individually from the four community types in each transect for isotopic analysis. Species not sampled individually in each community were pooled into composite samples and analyzed. We also obtained samples from well-established and representative forest and prairie communities in the area. Sieche Hollow State Park (45° 44" N and 97° 13" W) and Makoce Washte Prairie Preserve (43° 92" N 97° W) represent the best examples of forest and prairie, respectively, in the area.

Sample Preparation and Isotope Analysis

The soil cores were separated by horizon and pooled within each quadrat. Where extensive A or B horizons were found, they were subdivided into A2, A3, etc. based in changes in color and texture. Soils were de-rooted, dried, and pulverized with a mortar and pestle. We decarbonated the portion to be sampled (about 10 g) in 1N HCl for approximately 16 h. The decarbonated soil was centrifuged and rinsed to remove HCl. Soils were again dried, pulverized, and loaded into the mass spectrometer. The litter and organic layer (O) samples were ground, dried, and analyzed in the mass spectrometer, as were the dried and decarbonated roots. Homogeneously ground samples containing 0.5 to 1.0 mg C were combused in a Carlo Erba CHN analyzer coupled to a SIRA-10 Isotope Ratio Mass Spectrometer fitted with a special triple trap to cryogenically purify and isolate the CO$_2$. Samples were run with a lab standard, and random replicates confirmed a precision better than 0.2‰. Percent C and C:N ratios were calculated from the integrated output of the thermal conductivity detector on the gas chromatograph. Isotope ratios are expressed as δ^{13}C values relative to the PDB standard.

Results

Species Cover

The common species in the prairie relicts were *P. pratensis., A. gerardi, B. curtipendula, A. scoparius,* and *Bromus inermis* (smooth brome) with smaller amounts of other grasses and forbs. Of the prevalent species, *A. gerardi, B. curtipendula,* and *A. scoparius* utilize the C$_4$ pathway, yielding 35% relative C$_4$ cover in transect 1, and 59% in transect 2. The sumac communities (Table 1) possessed many of the same species including *P. pratensis, A. gerardi, A. scoparius, R. glabra, B. curtipendula,* and *Agropyron smithii* (western wheatgrass), yielding relative C$_4$ covers of 41% in the first transect and 32% in the second transect. The prevalent oak savanna (Table 1) understory species included *Zanthoxylem americanum* (prickly ash), *Sanguinaria canadensis* (bloodroot), *Ribes missouriense* (gooseberry), *Hydrophylum virginianum* (waterleaf), and *Symphoricarpos occidentalis* (wolfberry). The understory of the upand deciduous community (Table 1) was dominated by *Parthenocissus quinquefolia* (virginia creeper), *Galium triflorum* (bedstraw), *H. virginianum, Urtica dioica* (nettle), *Rhus radicans* (poison ivy), and *Solidago canadensis* (goldenrod).

Quercus macrocarpa had the highest density (370 ha^{-1}) in transect 1 of the oak savanna community and occurred with *Ostrya virginiana* (ironwood) (80 ha^{-1}), *U. americana* (60 ha^{-1}), and some *Juniperus virginiana* (red juniper) (20 ha^{-1}) (Table 2). The tree density in this community is low relative to the other communities studied, although individual *Quercus* were relatively large (140 cm bhc) and were used as bearing trees by the 1863 surveyor. The upland deciduous community of transect 1 (Table 2) was denser with *J. nigra* (600 ha^{-1}), *O. virginiana* (650 ha^{-1}), *Q. macrocarpa* (125 ha^{-1}), *U. americana* (75 ha^{-1}), and *T. americana* (50 ha^{-1}). Most of the trees were medium sized, with the largest *J. nigra* at 94 cm bhc. Overall tree density was higher than in the 1OS community but lower than the UD counterpart in transect 2. Trees were fairly regularly spaced. The pattern of lower density and even spacing may suggest a maturity of this forest relative to its counterpart in transect 2.

Quercus macrocarpa also dominated (930 ha^{-1}) the second transect, followed by *U. americana* (80 ha^{-1}), *T. americana*, and *Celtis occidentalis* (hackberry) (both at 20 ha^{-1}). This area was not especially dense, but the *Quercus* and *Tilia* were fairly large (bhc of 114cm and 168cm, respectively). Upland Deciduous trees (Table 2) were represented by *O. virginiana* (2,450 ha^{-1}), *T. americana* (1950 ha^{-1}), *U. americana* (950 ha^{-1}), *C. occidentalis* (600 ha^{-1}), and *Q. macrocarpa* (600 ha^{-1}). In contrast to the 1UD community, smaller densely packed trees dominated this community (under 65 cm bhc). *U. americana* was the largest tree species represented in the community, with an average bhc value of 126 cm. Because of its steep slope and southward orientation, this forest community may be more recent, thus not possessing the wider spacing indicative of the mature forest community in transect 1.

Table 1 - Mean cover estimates of the understory for prairie relict, sumac, oak savanna, and upland deciduous communites in each transect differentiated into growth form and photosynthetic pathway.

				PR % Cover			Su % Cover		
Common name	**Species**	**Form**	**Type**	**Tr1**	**Tr2**	**Mean**	**Tr1**	**Tr2**	**Mean**
Big bluestem	*Andropogon gerardi*	G	C_4	25	21	23	28	16	22
Little bluestem	*Andropogon scoparius*	G	C_4	3	14	8	20	13	16
Side oats grama	*Bouteloua curtipendula*	G	C_4	16	15	16	9	0	4
Blue grama	*Bouteloua gracilis*	G	C_4	0	1	1	0	0	0
Indian grass	*Sorghastrum nutans*	G	C_4	0	4	2	0	0	0
W. wheatgrass	*Agropyron smithii*	G	C_3	0	0	0	8	0	4
Smooth brome	*Bromus inermis*	G	C_3	3	0	1	0	8	4
Kentucky bluegrass	*Poa pratensis*	G	C_3	60	33	47	61	45	53
Porcupine grass	*Stipa spartea*	G	C_3	1	0	0.3	0	0	0
Sedge	*Carex* sp.	S	C_3	0	0	0	0	0	0
Meadow anemone	*Anemone canadensis*	F	C_3	0	0	0	0	0.3	0.1
Anenome	*Anemone patens*	F	C_3	0	0.3	0.1	0	0	0
Indian hemp	*Apocynum cannabinum*	F	C_3	1	0	0.4	1	0	0.3
Aster	*Aster* sp.	F	C_3	0	1	0.3	0	0	0
Slimflower scurfpea	*Psoralea* sp.	F	C_3	0	3	2	1	0	0.4
Spiderwort	*Tradescantia bracteata*	F	C_3	1	0	0.3	0	0	0
W. salsify	*Tragopogon* sp.	F	C_3	0.3	0	0.1	0	0	0
Dicot		F	C_3	1	0	0.4	1	1	1
Clover		F	C_3	1	0	0.4	0	0	0
Sumac	*Rhus glabra*	Sh	C_3	0	0	0	9	5	7
Unknown		F	C_3	0.3	0	0.1	0	3	1
	Relative % C_4 cover			35	59	47	41	32	37
	Relative % C_3 cover			65	41	53	59	68	63
	% Cover			110	91	101	136	90	113

				OS % Cover			UD % Cover		
Common name	**Species**	**Form**	**Type**	**Tr1**	**Tr2**	**Mean**	**Tr1**	**Tr2**	**Mean**
Dutchman's breeches	*Dicentra cucullaria*	F	C_3	0	0	0	0	9	4
Leafy spruge	*Euphorbia podperae*	F	C_3	0	0	0	8	0	4
Bedstraw	*Galium triflorum*	F	C_3	0	5	3	43	3	23
Waterleaf	*Hydrophylum virginianum*	F	C_3	5	2	3	25	23	24
Motherwort	*Leonurus cardiaca*	F	C_3	0	5	3	0	0	0
Moonseed	*Menispermum canadense*	F	C_3	0	0	0	5	1	3
Virgina creeper	*Parthenocissus quinquefolia*	F	C_3	0	5	3	38	33	35
Poison ivy	*Rhus radicans*	F	C_3	1	0	1	11	4	8
Bloodrot	*Sanguinaria canadensis*	F	C_3	10	0	5	10	0	5
Nettle	*Urtica dioica gracilus*	F	C_3	1	5	3	18	1	9
Violet	*Viola* sp.	F	C_3	0	0	0	0	0	0
Poa	*Poa pratensis*	G	C_3	0.3	29	15	3	11	7
Sedge	*Carex* sp.	S	C_3	0	0	0	0	4	2
Gooseberry	*Ribes missouriense*	Sh	C_3	6	5	6	0	5	3
Wolfberry	*Symphoricarpos occidentalis*	Sh	C_3	5	6	6	0	0	0
Prickly ash	*Zanthoxylum americanum*	Sh	C_3	14	5	9	0	0	0
Bur oak seedling	*Quercus macrocarpa*	Tr	C_3	0	0	0	0	5	3
Unknown		F	C_3	0	0	0	1	0	1
	Relative % C_3 cover			100	100	100	100	100	100
	% Cover			43	62	52	110	87	98

NOTE: G = Grass F = Forb Sh = Shrub S = Sedge Tr = Tree

Table 2. Tree composition in the oak savanna and upland deciduous communities as determined with the point quarter method with bhc measurements derived from nearest tree in each quarter.

Community and Common Name	Species	Transect 1 Density (#/ha)	Transect 1 bhc (cm)	Transect 2 Density (#/ha)	Transect 2 bhc (cm)
Oak Savanna					
Hackberry	*Celtis occidentalis*	0	0	20	81
Juniper	*Juniperus virginiana*	20	41	0	0
Ironwood	*Ostrya virginiana*	80	32	0	0
Bur oak	*Quercus macrocarpa*	370	140	930	114
Basswood	*Tilia americana*	0	0	20	168
Elm	*Ulmus americana*	60	68	80	33
	Total Density	530		1050	
Upland Deciduous					
Hackberry	*Celtis occidentalis*	0	0	600	44
Black walnut	*Juglans nigra*	600	94	0	0
Ironwood	*Ostrya virginiana*	650	39	2450	49
Bur oak	*Quercus macrocarpa*	130	33	150	36
Basswood	*Tilia americana*	50	23	1950	65
Elm	*Ulmus americana*	80	70	950	126
	Total Density	1510		6100	

Biomass Values

Live biomass from clipped quadrats in the 1PR community (Table 3) yielded a mean δ^{13}C value of -20.4‰, with the dead material at -21.5‰ and litter at -21.2‰. Thus, the 1PR input from vegetation was close to -21‰. The live and dead materials from the 1Su community were -16.6‰ and -17.6‰, respectively, suggesting an average vegetation input δ^{13}C near -17‰; however, the δ^{13}C value of the sumac leaves (-28.9‰) also must be considered as input. This explains the fact that 1Su O-layer values are close to -21‰ and suggests that the "understory" contributes most of the biomass. Isotopic values for individual species from the 1PR, 1Su, and other community types are presented in Table 4. Live biomass, dead, and litter from the 2PR community (Table 3) were more positive than the first transect and closer to an expected prairie δ^{13}C value of -15.1‰, with mean dead and litter values of -16.2‰ and -18.3‰, respectively. Vegetation input δ^{13}C values for this prairie community are probably close to -16‰. Live biomass in the 1Su community yielded a mean δ^{13}C value of -25.9‰, the same as the dead. The δ^{13}C values of the vegetation inputs in this sumac are near -26‰.

Table 3. Mean biomass δ^{13}C values (‰ ± Std Error) for prairie relict and sumac communities.

	Prairie Relict		Sumac	
Biomass	**Transect 1**	**Transect 2**	**Transect 1**	**Transect 2**
Live	-20.4±1.89	-15.1±0.71	-16.6±1.75	-25.9±1.17
Dead	-21.5±1.46	-16.2±0.44	-17.6±1.57	-25.9±1.40
Litter	-21.2±1.38	-18.3±0.84	na	na

Samples were obtained from clipped vegetation in each quadrat near the period of peak standing crop.

We used the δ^{13}C values for the individual species (Table 4) to estimate vegetation inputs for the OS and UD communities. Little variation occurred in the isotopic contents of the OS and UD communities between the transects, and the variations among species were small. For the OS community type, the ä^{13}C values of the tree leaves were between -27‰ and -28‰, whereas the understory yielded value between -29‰ and -30‰. For the UD community types, tree leaves yielded ä^{13}C values of between -27‰ and -28‰. The understory species of this community type yielded fairly consistent values between -29‰ and -31‰, with *Urtica* having the most negative value at -32.1‰. Vegetation input ä^{13}C values for both communities appeared near -28‰ and -29‰, assuming that tree leaves contribute a larger proportion of carbon to the SOM than the understory species.

Soil Values

In the 1PR community (Table 5, Figure 2), litter and O-layer δ^{13}C values were similar to the soil value of the A horizon. The values for the soil became more positive with depth (-21.8‰ in the A layer to -17.9‰ in the B3 horizon). The ANOVA indicates that the input material (litter and O-layer) and the A horizons are statistically different from the B horizons. In the 1Su community, litter and O-layer values are also similar to the A soil; the soil values throughout the core were also statistically similar. The 1OS litter and O-layer values were substantially depleted relative to their A horizons. Soil δ^{13}C values increased with depth (from -23.1‰ in the A to -17.7‰ in the B3 horizon). The OS inputs were statistically distinct from the B horizons, and the A and A2 horizons were each statistically distinct and intermediate between the statistically different inputs and B horizons. The 1UD community litter and O-layer values were approximately 2‰ depleted relative to the A horizon. Soil values increased from -25.5‰ in the A horizon to -23.6‰ in the B3 horizon. The inputs were statistically different from the statistically similar A2 to B3 horizons, and the A horizon was a statistically distinct intermediate between the inputs and the A2 to B horizons. In the OS and UD communities, the litter and O-layers were depleted substantially compared to the soil values.

Table 4. $\delta^{13}C$ (‰) values of mature leaves of common species collected from the understory or near the bottom or top of the canopy.

Species	PR	Su	OS	UD
Andropogon gerardi	-13.4	-15.4	0.0	0.0
Andropogon scoparius	-13.6	-14.0	0.0	0.0
Bouteloua curtipendula	-14.0	-13.8	0.0	0.0
Sorghastrum nutans	-13.2	0.0	0.0	0.0
Bromus inermis	0.0	-29.2	0.0	0.0
Poa pratensis	-26.1	-27.5	0.0	0.0
Stipa spartea	-27.2	0.0	0.0	0.0
Galium triflorum	0.0	0.0	0.0	-30.9
Hydrophylum virginianum	0.0	0.0	-29.3	-30.0
Parthenocissus quinquefolia	0.0	0.0	-31.0	-30.6
Ribes missouriense	0.0	0.0	-30.7	0.0
Sanguinaria canadensis	0.0	0.0	0.0	-29.2
Urtica dioica	0.0	0.0	-32.1	-31.9
Zanthoxylum americanum	0.0	0.0	-29.7	0.0
Pooled leaves	0.0	0.0	-29.9	-31.0
Celtis occidentalis bottom	0.0	0.0	0.0	-27.4
Celtis occidentalis top	0.0	0.0	0.0	-27.9
Juglans nigra bottom	0.0	0.0	0.0	-28.1
Juglans nigra top	0.0	0.0	0.0	-28.8
Juniperus virginiana bottom	0.0	0.0	-27.5	0.0
Juniperus virginiana top	0.0	0.0	-28.9	0.0
Ostrya virginiana bottom	0.0	0.0	0.0	-28.9
Ostrya virginiana top	0.0	0.0	0.0	-28.9
Quercus macrocarpa bottom	0.0	0.0	-28.2	0.0
Quercus macrocarpa top	0.0	0.0	-28.9	0.0
Tilia americana bottom	0.0	0.0	0.0	-28.6
Tilia americana top	0.0	0.0	0.0	-28.0
Ulmus americana bottom	0.0	0.0	0.0	-27.7
Ulmus americana top	0.0	0.0	0.0	-28.5

Table 5. Mean isotopic composition, ä^{13}C values, of soil organic matter and roots for each community and transect sampled at Newton Hills State Park.

Transect 1

PRAIRIE RELICT	**Depth (cm)**		**Soil $\delta^{13}C$**	**Root $\delta^{13}C$**	**% Carbon**
Litter		ab	-21.2±1.79		
O-Layer	0	a	-22.6±0.60		
A Horizon	3	ab	-21.8±0.57	-23.9±0.90	2.79±0.46
A2 Horizon	13	bc	-19.2±0.74	-22.6±1.52	1.70±0.26
B1 Horizon	29	c	-17.9±0.63	-22.3±2.58	1.24±0.20
B2 Horizon	49	c	-17.9±1.13	-25.3±0.91	1.58±0.32
			F=4.093		
			P=0.0017		

SUMAC	**Depth (cm)**		**Soil $\delta^{13}C$**	**Root $\delta^{13}C$**	**% Carbon**
Litter		a	-21.2±1.48		
O-Layer	0	a	-20.9±1.46		
A Horizon	3	a	-20.6±1.52	-22.5±2.36	1.99±0.23
A2 Horizon	10	a	-18.6±0.80	-20.7±2.49	1.11±0.16
B1 Horizon	22	a	-17.9±0.42	-21.9±1.92	0.69±0.16
B2 Horizon	39	a	-19.1±1.20	-21.0±2.21	0.40±0.03
B3 Horizon	52	a	-21.2±1.95	-26.3±0.71	0.44±0.20
			F=1.155		
			P=0.3682		

OAK SAVANNA	**Depth (cm)**		**Soil $\delta^{13}C$**	**Root $\delta^{13}C$**	**% Carbon**
Litter		a	-22.3±2.58		
O-Layer	0	a	-25.3±0.91		
A Horizon	3	b	-23.1±0.57	-27.7±0.18	3.05±1.0
A2 Horizon	11	c	-20.2±1.14	-27.6±0.08	2.54±0.4
B1 Horizon	25	d	-17.9±0.42	-27.2±0.25	1.70±0.23
B2 Horizon	43	d	-17.1±0.70	-27.2±0.16	0.86±0.05
B3 Horizon	54	d	-17.7±0.13	-27.4±0.30	0.54±0.1
			F=45.413		
			P=0.0001		

UPLAND DECIDUOUS	**Depth (cm)**		**Soil $\delta^{13}C$**	**Root $\delta^{13}C$**	**% Carbon**
Litter		a	-27.8±0.17		
O-Layer	0	a	-27.6±0.17		
A Horizon	3	b	-25.5±0.35	-27.9±0.45	2.85±0.21
A2 Horizon	11	c	-23.7±0.33	-27.3±0.61	2.98±0.11
B1 Horizon	25	c	-22.9±0.30	26.4±0.96	1.35±0.37
B2 Horizon	40	c	-23.5±0.69	-26.6±0.61	1.08±0.62
B3 Horizon	46	c	-23.6±0.95	-27.1±0.63	1.59±1.41
			F=25.202		
			P=0.0001		

Transect 2

PRAIRIE RELICT	**Depth (cm)**		**Soil $\delta^{13}C$**	**Root $\delta^{13}C$**	**% Carbon**
Litter		a	-19.6±1.11		
O-Layer	0	a	-19.6±0.93		
A Horizon	3	b	-16.5±0.72	-16.3±1.48	2.38±0.20
A2 Horizon	13	b	-15.8±0.46	-17.5±1.27	1.02±0.08
B1 Horizon	29	ab	-17.4±0.61	-16.5±1.52	0.33±0.08
B2 Horizon	49	a	-19.4±0.43	-17.7±2.80	0.20±0.03
			F=5.143		
			P=0.0042		

SUMAC	**Depth (cm)**		**Soil $\delta^{13}C$**	**Root $\delta^{13}C$**	**% Carbon**
Litter		a	-25.2±0.74		
O-Layer	0	a	-24.9±0.83		
A Horizon	3	b	-21.0±0.33	-25.6±0.70	3.02±0.72
A2 Horizon	14	c	-18.0±0.11	-25.2±0.91	1.71±0.27
B1 Horizon	34	c	-17.4±0.65	-25.4±0.60	0.97±0.2
B2 Horizon	53	c	-18.0±0.74	-24.2±1.11	0.49±0.08
			F=32.673		
			P=0.0001		

OAK SAVANNA	**Depth (cm)**	**Soil $\delta^{13}C$**	**Root $\delta^{13}C$**	**% Carbon**	
Litter		a	-26.5±0.13		
O-Layer	0	a	-26.6±0.43		
A Horizon	3	b	-23.7±0.28	-27.2±0.15	3.06±0.28
A2 Horizon	13	cd	-21.4±0.55	-27.3±0.29	1.66±0.24
B1 Horizon	29	d	-19.8±0.98	-26.4±0.25	0.67±0.37
B2 Horizon	46	d	-20.1±0.77		0.58±0.14
			F=20.292		
			P=0.0001		

UPLAND DECIDUOUS	**Depth (cm)**	**Soil $\delta^{13}C$**	**Root $\delta^{13}C$**	**% Carbon**	
Litter		a	-26.8±0.14		
O-Layer	0	a	-26.3±0.29		
A Horizon	3	a	-25.4±0.43	-27.6±0.12	3.80±1.24
A2 Horizon	12	cb	-23.5±0.47	-27.6±0.48	2.15±0.77
B1 Horizon	31	c	-21.2±0.70	-27.3±0.35	0.79±0.09
B2 Horizon	51	c	-21.5±0.89		0.36±0.11
			F=20.118		
			P=0.0001		

One factor ANOVA of soils with letters grouping similar horizons. Depths are approximate and estimated from the means of the horizons for all pooled cores.

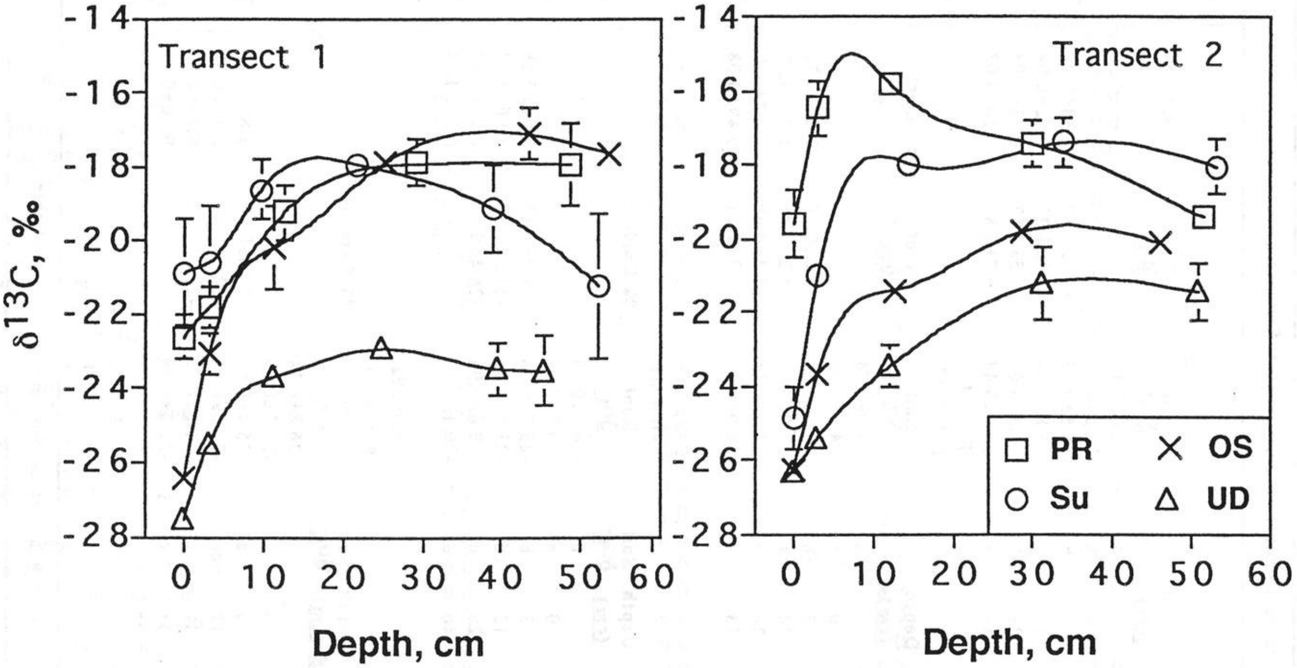

FIG. 2. Isotopic composition of soil organic matter derived from cores pooled within each of four quadrats per community. Sample points are approximate depths derived from the means of horizons at that position. The value at depth "0" represents the organic horizon of the soil profile. Bars are standard errors. PR = Prairie Relict, Su = Sumac, OS = Oak Savanna, UD = Upland Deciduous forest.

The PR samples from transect 2 (Table 5) possessed litter and O-layers around 3‰ depleted relative to the A horizon. Again, as in all communities, depth (horizon) accounted for the variation in soil isotopes through the profile. The 2PR soils became more positive through A2 and B1, and values with depth were similar to those of 1PR (around -17‰). The 2Su litter and O-layer values were approximately 4‰ depleted relative to the A horizon at -21‰, and 7‰ depleted relative to the B2 horizon at -18‰. The 2Su inputs were statistically different from the A horizon, which was, in turn, statistically different from the A2 to B2 horizons. 2OS litter and O-layer values were aproximately 3‰ depleted relative to the A horizon soil. The soil $\delta^{13}C$ values increased slightly from -23.7‰ at the A horizon to the A3 horizon and then became more negative (-22.8‰) in the B3 horizon. Litter and O-layer values from 2UD were 1‰ depleted relative to the A horizon. The soil $\delta^{13}C$ values gradually increased from -25.4‰ in the A horizon to -19.1‰ in the B3 horizon. As in transect 1, the input $\delta^{13}C$ values were depleted substantially compared to the soil values. The inputs and the A horizon were statistically similar, as were the isotopic values for the B horizons.

Root Values

Isotope values for roots were similar within community types at different depths, except for a slight difference in the OS communities (Table 5). Mean $\delta^{13}C$ values from 1PR were -23.9‰ in the A horizon and reached -25.2‰ with depth. The 1Su means ranged from -22.5‰ in the A horizon to -26.3‰ at depth and were statistically similar. 1UD root $\delta^{13}C$ values were similar between -26‰ and -27‰ for all depths. Mean 2PR values between -16‰ and -17‰ did not differ with depth, as was the case with the 2Su community where the values were more negative, between -24‰ and -25‰. In the 2OS community, average root $\delta^{13}C$ values were between -26‰ and -28‰, with the B1 horizon being statistically distinct. Finally, 2UD community roots were also similar at all depths, yielding values between -26‰ and -27‰. Linear regressions indicated that the root ä^{13}C values approximated the isotopic values of the vegetation from which they were removed (R^2=0.005 for OS & UD, and 0.188 for PR & Su). Root values were not associated closely with the soil values from which they were derived (R^2=0.219).

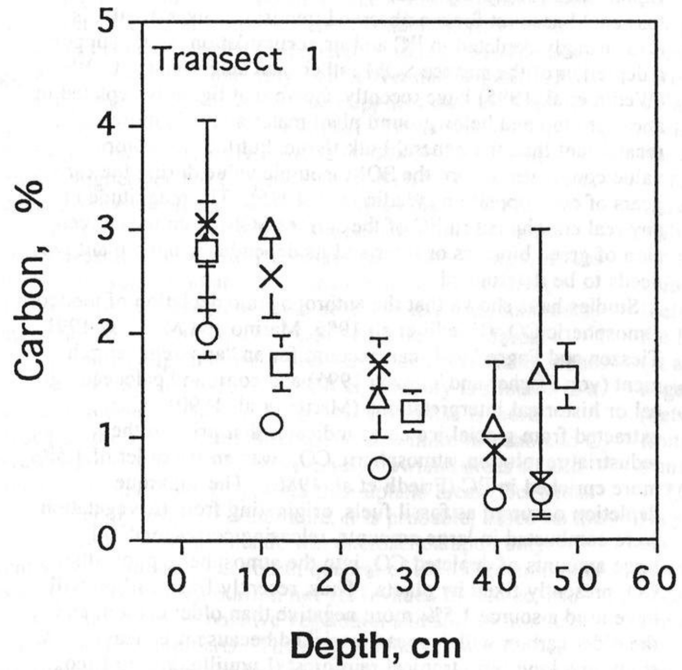

FIG. 3. Percent carbon in the SOM samples described in figure 2.

Percent Carbon

Carbon contents of the soil (see Table 5, Figure 3) ranged between 2% and 3.8% in the upper A horizon to values as low as 0.2% in the lower B horizons. Patterns of decreasing carbon were similar in all communities, although the "lowland" prairie site (1PR) had 1.6% carbon at 49 cm, possibly reflecting the results of downslope deposition.

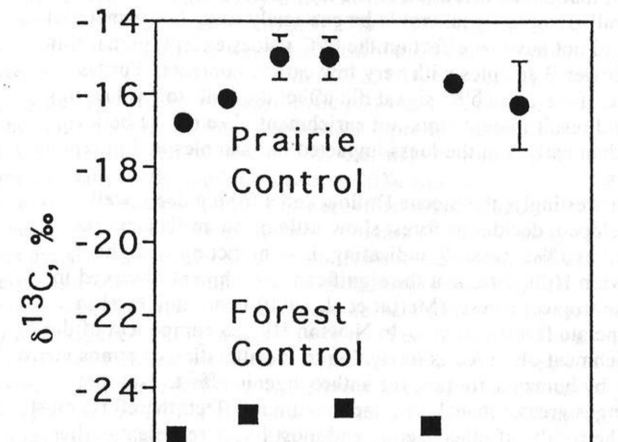

FIG. 4. Mean carbon isotope composition of SOM samples through the profiles from prairie controls (Makoce Washte) and a forest control (Sieche Hollow).

Prairie and Forest Comparison

We obtained samples from a virgin prairie and a well-developed forest in order to provide clearer estimates of SOM isotope values that were in a long-term equilibrium with the vegetation. The mean values of four soil cores taken at the Makoce Washte Prairie Preserve (Figure 4) served as our representative prairie endpoint and was similar to the mixed prairie system found in the loess hills (Novacek et al. 1985). The sites for cores were selected for their topographical similarity to the Newton Hills PR sites. The $\delta^{13}C$ values increased from -16.8‰ in the A horizon to -15‰ in the A3 and A4 horizons and fell again to -16.3‰ with depth in the B2 horizon. The forest samples from Sieche Hollow State Park revealed little change with depth, with mean $\delta^{13}C$ values between -24.5‰ and -25.3‰ throughout the cores.

Table 6. Correlation matrix of the isotope values from all soil organic matter samples, O layers, and inputs calculated from weighted values for live, litter, and dead biomass.

	Input	Litter	O	A1	A2	B1	B2
Input	1.00						
Litter	.921	1.00					
O	.948	.942	1.00				
A1	.824	.742	.800	1.00			
A2	.776	.681	.738	.930	1.00		
B1	.575	.530	.532	.671	.833	1.00	
B2	.241	.241	.199	.420	.586	.818	1.00

Correlations are across all communities and both transects.

Discussion

Inputs and the Isotopic Signal

The correlation matrix (Table 6) across all communities and transects illustrates that the isotopic value of the near-surface SOM carbon is related to the signal of the live and dead biomass on the surface. To a significant extent, then, the upper layers reflect the percent C_4 of the current vegetation at those quadrats. Regression analysis of the relationship between percent C_4 and $d^{13}C$ values indicates a strong positive relationship ($P =< 0.0001$) with the litter and O-layer compartments. The percent C_4 also correlates strongly with the A horizons, though with less significance ($P =< 0.0012$). These data confirm that materials in the early stages of decomposition to SOM reflect the isotopic signal presented by the recent vegetation. Under a steady state condition with minimal diagenetic alteration, the vegetation value should be in equilibrium with the litter, O-layer, and the soil.

Other factors potentially affecting the $d^{13}C$ signal, such as leaf litter accumulation from surrounding trees, were analyzed. Leaves were collected from each PR quadrat and weighed in an attempt to assess the possible impact of this depleted leaf material on the otherwise positive prairie signal. In the PR community types, leaves frequently accounted for up to one third of the biomass input. The leaf $d^{13}C$ values, at approximately -28‰, give the PR litter, O-layer, and, to a lesser degree, the SOM, a depleted character and account for the somewhat negative $d^{13}C$ values noted in the PR communities. Organic matter near the surface layers of these prairie relicts, which have not been invaded by live C_3 species from adjoining woodlands, are already recording a C_3 signal imported from the litter of nearby oak trees.

Decomposition Dynamics and SOM Enrichment

Our data indicate that all communities except 1PR and 1Su had inputs more negative than the A soil by 2 to 3‰, especially in the OS and UD community types. Enrichment often increased with depth (especially in the B horizons where the values were statistically more positive than surface layers) in both upland deciduous communities, which are presumed to have been C_3 for quite some time. These enrichments between the A horizon and the B3 horizon (Figure 3) were approximately 2‰ in transect 1 and on the order of 4‰ in transect 2. Similar enrichment has been noted both between vegetation and surface layers (Vitorello et al 1989 and Balesdent 1990) and at greater depth (Pentico and Tieszen 1991, Balesdent et al. 1988, Natelhoffer and Fry 1988, Stout and Rafter 1978).

Several explanations have been proposed for this observed enrichment. Slight fractionation may occur with decomposition and SOM mineralization (Vitorello et al. 1989, Natelhoffer and Fry 1988, Dzurec et al. 1985), although the mechanism and the extent of enrichment by decompositional fractionation are not well documented. However, we now know that the incoming litter is isotopically heterogeneous because of differences in the isotopic composition of plant biochemicals (Tieszen 1991, Tieszen 1994, Fagre et al. 1991). Some immediate enrichment may occur during early decomposition if most of the substances in plant material that are metabolized initially by decomposers are depleted in ^{13}C (Balesdent et al. 1988). The loss of these depleted substances from the more recalcitrant plant material that becomes incorporated into SOM would result in an enrichment of ^{13}C in the surface soil carbon (see Martin et al. 1990, Natelhoffer and Fry 1988). This can account for the observed isotopic changes between the input material (litter and O-layer) and soil (Figure 2) but does not adequately account for the enrichment observed with depth. Cellulose generally is the major component of plant litter and largely determines the bulk isotopic input. Lipids are strongly depleted, relative to cellulose, and their rapid loss could account for the observed trends; however, lignin, is also strongly depleted in ^{13}C and its accumulation would support a depletion of the surface SOM rather than an enrichment. We (Wedin et al. 1995) have recently shown that lignin is depleted in aboveground and belowground plant material and is more recalcitrant than the general bulk tissue, but that its isotopic value converges toward the SOM isotopic value during the early years of decomposition (Wedin et al. 1995). The magnitude of any real enrichment in ^{13}C of the surface SOM from the conversion of green biomass or litter and its dependence upon plant type needs to be determined.

Studies have shown that the anthropogenic depletion of modern atmospheric CO_2 (Friedli et al. 1986, Marino and McElroy 1991, Tieszen and Fagre 1994) can account for an "apparent" enrichment (von Fischer and Tieszen 1995) and confound paleoecological or historical interpretations (Martin et al. 1990). Gas extracted from glacial ice cores indicates that prior to the industrial revolution, atmospheric CO_2 was on the order of 1.5‰ more enriched in ^{13}C (Friedli et al. 1986). The subsequent depletion occurred as fossil fuels, originating from C_3 vegetation, were combusted in large amounts, releasing correspondingly large amounts of depleted CO_2 into the atmospheric pool - the CO_2 presently fixed by plants. Thus, recently fixed carbon will have used a source 1.5‰ more negative than older carbon, and the older carbon will "appear" enriched because it is heavier. A study in a long-term tropical rainforest (Luquillo, Puerto Rico, von Fischer and Tieszen 1995) suggested that, under these conditions, most of the "enrichment" with decomposition and or depth is accounted for by the depletion in ^{13}C of the atmospheric source CO_2.

The $\delta^{13}C$ values of the lower B horizons could be influenced by the $\delta^{13}C$ values of the carbon remaining in the original loess material. Unexposed loess soil samples were removed from an eroded hillside in the region. The $\delta^{13}C$ value of the carbon in the deep loess ranged from -25.9‰ to -28.1‰. However, the carbon content of the loess material was very low, ranging from 0.08% at the top of the core to 0.05% at the bottom. The low %C values mean that the contribution of the remnant loess carbon to the overall isotopic signal would be extremely low. Loess material should not have an effect on the $\delta^{13}C$ values except, perhaps, in the lower B samples with very low carbon contents. Furthermore, if the loess $\delta^{13}C$ signal did affect the bulk soil value, it would result in depletion, not enrichment. We do not believe residual carbon in the loess impacted our samples and interpretations.

Interestingly, the Sieche Hollow cores from a deep, well developed, deciduous forest show little or no enrichment (as small as 1‰), possibly indicating, in conjunction with the Newton Hills data, that the significant enrichment observed in some tropical forests (Martin et al. 1990) is not universal in temperate forest systems. In Newton Hills, a component of the enrichment observed is likely due to the alteration of atmospheric CO_2 by human activities, the anthropogenic effect. Isotopic changes greater than 1.5‰, the maximum effect, therefore, must be the results of other factors and most likely represent earlier Holocene grassland signals and record vegetation changes through time (Tieszen and Boutton 1989, Dzurec et al. 1985).

Transect Comparison

Although the isotopic compositions show similar profiles and usually were statistically similar across communities, the first transect was characterized by a depleted prairie and correspondingly enriched sumac community. The cover data showed a low percent C_4 grass (only 35%), and the clippings data indicate very negative inputs (around -20‰ or -21‰). The corresponding sumac values were relatively positive (-16‰ or -17‰) and showed a higher percent C_4 grasses (over 41%). We believe this is explained by differences in topography and is similar to topographic differences observed at other sites, including the Makoce Washte prairie reserve. South- and west-facing hillsides receive more solar irradiance than the north- and east-facing hillsides. This orientation to some degree determines community composition, as was previously examined in terms of forest expansion mostly up cool and moist, north- and east-facing slopes (Hanson and Hazlett 1971). The 1PR community is situated in a lowland or toeslope position. However, the sumac is more exposed on the south-facing hillside, an area more favorable to C_4 grasses (Barnes et al. 1983). Conversely, lowland areas should contain relatively fewer C_4 grasses than upland areas (Heineman 1982, Ode et al. 1980). Furthermore, it is probable, based on the soil $d^{13}C$ values, that the hillside was encroached upon only recently by the sumac. The fourth quadrat of the 1PR community was on the hillside, on a portion not yet invaded by sumac, and yielded decidedly more positive vegetation and soil values than its three lower counterparts. Thus, the sumac hillside yielded more positive $\delta^{13}C$ than the lowland prairie because its topography favored C_4 species, and it is a recent encroachment, not yet able to eliminate C_4 competitors and their $\delta^{13}C$ signals. This example may illustrate the potential of carbon isotope tracers to document recent and very localized changes in species and patch movements.

Community Trends and Changes

Soil $\delta^{13}C$ values were associated strongly with community type (F = 56.9, P = .0001) and percent C_4 composition (F = 64.9, P =.0001). Mean $\delta^{13}C$ values for the litter and O-layer of transect 1 indicated that the PR and Su areas were statistically similar (around -21‰) but statistically different from the statistically similar OS and UD areas (at around -27‰). The vegetation inputs at the present time were statistically different between grassland (PR & Su) and woodland (OS & UD) community types largely due to differing photosynthetic pathways. A comparison of the isotope signal between community types of transect 1 in the A horizon soils shows that the PR, Su, and OS community types are statistically similar (between -20‰ and -23‰). However, the OS value (-23‰) is more of an intermediate between PR, Su, and UD, because the OS and UD community types are also statistically similar (at between -23‰ and -25‰). These observations are consistent with the hypothesis that oak savanna areas are precursors to a more densely forested community and originate from grassland systems. For the A horizons as a whole, the statistically similar PR and Su community types (around -19‰) were statistically different from both the OS and UD types. OS and UD areas, in turn, were statistically different from each other and the PR and Su community types, with OS values being more negative (about -21‰) and the UD values even more negative (at about -24‰). The PR, Su, and OS $d^{13}C$ values are statistically similar in the A2 horizon (around -19‰) and different from the more negative UD community type (at about -24‰). This trend continues throughout the B horizons, and the isotopic convergence suggests that in the past, the PR, Su, and OS positions supported a common grassland and C_4 character, whereas the upland deciduous community type was still largely forest. The statistical singularity of the negative values for upland deciduous community is notable even though the B3 horizon which becomes slightly more negative in, for example, Su, and approaches the range of the UD values.

The average litter and O-layer $\delta^{13}C$ values for transect 2 showed that the UD, OS, and Su types were similar and statistically distinct (between -25‰ and -27‰) from the more positive PR litter (at about -19‰). Throughout the A horizons, all community types were significantly different from one another (between -16‰ and -25‰), and no convergence occurred until the B1 horizon, where the statistically similar PR and Su values (at about -17‰) were relatively positive and distinct from the negative values of the statistically similar OS and UD values (between -20‰ and -21‰). This suggests that the divergence from common communities occurred some time ago along this transect.

The spatial distributions of community types along this transect (Figure 1) again provide a possible explanation for similar isotopic values in the B horizon. The UD community, along the creek, could be expected to remain wooded and, thus, more negative (as suggested by its B2 $\delta^{13}C$ value), even under variable fire and climate regimes. More distant from the creek and up the hill, the Su community type would be more exposed to fire and likely remain grassland with some C_4 component. The two communities in between the hilltop Su and valley UD (PR and OS) might have been covered by shifting vegetation as fire frequency varied and would express an intermediate isotopic value. The negative UD value in the lower B horizons (about -22‰) again suggests that the prairie, sumac, and oak savanna systems, with their more positive $\delta^{13}C$ values, have a common grassland origin, and that the upland deciduous component, with its negative character, has existed for some time (Figure 3).

Community Origins

Isotopic analysis of soil $\delta^{13}C$ values clearly differentiate between the origins of the several main community types and allow us to understand the origin of the park in the context of community change and composition. The nucleus of the wooded systems at Newton Hills is along the creek. This is reinforced by the surveyors' notations of forest cover made over 100 years ago. The surveyors recorded vegetation patterns and soil quality as they traversed the line between Sections 13 and 14 (the location of the first transect) and recorded roughly 60 m of timber growing along Sargeant Creek in the exact location of today's UD community of transect 1. Today, 1240 m of timber extend far to the north and south of the creek. The UD community type of transect 1 was specifically defined and described as wooded by the surveyors. These notes, combined with isotopic analysis, mutually reinforce the suggestion that the present extensive woodland originated and spread primarily from the fire-protected valleys along the creek. The isotopic data clearly show that forest has existed along the creek for some time, perhaps several thousand years, based on reasonable estimates of turnover of SOM. We also can conclude from the positive isotopic values at depth that the prairie relict, sumac, and oak savanna communities share a common origin more reminiscent of grassland with distinct C_4 components (Pentico and Tieszen 1991). This area then appears to have consisted of very localized closed forest immediately adjacent to the creek with more substantial prairie communities on the surrounding hillsides. Expansion of forest into prairie has been relatively recent and cannot be dated accurately without ^{14}C dating of SOM or other analyses.

Forest to grassland changes certainly can occur as a result of short-term climatic shifts, but the primary factor allowing the massive expansion of wooded land in the park was probably the absence of fire as a major abiotic factor in the ecosystem. The extent of fire has been shown to be a significant factor in the competition between forest and prairie in general (Clark 1990, Grimm 1983), and in the loess hills (Heineman 1982) in particular. From a comparison of the surveyors' notes and the isotopic record in the soil, we conclude that the majority of woodland expansion, the results of which we see today in the extensive forest of Newton Hills, likely has occurred in the last 100 to 200 hundred years. This estimate is consistent with the approximate time of fire cessation associated with European settlement and supports the hypothesis that woodland expansion occurs with fire supression.

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Literature Cited

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

Anderson RC. 1990. The historic role of fire in the North American grassland. In Fire in North American Tallgrass Prairies. Collins SL and Wallace LL eds. University of Oklahoma Press, Norman. pp 8-18.

Balesdent J. 1990. Effect of tillage on soil organic carbon mineralization estimated from ^{13}C abundance in maize fields. Journal of Soil Science 41: 587-596.

Balesdent J, GH Wagner, and A Mariotti. 1988. Soil organic matter turnover in long-term field experiments as revealed by carbon-13 natural abundance. Soil Science Society of America Journal 52: 118-124.

Balesdent J, A Mariotti, and B Guillet. 1987. Natural ^{13}C abundance as a tracer for studies of soil organic matter dynamics. Soil Biological Biochemistry 19: 25-30.

Barnes PW, LL Tieszen, and DJ Ode. 1983. Distribution, production, and diversity of C_3- and C_4-dominated communities in a mixed prairie. Canadian Journal of Botany 61: 741-751.

Cambardella CA. 1993. Carbon and nitrogen distribution in aggregates from cultivated and native grassland soils. Soil Science Society of America Journal 57: 1071-1075.

Cambardella CA and ET Elliott. 1994. Carbon and nitrogen dynamics of soil organic matter fractions from cultivated grassland soils. Soil Science Society of America Journal 58: 123-130.

Cavagnaro JB. 1988. Distribution of C_3 and C_4 grasses at different altitudes in a temperate arid region of Argentina. Oecologia 76: 273-277.

Cerling TE, J Quade, Y Wang, and JR Bowman. 1989. Carbon isotopes in soils and paleosols as ecology and paleoecology indicators. Nature 341: 138-139.

Clark JS. 1990. Fire and climate change during the last 750 yr in northwestern Minnesota. Ecological Monographs 60: 135-159.

Driessen. 1976. Soil Survey Lincoln County South Dakota. United States Dept. of Agric., SCS, U.S. Government Printing Office, Washington, DC. 102 pp.

Dzurec RS, TW Boutton, MM Caldwell, and BN Smith. 1985. Carbon isotope ratios of soil organic matter and their use in assessing community composition changes in Curlew Valley, Utah. Oecologia 66: 17-24.

Ehleringer JR and RK Monson. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annual Review of Ecology and Systematics 24: 411-439.

Fagre T, LL Tieszen, and S Rodriguez. 1991. Variations in the stable carbon isotope values of biochemicals: Extraction procedures and results. Proceedings of the South Dakota Academy of Science 70: 83-98.

Friedli H, H Lotscher, H Oeschger, U Siegenthaler, and B Stauffer. 1986. Ice core record of the ^{12}C/^{13}C ratio of atmospheric CO_2 in the past two centuries. Nature 324: 237-238.

Grimm EC. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. Ecological Monographs 54: 291-311.

Grimm EC. 1983. Chronology and dynamics of vegetation change in the prairie-woodland region of southern Minnesota, U.S.A.. New Phytology 93: 311-350.

Hanson R and D Hazlett. 1971. An ordination study of the forest vegetation of Newton Hills State Park. Proceedings of the South Dakota Academy of Science 50: 280-285.

Heineman PL. 1982. Woody plant invasion of Iowa loess bluff prairies. Master's Thesis, University of Nebraska at Omaha.

Knight CL, JM Briggs, and MD Nellis. 1994. Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas, USA. Landscape Ecology 9: 117-125.

Kuchler AW. 1964. The potential natural vegetation of the conterminous United States. Special Publication No. 36. American Geographical Society, New York. pp 38.

Lobo Sternberg LS, SS Mulkey, and SJ Wright. 1989. Ecological interpretation of leaf carbon isotope ratios: Influence of respired carbon dioxide. Ecology 70: 1317-1324.

McPherson GR, TW Boutton, and AJ Midwood. 1993. Stable carbon isotope analysis of soil organic matter illustrates vegetation change at the grassland/woodland boundary in souteastern Arizona, USA. Oecologia 93: 95-101.

Marino BD and MB McElroy. 1991. Isotopic compostion of atmospheric CO_2 inferred from carbon in C_4 plant cellulose. Nature 349: 127-131.

Martin A, A Mariotti, J Balesdent, P Lavelle, and R Vuattoux. 1990. Estimate of soil organic matter turnover rate in a savanna soil by ^{13}C natural abundance measurements. Soil Biological Biochemistry 22: 517-523.

Mutel CF. 1990. Fragile Giants: Natural History of the Loess Hills. University of Iowa Press, Iowa City.

Natelhoffer KJ and B Fry. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Science Society of America Journal 52: 1633-1640.

Nordt LC, TW Boutton, CT Hallmark, and MR Water. 1994. Late quaternary vegetation and climate changes in central Texas based on the isotopic composition of organic carbon. Quaternary Research 41: 109-120.

Novacek JM, DM Roosa, and WP Pusateri. 1985. The vegetation of the Loess Hills landform along the Missouri River. Proceedings of the Iowa Academy of Science 92:199-212.

Ode DJ, LL Tieszen, and JC Lerman. 1980. The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. Ecology 61: 1304-1311.

Parton WJ, DS Schimel, CV Cole, and DS Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51: 1173-1179.

Pentico ED and LL Tieszen. 1991. Community and stable carbon isotope ratios: Forest-grassland transitions at Wind Cave National Park. Proceedings of the South Dakota Academy of Science 70: 69-82.

Rogers DJ. 1972. The use of land survey records in determining past vegetation in eastern South Dakota. Proceedings of the South Dakota Academy of Science 51: 73-79.

Schleser GH and R Jayasekara. 1985. δ^{13}C-variation of leaves in forests as an indication of reassimilated CO_2 from the soil. Oecologia 65: 536-542.

Schwartz D, A Mariotti, R Lanfranchi, and B Guillet. 1986. ^{12}C/^{13}C ratios of soil organic matter as indicators of vegetation changes in the Congo. Geoderma 39: 97-103.

Shotola SJ, GT Weaver, PA Robertson, and WC Ashby. 1992. Sugar maple invasion of an old-growth oak-hickory forest in southwestern Illinois. American Midland Naturalist 127: 125-138.

Steuter AA, B Jasch, J Ihnen, and LL Tieszen. 1990. Woodland/grassland boundary changes in the Middle Niobrara Valley of Nebraska identified by δ^{13}C values of soil organic matter. American Midland Naturalist 124: 301-308.

Stout JD and TA Rafter. 1978. The 13C/12C isotopic ratios of some New Zealand tussock grassland soils. New Zealand Department of Scientific and Industrial Research Bulletin 220: 75-83.

Terri JA and LG Stowe. 1976. Climatic patterns and distribution of C_4 grasses in North America. Oecologia 23: 1-12.

Tieszen LL. 1991. Natural variations in the carbon isotope values of plants: Implications for archaeology, ecology, and paleoecology. Journal of Archaeological Science 18: 227-248.

Tieszen LL. 1994. Stable isotopes in the Great Plains: Vegetation analyses and diet determinations. In Skeletal Biology in the Great Plains: A Multidisciplinary View. Owsley DW and Jantz RL (eds) Smithsonian Press, Washington DC, pp. 261-282.

Tieszen LL and S Archer. 1990. Isotopic assessment of vegetation changes in grassland and woodland systems. In Ecological Studies 80. Plant Biology of the Basin and Range, Osmond CB (ed) Springer Verlag, New York, pp. 293-321.

Tieszen LL and TW Boutton. 1989. Stable carbon isotopes in terrestrial ecosystem research. In Stable Isotopes in Ecological Research, Ecological Studies Series 68, Rundel PW, Ehleringer JR, and Nagy KA (eds), Springer-Verlag, Heidelberg, pp. 167-195.

Tieszen LL and T Fagre. 1993. Carbon isotopic variability in modern and archaeological maize. Journal of Archaeological. Science 20: 25-40.

Tieszen LL, BC Reed, NB Bliss, BK Wylie, and DD DeJong. 1995. NDVI characteristics, potential C_3 and C_4 grass production, and δ^{13}C values in grassland land cover classes of the Great Plains. Ecological Applications (Accepted):

Tieszen LL, MM Senyimba, SK Imbamba, and JH Troughton. 1979. The distribution of C_3 and C_4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. Oecologia 37: 337-350.

Tieszen LL and AA Steuter. 1991. Relationship between community carbon isotope values and nutrient concentrations in northern mixed prairie. Proceedings of the South Dakota Academy of Science 70: 55-68.

Vitorello VA, CC Cerri, F Andreux, C Feller, and RL Victoria. 1989. Organic matter and carbon-13 discrimination in forested and cultivated oxisols. Soil Science Society of America Journal 53: 773-778.

Volkoff B and CC Cerri. 1987. Carbon isotopic fractionation in subtropical Brazilian grassland soils. Comparison with tropical forest soils. Plant and Soil 102: 27-31.

von Fischer JC and LL Tieszen. 1995. Carbon isotope charaterization of soil organic matter from four tropical forests in Luquillo, Puerto Rico. Biotropica 27: 138-148.

Wedin DA, LL Tieszen, B Dewey, and J Pastor. 1995. Carbon isotope dynamics during grass decomposition and soil organic matter formation. Ecology 76: 1383-1392.

White EM, JR Johnson, JT Nichols. 1969. Prairie-forest transition soils of the South Dakota Black Hills. Soil Science Society of America Proceedings 33: 932-936.

Establishment of Prairie Species by Overseeding into Burned Roadside Vegetation

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Abstract. Seeding experiments were carried out on a Linn County, Iowa, secondary roadside beginning in 1991 to determine the ability of certain prairie grass and forb species to establish in preexisting cool-season roadside vegetation. Three blocks of plots were burned or left unburned prior to a late April broadcast seeding of grasses. Plots were overseeded with several prairie forb species in early May, 1992. Vegetation was scored by species for cover each fall in 1991,'92 and '93. ANOVA (P>0.05) of total cover showed no differences for burned and unburned plots or between blocks for each year. Plants of several seeded species were observed first between August and November of 1993. *Sorghastrum nutans, Andropogon gerardii, Rudbeckia hirta, Ratibida pinnata*, and *Heliopsis helianthoides* established in several seeded plots but were not present in unseeded plots. *S. nutans* was three times more abundant in burned plots, and *R. hirta* was 70 times more abundant. *R. pinnata* and *H. helianthoides* established only in burned plots. Results indicate that overseeding into established roadside cover is an alternative to more intensive cultural methods for introducing prairie species along roadsides.

Key words: burn, establishment, overseed, prairie, roadside,

Introduction

Establishing prairie species in roadside rights-of-way often is approached with intensive cultural methods requiring herbicide treatment or cultivation or sometimes both (Christiansen and Lyon 1973, Thompson 1992). Successful stands are usually established, but at considerable investment in labor and money. Several observations I have made over the past 25 years lead me to believe that less intensive methods might be successful, though not as rapid or as complete as the methods described above. In the spring of 1967, I scattered a quantity of prairie seeds in a roadside ditch in Mitchell County, Iowa. Seeds of approximately 35 prairie species had been stratified in moist potting soil during the previous winter and were scattered on the backslope and bottom of the ditch for a distance of about 100m. Competing vegetation consisted of Kentucky bluegrass (*Poa pratensis*) (Eilers and Roosa 1994), red clover (*Trifolium pratense*), and other typical roadside species. Small numbers of porcupine grass (*Stipa spartea*), wild rose (*Rosa arkansana*), smooth aster (*Aster laevis*), pale purple coneflower (*Echinacea pallida*), and rosette panic grass (*Dicanthelium oligosanthes* var. *scriberianum*) plants were also present. After a period of 6 to 8 years, plants of a number of the seeded species began to appear. Among them were golden alexanders (*Zizia aurea*), false boneset (*Brickellia eupatorioides*), purple prairie clover (*Dalea purpureum*), switchgrass (*Panicum virgatum*), big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), and little bluestem (*Schizachyrium scoparium*). During the next several years and after occasional spring burns, the introduced prairie species dominated the seeded area.

In a 1971 roadside-vegetation experiment, seeds of several prairie grasses were hydroseeded, along with mulch, on a Linn County, Iowa, vegetated roadside in June at two locations (Christiansen and Lyon 1973). One location had sandy soil (Sparta loamy fine sand, 2-5% slopes) whereas the other was an upland mesic site (Fayette silt loam, 2-5% slopes) (Schermerhorn & Highland 1975). No positive results were evident at the end of the third growing season and were so reported (Christiansen and Lyon 1973). However, after several more years had passed, clumps of prairie grasses began to appear. In 1988, measurements indicated that prairie grasses comprised up to 25% cover. Casual observations indicated that prairie cover continued to increase over the next several years. No burning or mowing of the site was done during the 20 years following seeding.

These two situations, where overseeded prairie species managed to become established over a number of years, indicated that establishment of prairie species might be possible with less intervention than has become common practice. I devised an experiment to test the hypothesis that 1) seeding into established roadside vegetation would lead to establishment and 2) spring burning of roadside vegetation, followed by seeding, would be more successful than seeding without prior burning.

Methods

Plots were laid out on the north side of Linn Ridge Road just to the west of Linn Grove Road in Franklin Township, Linn County, Iowa (T-83, R-05, S-22) on a gentle slope resulting in a moisture cline from mesic (block 1) to wet-mesic (block 3). The soil type was Downs silt loam, moderately eroded, with 5-9% slopes, (Schermerhorn & Highland 1975). Treatment plots were 20m long and the width of the roadside ditch.(approximately 5 m). Four treatments were laid out; 1) burn/seed, 2) no-burn/seed, 3) burn/no-seed, and 4) no-burn/no-seed. Each treatment was set out in each of three blocks. Burn plots were burned on 17 April, 1991. Broadcast seeding of grasses was done on 27 May, 1991 (Table 1).

Table 1. Grass seed mixture (PLS)[1] applied to each seeded plot (1991).

Species	Kg per ha
Sorghastrum nutans	3.75
Andropogon gerardii	4.69
Schizachyrium scoparuium	3.47
Bouteloua curtipendula	1.87
Elymus canadensis	1.30
Panicum virgatum	1.98
Sporobolus asper	2.57

1/ PLS=pure live seed

The same burn plots were burned again on 29 April, 1992. Several species of prairie forbs as well as one grass species were broadcast seeded on 1 May, 1992 (Table 2). In addition to the species listed, a mixture of seeds of gray-headed coneflower (*Ratibida pinnata*), windflower (*Anemone cylindrica*), tall goldenrod (*Solidago canadensis*), wild bergamot (*Monarda fistulosa*), and black-eyed Susan (*Rudbeckia hirta*) was broadcast on each seeded plot at the rate of 0.33 kg/ha. Burn plots were not burned in 1993 but were burned on 28 March, 1994.

Table 2. Forb and grass seed mixture (PLS)[1] applied to each seeded plot (1992) .

Species	Kg per ha
Rudbeckia hirta	0.019
Heliopsis helianthoides	0.246
Baptisia lutea	0.032
Parthenium integrifolium	0.011
Silene stellata	0.016
Sporobolus heterolepis	0.026

1/ PLS=pure live seed

Plots were inventoried by species in cover categories on 28 August, 1991. Cover classes were as follows: very common (>20% cover), common (10 to 20% cover), uncommon (<10% cover), and rare (one or a few individual plants). Inventories also were made on 4 November, 1992, and 5 September, 1993.

Measurements of vegetative cover were converted to percent relative cover (percent cover of each species/total percent cover) for cover analysis. Differences in vegetative percent relative cover by year were evaluated by ANOVA (P>0.05)

Counts of seeded forb plants were made first on 27 July and 5 September, 1993. Plants of seeded grass species were counted on 20 November, 1993. In addition, counts of oxeye (*Heliopsis helianthoides*), black-eyed Susan, and gray-headed coneflower were made on 7 June, 1994.

Meteorological conditions during the 1991-1993 growing seasons (April through September) were as follows. Average monthly departure from normal for temperature was: -0.63C, 1991; -1.75C, 1992; -1.98C, 1993. Average monthly departures from normal for precipitation were; -27.4 mm, 1991; -21.3 mm, 1992; +121.4 mm, 1993.

Results

Smooth bromegrass (*Bromus inermis*) dominated the existing vegetation in all 3 years. Kentucky bluegrass and redtop (*Agrostis alba*) were also prominent (Table 3). Yellow foxtail (*Setaria glauca*) was a constant component and giant foxtail (*Setaria faberi*) increased from 1991 to 1992 and then decreased in 1993. Among the forbs, tall goldenrod remained at about the same cover, whorled milkweed (*Asclepias verticillata*) decreased, heath aster (*Aster ericoides*) increased, and wild lettuce (*Lactuca canadensis*) fluctuated widely (Table 3). Seeded species made up less than 1% of the relative cover.

Table 3. Percent relative cover of dominant species across all blocks.

Species	1991	1992	1993
Grasses			
Bromus inermis	37.74	32.91	35.43
Poa pratensis	23.90	11.35	19.51
Setaria lutescens	9.56	11.58	13.37
Setaria faberi	3.90	12.14	2.81
Agrostis alba	6.92	9.65	6.82
Forbs			
Asclepias verticillata	7.54	5.11	4.14
Solidago canadensis	8.80	8.51	8.95
Lactuca canadensis	0.76	5.79	1.33
Aster ericoides	0.76	2.95	3.62
Physalis heterophylla	0.12	0.00	1.01

No searches for seedlings of seeded prairie species were made in 1991 or 1992. Two species of seeded prairie grasses, big bluestem and Indiangrass, were observed in 1993 (the third growing season following seeding). Big bluestem was represented by only one plant in two burn/seed treatments and two plants in one no-burn/seed treatment (Table 4). Indiangrass was represented by six and 12 plants in burn/seed treatments and three and two plants in no-burn/seed treatments. One block did not have any establishment (Table 4).

Table 4. Establishment of prairie grasses, 1993.

	Plants per plot		
Treatment	Block 1	Block 2	Block 3
Andropogon gerardii			
Burn/seed	1	1	0
No-burn/seed	0	2	0
Burn/no-seed	0	0	0
No-burn/no-seed	0	0	0
Sorghastrum nutans			
Burn/seed	6	12	0
No-burn/seed	2	3	0
Burn/no-seed	0	0	0
No-burn/no-seed	0	0	0

Black-eyed Susan was present in all blocks in 1993, the second growing season. Forty to 54 flowering plants were counted in the three burn/seed plots (Table 5). The only other establishment was in one block of the no-burn/seed treatment (Table 5). In 1994, 82 and 73 flowering plants were counted in two burn/seed treatments, but one block did not have any flowering plants (Table 5). Twelve flowering plants were present in one no-burn/seed treatment.

Table 5. Establishment of prairie forbs, 1993 and 1994.

Treatment	Year	Block 1	Block 2	Block 3
Rudbeckia hirta				
Burn/seed/	1993	44	54	40
	1994	82	73	0
No-burn/seed	1993	2	0	0
	1994	12	0	0
Burn/no-seed	1993	0	0	0
	1994	0	0	0
No-burn/no seed	1993	0	0	0
	1994	0	0	0
Heliopsis helianthoides				
Burn/seed	1993	1	2	6
	1994	46	37	26
No-burn/seed	1993	0	0	0
	1994	4	0	0
Burn/no-seed	1993	0	0	0
	1994	0	0	0
No-burn/no-seed	1993	0	0	0
	1994	0	0	0
Ratibida pinnata				
Burn/seed	1993	7	0	0
	1994	21	15	7
No-burn/seed	1993	0	0	0
	1994	0	0	0
Burn/no-seed	1993	0	0	0
	1994	0	0	0
No-burn/no-seed	1993	0	0	0
	1994	0	0	0

Oxeye was observed only in the burn/seed treatments in 1993, with one to 6 plants per plot (Table 5). In 1994, many more plants were present, 26 to 46 per treatment in burn/seed treatments (Table 5) and one block had 4 plants present in the no-burn/seed treatment.

Gray-headed coneflower was present only in the burn/seed treatment of one block in 1993, but by 1994, plants were present in the burn/seed treatments of all blocks (Table 5).

A number of species have not been observed in the treatment plots, including grass species — little bluestem, side-oats grama (*Bouteloua curtipendula)*, Canada wildrye (*Elymus canadensis)*, switchgrass, tall dropseed (*Sporobolus asper*), and prairie dropseed (*Sporobolus heterolepis*).and forbs — wild indigo (*Baptisia lactea)*, feverfew (*Parthenium integrifolium*), and starry campion (*Silene stellata*).

Discussion

The overall vegetative cover of the experimental site was not affected greatly by burning or seeding treatments during the 3-year study. Giant foxtail increased in 1992, and burning was suspended for the spring of 1993 to allow smooth bromegrass, Kentucky bluegrass, and other cool-season grasses to recover. Levels of seeded species establishment were not sufficient to alter dominant cover of the plots.

Substantial numbers of several seeded species were established, and previous experience indicates that additional establishment, especially of grasses, will become apparent in the future.

Detection of forb establishment is somewhat easier, and reliable estimates of establishment can be made in the first or second season after seeding. Black-eyed Susan and oxeye followed expected patterns of flowering. Black-eyed Susan, a biennial, flowered in the second year, and oxeye flowered to a small extent in the second year but increased greatly in the third growing season. Gray-headed coneflower will probably flower in 1994.

Great differences were apparent between burned and unburned treatments in establishment of both grasses and forbs. In 1994, 307 forb plants were counted in burn/seed treatments whereas only 16 were present in no-burn/seed treatments. No plants of seeded forb species were present in no-seed treatments. Although not as dramatic, differences in burn v. no-burn treatments for grasses were also apparent; 20 v. 7 plants. No seeded prairie grasses were observed in no-seed treatments.

After 3 years, establishment of several prairie grasses and forbs was apparent in a roadside overseeded with prior burning and with seeding rates comparable to those used in other establishment techniques, but without intensive seedbed preparation. This technique appears to be useful for establishing prairie species in existing roadside vegetation without requiring destruction of pre-existing cover.

Literature Cited

Christiansen, P. A. and D. L. Lyon. 1973. Roadside vegetation management. Report to the Iowa Department of Transportation, Ames, IA.

Eilers, L. J. and D. M. Roosa. 1994. The Vascular Plants of Iowa. University of Iowa Press, Iowa City, IA.

Schermerhorn, E. J. and J. D. Highland. 1975. Soil Survey of Linn County, Iowa. United States Department of Agriculture, Soil Conservation Service, Washington, DC.

Thompson, J. R. 1992. Prairies, Forests, & Wetlands: The Restoration of Natural Landscape Communities in Iowa. University of Iowa Press, Iowa City, IA.

Phreatophyte Survey and Water-Use Estimates for Nine River Systems in Kansas

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Abstract. This study estimated phreatophyte and associated woody plant acreage, species composition, and evaporation losses and evapotranspiration losses for each of nine river basins in Kansas. These river basins contain approximately 40,000 acres of riparian woodland that yielded an estimated 140,000 acre-f/y to evapotranspiration. Of the l0 most common taxa of phreatophytes and associated woody plants, cottonwoods and willows constituted 83%. Shrubs, elm, ash, and saltcedar contributed about 3% each to the composition of the riparian woodlands. Combined evaporation losses and evapotranspiration losses were compared to other water demands on the river systems and found to be much less than agricultural irrigation usage.

Introduction

Concern is growing over the quality and quantity of surface and subsurface water supplies in Kansas. The water-table declines from perennial overdrafts, droughts, sedimentation, pollution, surface water evaporation (E) losses, and evapotranspiration (ET) losses from riparian vegetation have jeopardized the future of this vital natural resource. The state, counties and municipalities face difficulties in meeting the needs of primary users in agriculture, industry, and domestic areas. Surface water in reservoirs and streams represents the most accessible and affordable water in many areas of eastern Kansas and also recharges or receives discharge from ground water in stream-aquifer systems. Although all surface water depletion and degradation factors are of great concern, the role of E and ET demands on water supplies is documented poorly in Kansas.

In areas where the water is near the surface, roots of many woody plants penetrate to the water table or to the capillary fringe just above it and draw upon a year-long water supply. Plants of this type are known as phreatophytes. Robinson (1965) estimated that approximately 15,000,000 acres of phreatophytic vegetation occurred in the 17 western states and losses by ET were between 20 and 30 million acre-feet each year. Research on the physioecology and economic significance of phreatophytes has been concentrated in the southwestern states. This study, conducted during 1989, estimated E and ET demand from streams and reservoirs in nine river basins in Kansas that drain approximately 55,000 sq mi (Figure 1). Evaporation and ET losses determined in this study were compared to existing E and ET estimates and contrasted with demands from agricultural, industrial, and domestic users in Kansas.

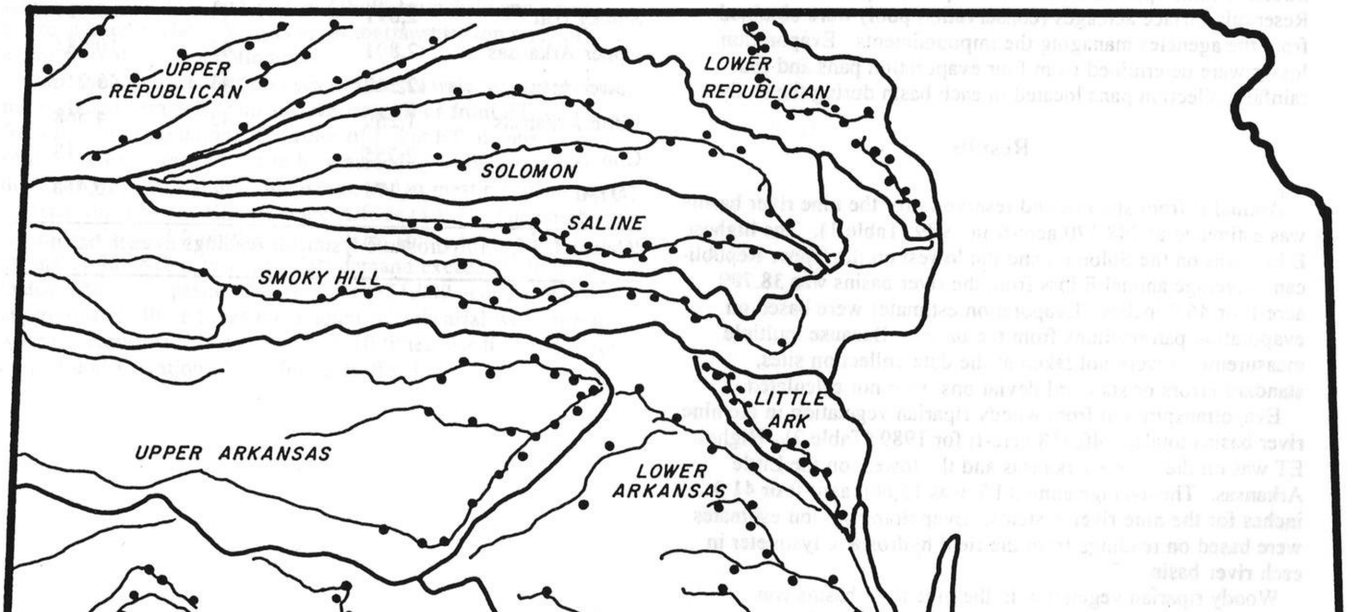

FIG. 1. The nine river basins included in the study with transect locations (indicated by dots).

Methods

Acreage of woody riparian vegetation in each of the nine river basins was estimated from Natural Resources Conservation Service (NRCS) aerial photographs, NRCS county soil survey maps, and the Kansas Forest Inventory (Spencer *et al.* 1981). A direct acreage map-reading scale (C Thru Ruler Company) recommended by the Soil Conservation Service (SCS) was used to determine approximate coverage of woody vegetation along the rivers and tributaries. Measurements were recorded in feet to conform to the standard acre-ft designation of reporting losses from E and ET. The Kansas Forest Inventory estimates of the percent of forested acres in each county were used to adjust riparian acreage estimates from SCS aerial photographs. Further refinements of land-use cover maps produced by the Kansas Applied Remote Sensing (KARS) program should provide a future source for delineating and identifying riparian vegetation in the river basins.

Composition of the woody riparian vegetation in each river basin was determined by counts of species along 20 line transects (120 ft long) set perpendicular to the stream, with one-half of the transect on each side of the water (Figure 1). Transects were placed near access roads but beyond road construction disturbances to the stream geometry and riparian vegetation. Also, transect sites were selected as representative of the pattern of woody riparian cover along the river system.

Calculations of ET by woody species were made from each basin with a field hydrostatic lysimeter constructed from a design by Courtin and Bliss (1971). Hydrostatic lysimeter readings were projected to obtain annual ET losses.

Surface acreage for rivers and tributaries for each river system was calculated by measurements of stream lengths from aerial photographs and from average stream widths during summer flow at vegetation survey sites. Additional three to five width measurements were made on each tributary in the river system. Stream widths approximated those reported by Burns (1971). Reservoir surface acreages (conservation pool) were obtained from the agencies managing the impoundments. Evaporation losses were determined from four evaporation pans and four rainfall collection pans located in each basin during the study.

Results

Annual E from streams and reservoirs for the nine river basins was estimated at 348,370 acre-ft in 1989 (Table 1). The highest E loss was on the Solomon and the lowest on the Upper Republican. Average annual E loss from the river basins was 38,709 acre-ft or 46.9 inches. Evaporation estimates were based on evaporation pan readings from the basins. Because multiple measurements were not taken at the data collection sites, standard errors or standard deviations were not calculated.

Evapotranspiration from woody riparian vegetation in the nine river basins totaled 140,458 acre-ft for 1989 (Table 2). Highest ET was on the Lower Arkansas and the lowest on the Little Arkansas. The average annual ET was 15,606 acre-ft or 41.9 inches for the nine river systems. Evapotranspiration estimates were based on readings from the field hydrostatic lysimeter in each river basin.

Woody riparian vegetation in the nine river basins was dominated by cottonwood (*Populus deltoides*; 63.6%) and willows (*Salix* spp.; 19.7%). Elms (*Ulmus* spp.), shrubs and woody vines, green ash (*Fraxinus pennsylvanica*), and saltcedar (*Tamarix ramosissima*) each contributed approximately 3 % to the average composition of the riparian vegetation. Plant names are from The Breat Plains Flora Association (1986). The remaining four species each contributed less than 2 % to the average of the basin's riparian woody vegetation (Table 3).

Table 1. Estimates of annual surface water evaporation (E) in acre-ft from rivers, tributaries,and reservoirs of nine river basins in Kansas.

River Basin	Streams	Reservoirs	Total
Upper Republican	2,041		2,041
Lower Republican	3,591	80,350	83,941
Solomon	2,508	99,751	102,259
Saline	2,367	38,700	41,067
Smoky Hill	3,694	44,802	48,495
Upper Arkansas	6,092		6,092
Lower Arkansas	15,824	41,022	56,846
Little Arkansas	4,944		4,944
Cimarron	2,685		2,684
Total	43,745	304,625	348,370

Table 2. Estimated annual evapotranspiration (ET) in acre-ft and inches from woody riparian acres in each of nine river basins in Kansas.

River Basin	Acres	ET (inches)[1]	ET acre-ft
Upper Republican	3,766	41	12,804
Lower Republican	4,755	41	16,167
Solomon	7,689	41	26,143
Saline	1,685	41	5,729
Smoky Hill	2,891	41	9,829
Upper Arkansas	2,801	43	10,084
Lower Arkansas	12,560	43	45,216
Little Arkansas	1,269	43	4,568
Cimarron	2,755	43	9,918
TOTAL	40,171		140,458

[1] Calculated from hydrostatic lysimeter readings in each basin.

Table 3. Percent composition of woody riparian species in each of nine river basins in Kansas.

Riparian woody species	Up Rep	Lo Rep	Sol	Sal	Smo Hill	Up Ark	Lo Ark	Li Ark	Cim	Mean %
Cottonwood	64	69	58	62	67	72	68	61	52	63.6
Willows	17	10	25	31	18	16	15	15	31	19.7
Elm	4	3	4	2	3	2	3	5	1	3.0
Vines & shrubs	5	4	5	2	1	2	1	4	2	2.9
Ash	1	5	3	1	4	2	2	6	1	2.9
Saltcedar	1	-	1	1	4	1	4	3	11	2.8
Bur oak	2	5	1	-	2	2	3	2	-	1.9
Box elder	2	3	2	1	1	1	2	2	1	1.7
Mulberry	1	1	1	-	1	1	1	1	1	0.9
Osage orange	1	-	-	-	-	1	1	1	-	0.9

Discussion

The average annual E of 46.9 inches fell within ranges reported previously. Wide variations in E values for surface waters in the Great Plains region are found in the climatological data. Flora (1948) reported the mean evaporation (April-Sept.) during 1914-1945 as 43.155 inches at Colby, Kansas and 60.426 inches of evaporation at Tribune, Kansas during the same period. Van Der Leeden *et al* (1991) noted annual E values ranging from 51 to 62 inches in the region. The ET rates were similar to those reported by Tomanek and Ziegler (1960) from field and greenhouse studies at Hays, Kansas on evapotranspiration rates of saltcedar, willow, and cottonwood.

Data from publications on uses of Kansas water resources have not included demands from surface water E or from ET losses from riparian vegetation. The roles of E and ET in consumption of Kansas water resources can be assessed by comparing these demands with agricultural, industrial, and domestic consumption as determined by the Kansas Water Office (1987). The combined E and ET demand from the nine systems studied totaled an estimated 488,828 acre-ft/yr. This demand exceeded all estimated, annual domestic uses of water (351,000 acre-ft) and was approximately three times the amount of industrial water use in Kansas. However, it was more than 10 times less than usage for agricultural irrigation (6,375,000 acre-ft/yr).

Literature Cited

The Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas. Lawrence, 1392 pp.

Burns, C. V. 1971. Kansas Stream Flow Characteristics. Part 8. Water Resources Board. State of Kansas. 31 pp.

Courtin, G. M. and L. C. Bliss. 1971. A hydrostatic lysimeter to measure evapotranspiration under remote field conditions. Arctic and Alpine Research 3:81-89.

Flora, S. D. 1948. Climate of Kansas. Kansas State Board of Agriculture. State Printing Office, Topeka. 320 pp.

Kansas Water Supply and Demand Report. 1987. Kansas Water Office, Topeka.

Robinson, T. W. 1965. Introduction, spread and extent of saltcedar in the Western states. Geological Survey Professional Paper 491-A. Government Printing Office, Washington, DC 11 pp.

Spencer, J. S., J. K. Strickler, and W. J. Moyer. 1981. Kansas forest inventory. U.S.D.A. Research Bulletin NC-83. 134 pp.

Tomanek, G. W., and R. L. Ziegler. 1960. Ecological studies of saltcedar. Division of Biological Sciences. Fort Hays State University, Hays, KS. 128 pp.

Van der Leeden, F., F. L. Troise, and D. K. Todd. 1991. The Water Encyclopedia. 2nd Ed. Lewis Publishers, Chelsea, MI. p 94.

Literature Cited

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Table [illegible]

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Discussion

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Planning and Implementation of a Right-of-Way Native Planting for Wisconsin Highway 51

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Abstract. In 1987, the Wisconsin Department of Transportation and the University of Wisconsin Department of Landscape Architecture developed plans for establishing prairie plantings along 67-km of freeway through Wisconsin's central sand plains. Goals included (1) reducing maintenance costs, (2) enhancing erosion control, and (3) linking plantings to the natural regional landscape. The 520 ha project is surrounded by agricultural lands and oak and jack pine openings. Planting patterns were assigned based on four factors: (1) road structure, (2) adjacent land use, (3) topography, and (4) habitat. Planning resulted in 55 prairie stands and 12,000 native tree and shrub plantings. A 6-year research and monitoring program at this site is examining several factors relevant to highway environments and management that can influence the success of prairie plantings in rights-of-way. This paper will discuss the planting patterns developed in the landscape process, the initial success of some of the plantings, and implementation problems.

Key words: Highway right-of-way, natural landscapes, prairie, landscaping, restoration

Introduction

During the late 1970s and the 1980s, the high costs of highway right-of-way (ROW) maintenance and greater ecological awareness by both highway personnel and citizen groups have encouraged the search for alternative solutions to traditional highway ROW plantings. Such plantings typically were composed of agronomic grasses and legumes requiring mowing and herbicide applications several times each year. In attempts to reduce mowing and herbicide use and, at the same time, increase aesthetics, transportation departments have begun experimenting with native grasses and forbs in their ROWs (Harrington 1991, Elmhirst and Cain 1990, Iowa Department of Transportation 1990, Jacobson et al. 1990). In 1987, the Wisconsin Department of Transportation (WiDOT) approached the University of Wisconsin Department of Landscape Architecture to develop a planting plan for a 67-km stretch of Highway 51. Highway 51 is a reconstructed freeway directing traffic north and south through Wisconsin's central sand plains. Reconstruction in 1987 added two lanes that often are separated from the original lanes by more than 100 m of rolling topography. The 520-ha project site is surrounded by agricultural lands, red pine plantations, tamarack swamps, and oak and jack pine openings.

WiDOT's goals for the project were to: (1) reduce maintenance costs and labor, (2) increase erosion control, (3) enhance the aesthetic experience of highway travelers, (4) promote and protect the natural landscape, and (5) initiate research on the influence of the roadside environment and DOT planting/management policies on the establishment of indigenous plantings . This paper describes the planning and implementation process, makes observations on the initial success of some of the prairie and tree and shrub plantings, and discusses implementation limitations.

Planning Methods

The planning process called for developing planting types or patterns for various sections of the ROW based on four factors: (1) road structure, (2) adjacent land use, (3) topography, and (4) habitat.

Road Structure

Road structure was subdivided into categories of median, overpass, interchange, inner shoulder, and outer shoulder. State and federal policies restrict the types of planting patterns that can occur in many of these road structure categories. For example, medians that are less than 18.3 m in width are mowed annually for safety reasons. Trees greater than 10.2 cm in diameter are prohibited within 15.25 m of the roadbed to reduce obstacles for errant vehicles. Therefore, prairie and tree plantings were restricted to medians with widths greater than 18.3 m and 45.75 m, respectively. The inner shoulder, between pavement and the ditch line, also is mowed at least once each year.

Visual clearance is a prime objective in landscaping interchange triangles. Short grass species were planted in interchanges where habitat conditions were appropriate. Grasses with heights greater than 1.2 m were prohibited, and, unfortunately, this restriction limited the species composition in the few areas where a moist substrate occurred. However, during 1992 and 1993, big bluestem (*Andropogon gerardii*) began to invade the stands. It is not known whether this species was inadvertently placed into the planting mix or is invading from surrounding regions. Trees such as bur oak (*Quercus macrocarpa*) and jack pine (*Pinus banksiana*) were planted in interchanges 1/2 ha or more in size. In areas where the objective was to mimic oak savanna, tree plantings were restricted to fewer than four individuals per 1/2 ha.

Adjacent Land Uses within the ROW

Adjacent land uses were subdivided into those that occur within the ROW and those that occur outside the ROW. Within the ROW, land use was defined largely by vegetation. In areas where the ROW is extremely wide, construction did not destroy all existing vegetation. In the development of patterns for this plan, existing ROW vegetation was divided into categories of upland woods, native grassland, exotic grassland, and wetland.

Existing upland woods were limited to median strips greater than 70 m in width. Dominant species included black oak (*Quercus velutina*), white oak (*Quercus alba*), shagbark hickory (*Carya ovata*), and white birch (*Betula papyrifera*). Numerous openings contained herbaceous species indicative of oak barrens and savanna communities, including bird's foot violet (*Viola pedata*), puccoon (*Lithospermum canescens*), lupine (*Lupinus perennis*), and penstemon (*Penstemon digitalis*).

The majority of the grassed ROW was dominated by exotic species, particularly brome grass (*Bromus inermis*) and quack grass (*Agropyron repens*). Small vegetation patches dominated by big bluestem, little bluestem (*Andropogon. scoparius*), butterfly milkweed (*Asclepias tuberosa*), leadplant (*Amorpha canescens*), and roundheaded bushclover (*Lespedeza capitata*) were found in areas undisturbed by construction.

Adjacent Land Uses

Vegetation adjacent to the ROW was subdivided into woodland, grassland, wetland, pasture, cropland, and red pine plantation. Other land uses include industry such as sand and gravel quarries, commercial enterprises, parallel roads, and cul du sacs. Trees and shrubs seldom were used for screening purposes but were used to provide variation in the degree of exposure to adjacent land uses. The planted vegetation structure attempts to extend the character of the adjacent vegetation into the ROW. For example, where the ROW abutted pasture, prairie was often planted to take advantage of the open character of the land. Where the ROW abutted red pine plantations, additional pines, birches, and maples were planted to naturalize the abrupt edge of the plantation. Serviceberry (*Amelanchier laevis*) and choke cherry (*Prunus virginiana*) were planted to increase interest along and extend wood edges (Figure 1). In draws, where soil moisture increased, wild plum (*Prunus americana*) and prairie crabapple (*Malus ioensis*) were planted to mimic the natural occurrence of shrubs in the prairie.

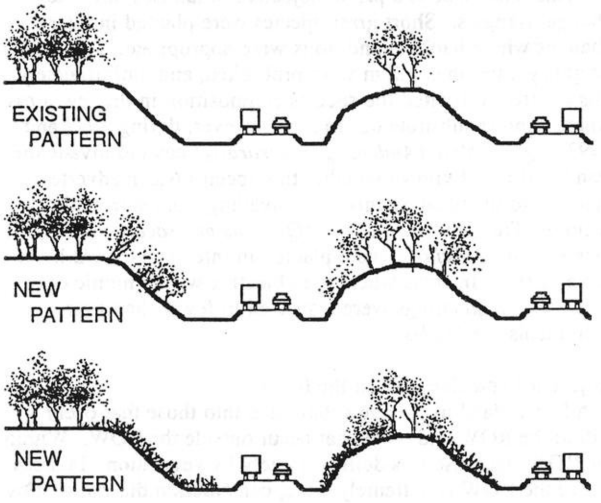

FIG. 1. Planting pattern along steep valley slopes, wide elevated medians, and oak-dominated stands. The patterns attempt to bring the character of the oak woods down the slope. Saplings that are tolerant of the sun and wind exposure on these slopes will eventually allow for the invasion of herbaceous species that may find these open sites to be currently inhospitable.

Topography

Topography was subdivided into level, valley or cut , and ridge or fill. The slopes along the highway vary from 2 1/2:1 to 4:1. As well as being erosion concerns, steep slopes have the highest visibility of any land form in the ROW. Slopes greater than 3:1, however, did not receive prairie plantings and had limited tree planting to minimize erosion problems in the loose sand. Where slopes were greater than 2-1/2:1, prairie plantings were targeted for west aspects over east aspects. Narrow valleys through which the highway passed became an issue for smoke management when prescription burns were introduced.

Habitat

Soils, as well as topography and existing vegetation, dictated the species that could be planted, regardless of other assignment factors. Soil surveys, prior to and during construction, indicated a substrate that is largely sand, drought-prone, and infertile. Samples from eight random locations along Highway 51 were analyzed by the University of Wisconsin-Soils Lab. The proportion of sand ranged from 72% to 90% (mean 85.75%); silt ranged from 5% to 22% (mean 9.75%), and clay ranged from 3% to 6% (mean 4.5%). This high proportion of sand combined with the drought conditions of the region increased the difficulty in establishing plants regardless of their origins.

Planting Plans

After planting patterns were established, plans were developed that resulted in 55 prairie stands ranging in size from 1/2 to 7 ha. The prairie stands were arranged in random pockets along both shoulders of the highway as well as in medians in an attempt to "surround" the traveler. We expect that, if the stands become established, the prairie will spread slowly throughout the ROW wherever competition from cool-season grasses is scarce. Within the last 2 years, we have observed invasion of a few native species, including blue-eyed grass (*Sisyrinchium campestre*), saxifrage (*Saxifraga pensylvanica*), and pale spiked lobelia (*Lobelia spicata*), in moist sites. The tree and shrub plantings were selected and placed to idealize, but not restore, the oak woods and openings of central Wisconsin (Figure 2). The species mixes (Table 1) were composed by utilizing information from Curtis (1959) with modification by the author for safety and functional needs.

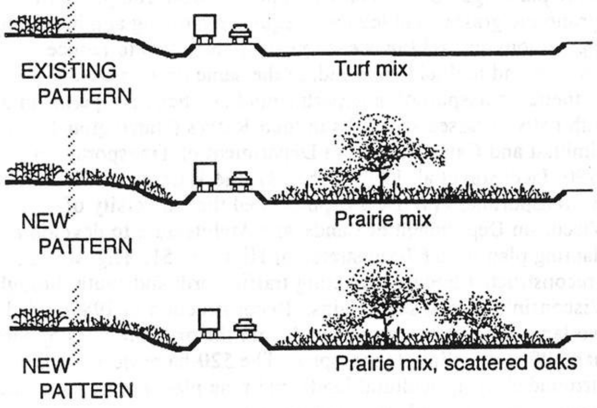

FIG. 2. Planting pattern along level topography, wide medians, and adjacent cornfields. This pattern attempts to mimic the spatial character of oak openings and barrens. Prairie species are planted in the understory with oaks, wild plum, and prairie crabapples in the middle and upper stories. In the last 2 years, unplanted prairie species have appeared in medians of sandy substrate where groundcovers have remained sparse.

Table 1. Percent presence of planted prairie species in highway 51 stands

Species	Number of stands in which planted	Average presence in 1993*
Bergamot (*Monarda fistulosa*)	46	41.30
Black-eye Susan (*Rudbeckia hirta*)	46	91.30
Butterfly milkweed (*Asclepias tuberosa*)	16	12.50
Canada wild rye (*Elymus canadensis*)	46	45.65
Flowering spurge (*Euphorbia corollata*)	45	28.89
Heath aster (*Aster ericoides*)	46	2.17
Horsemint (*Monarda punctata*)	45	44.44
Indian grass (*Sorghastrum nutans*)	45	33.33
Lance-leaved coreopsis (*Coreopsis lanceolata*)	31	80.65
Large beardtongue (*Penstemon grandiflora*)	45	31.11
Little bluestem (*Schizachrium scoparium*)	46	80.43
Lupine (*Lupinus perennis*)	46	17.39
Purple prairie clover (*Dalea purpurea*)	46	4.35
Rough blazingstar (*Liatris aspera*)	31	12.90
Round-headed bushclover (*Lespedeza capitata*)	46	13.04
Showy goldenrod (*Solidago speciosa*)	31	6.45
Side oats grama (*Bouteloua curtipendula*)	46	60.87
Sky-blue aster (*Aster azureus*)	31	3.23
Spiderwort (*Tradescantia ohiensis*)	46	13.04
Stiff goldenrod (*Solidago rigida*)	15	20.00
Thimbleweed (*Anemone cylindrica*)	17	17.65
Wild rose (*Rosa blanda*)	15	26.67
Yellow coneflower (*Ratibida pinnata*)	45	75.56

*Presence refers to the number of stands in which a species occurs out of all the stands in which it was planted.

Tree stock came from area nurseries or, in the case bur oak and old field juniper (*Juniperus communis 'depressa'*), was dug from nearby farms. The sizes of trees at the time of planting were 3.8 cm to 5 cm caliper; shrub heights were .75 m to 1 m. Tree plantings occurred during the spring and fall of both 1988 and 1989. Specifications required that prairie seed come from plant stock growing within 320 km of the site. This specification was a compromise of a variety of views on ecotypes and demonstrated the need for additional research on the genetics of prairie species. Seed rates varied from 9 kg to 13 kg/ha with approximately 20 species planted in each stand.

Because this was WiDOT's first major prairie planting, there was a desire to evaluate the ease and success of several methods. Three planting methods were assigned randomly to the prairie sites: drilling, no-till seeding, and hydro-seeding. Planting depths were approximately 1 cm. Roundup (glyphosate) was applied to no-till sites at a rate of 5 liters/ha. In situations where dense stands of quackgrass (*Agropyron repens*) occurred, more than one herbicide application was required at intervals of approximately 3 wks. Any remaining litter was raked. Sites targeted for drilling were plowed once and lightly disked several times over a period of 8 wks. A weed-free straw mulch was applied at 3.75 tons/ha. The prairie stands were planted in spring (May 15-July 1) and fall (November) of 1988 and 1989.

Much of our study uses relatively uncomplicated monitoring methods to evaluate planting success. For instance, 50 of the 55 prairie stands are sampled using a minimum of 15 randomly placed 1/4 sq m quadrats along three transects located parallel to the highway. Presence, cover, and density measurements are taken annually. The remaining stands are used for research requiring individual sample designs. Tree and shrub survival is being evaluated every June and categorized by percent of aboveground living tissue.

Results

Plantings were initiated in May 1988. Unfortunately, 1988 turned out to be the beginning of a 2-year drought. Trees and shrubs were watered weekly by the contractor during the summers of 1988 and 1989 to compensate for the lack of precipitation, and losses during this period were less than 20%. The prairie received no care except for mowing at a height of 15-20 cm during July 1989. Grass seedlings appeared during the first growing season but were observed to desiccate and disappear. Contracts did not allow for a rapid response to weather conditions and, although a halt to the planting was recommended at the end of May, plantings continued through June.

Prairie Establishment

Because of the drought, inadequate site preparation, and lack of early management, the prairie stands are not of the quality one would expect after four growing seasons. Of the 50 prairie stands sampled along the highway, 36 of these stands continually show an apparent increase in the percent area covered with native grasses since the plantings were initiated. Six prairie stands showed an increase of more than 15% in native grass cover in 1993. However, no stand has a native grass cover greater than 50%, and 30 stands have an average exotic grass cover of 40%. Our goal was to have a relative native grass cover between 60% and 80%, with the remaining cover supplied by native forbs. In this regard, the plantings are not successful, and yet the trend in increased native grass cover requires a delay in any final judgment. However, our goal for forb diversity and cover probably will not be met without additional planting.

Tree and Shrub Establishment

A total of 12,334 trees and shrubs was planted along Highway 51. All of the tree species and 80% of the shrub species are native to central Wisconsin and to the particular soils in the area. Approximately 10% of the trees died each year through 1990. Since 1991, the overall tree and shrub population has been stable with a survival rate of 68%. Stem numbers for thicket-forming species have increased and are noted during our surveys. Some of the plant deaths can be attributed to the drought, but it is difficult to pinpoint the extent. The poor performance of some species can be attributed to other causes, such as accidental mowing in the case of New Jersey tea (*Ceanothus americana*); heavy grass competition in the case of tamarack (*Larix laricina*); and stock quality, transplant tolerance, rodent damage, and fungal diseases in the case of aspen (*Populus tremuloides*). The poor performance of the latter species also may be an indirect result of the drought. At the same time, many species have done well, particularly given the weather during the first years after planting (Table 2A/B).

Table 2A. Tree survival in planting along Highway 51 as of 1993

Species	Number planted	Percent alive as of 1993
Aspen, trembling (*Populus tremuloides*)	624	49.04
Birch, paper (*Betula papyrifera*)	78	42.31
Birch, river (*Betula nigra*)	34	94.12
Cherry, black (*Prunus serotina*)	40	87.50
Hackberry (*Celtis occidentalis*)	84	91.67
Maple, red (*Acer rubrum*)	64	51.56
Maple, silver (*Acer saccharinum*)	1	100.00
Oak, bur (*Quercus macrocarpa*)	66	39.39
Oak, red (*Quercus rubra*)	67	53.73
Oak, swamp White (*Quercus bicolor*)	23	65.22
Pine, jack (*Pinus banksiana*)	114	72.81
Pine, red (*Pinus resinosa*)	67	80.60
Pine,white (*Pinus strobus*)	109	88.07
Cedar, red (*Juniperus virginiana*)	55	100.00
Tamarack (*Larix laricina*)	42	26.19

Table 2B. Shrub survival in planting along Highway 51 as of 1993

Species	Number planted	Percent alive as of 1993
Bittersweet, American (*Celastrus scandens*)	10	100.00
Cherry, choke (*Prunus virginiana*)	161	79.50
Chokeberry, red (*Aronia arbutifolia*)	165	41.21
Chokeberry, black (*Aronia melanocarpa*)	330	89.09
Crabapple, prairie (*Malus ioensis*)	106	91.51
Dogwood, grey (*Cornus racemosa*)	1320	54.77
Dogwood, silky (*Cornus amomum*)	540	61.85
Elderberry (*Sambucus canadensis*)	521	69.48
Hawthorn (*Crataegus* spp.)	224	98.66
Hazlenut (*Corylus americana*)	771	46.82
Ironwood (*Ostrya virginiana*)	24	45.83
New Jersey tea (*Ceanothus americanus*)	198	4.04
Ninebark, common (*Physocarpus opulifolius*)	61	90.16
Juniper, old field (*Juniperus communis 'depressa'*)	99	63.64
Plum, American (*Prunus americana*)	551	92.56
Rose, prairie (*Rosa setigera*)	539	72.91
Rose, Virginia (*Rosa virginiana*)	988	71.96
Serviceberry, Allegheny (*Amelanchier laevis*)	202	63.37
Serviceberry, running (*Amelanchier humilis*)	401	76.31
Sumac, fragrant (*Rhus aromatica*)	315	99.37
Sumac, smooth (*Rhus glabra*)	1191	61.96
Sumac, staghorn (*Rhus typhina*)	661	79.88
Viburnum, arrowwood (*Viburnum dentatum*)	599	53.76
Viburnum, nannyberry (*Viburnum lentago*)	468	72.86
Virgin's bower (*Clematis virginiana*)	46	58.70
Winterberry (*Ilex verticillata*)	375	1.60
TOTAL FOR BOTH TREES AND SHRUBS	12334	67.90

Discussion

One issue we wished to address in this project was whether prairie plantings are reasonable alternatives to traditional plantings in highway ROWs. The response to this question largely depends on the commitment of WiDOT to retool its management and planting programs.

WiDOT is developing a strong state program in planting indigenous species and research but has been slow in restructuring management practices and increasing county interest and has almost no personnel educated in aspects of restoring native plant communities. This was one of several limitations in WiDOT's ability to initiate a large-scale native planting project at the Highway 51 site. Although WiDOT had several individuals interested in the prairie plantings, it became apparent that a limited number of personnel recognized that prairie plantings have planning, implementation, and management practices distinct from those for more traditional "lawn-like" landscapes.

This problem extends beyond the planting of prairie to plantings in general. Highway departments control vast amounts of land, but only a few have personnel with backgrounds in botany, ecology, or the natural sciences. This became problematic in the day-to-day supervision of the planting assigned to WiDOT personnel with backgrounds in civil engineering. The lack of training in landscape design, ecology, and/or restoration for these DOT personnel restricted their ability to make suitable alterations to the plan when field conditions required them and, more importantly, to recognize the occurrence of such situations.

Other limitations that became apparent were the lack of specifications for selecting contractors with prairie planting experience and for seed quality standards and an initial reluctance to consider prescribed burning as an acceptable management tool. Fire is a preferred method of management, because it stimulates growth and tillering in grasses. However, even though some highway departments are experimenting with fire, many DOT managers are reluctant to consider its use largely because of smoke management and the distraction to drivers (Harrington 1991). Currently, WiDOT is reviewing other agencies' management practices and developing a prescription burn policy for its ROWs. WiDOT has begun experimenting with fire in eight of the plantings during the last 2 years.

Recently developed policies suggest that WiDOT is committed to building a strong ROW program that focuses on the use of indigenous species planted in natural appearing patterns. WiDOT also has begun to inventory its roadsides for remnants for consideration in planning future highway projects and maintenance activities. However, these commitments need to be followed through with the hiring of personnel who have the ability and authority to implement them and use study findings such as the research and inventories that are being undertaken currently.

WiDOT is working with the University of Wisconsin Department of Landscape Architecture faculty and graduate students on six research projects at the Highway 51 site, the majority of which will end in 1995:

(1) examining the success of prairie establishment under three implementation methods--drilling, hydroseeding, and no-till seeding,
(2) evaluating the tolerance of prairie seeds and seedlings to salt runoff (Harrington and Miekle 1994),
(3) evaluating the response of native grasses and wildflowers to mowing times and frequencies,
(4) evaluating the response of prairie seeds to soil amendments that increase soil moisture- holding capacity and fertility,
(5) evaluating species composition in stands where burning has been allowed after several years of neglect, and
(6) evaluating the performance of 41 native trees and shrubs in sandy, drought-prone soils.

These studies, although not comprehensive, will assist WiDOT in determining if prairie plants can establish and function given the parameters of the highway environment and the Department's management structure.

Literature Cited

Curtis, J.T. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison. 657 pages.

Elmhirst, J.F. and N.P. Cain. 1990. Review of Roadside Wildflower Programs and Assessment of Feasibility in Ontario. Technical Report MAT-90-05. Research and Development Branch, Ministry of Transportation, Ontario.

Harrington, J. 1991. Survey of landscape use of native vegetation on Midwest highway rights-of-way. Safety Rest Areas, Roadway Vegetation, and Utility and Highway Issues, Transportation Research Record 1326: 19-30.

Harrington, J. A. and Tim Miekle. 1994. The effect of salinity on the germination and growth of Wisconsin roadside prairie species. *In* R.G. Wickett, P. N. Lewis, A. Woodliffe and P. Pratt (eds.) Proceedings of the Thirteenth North American Prairie Conference, Spirit of the Land--Our Prairie Legacy. Department of Parks and Recreation, Windsor, Ontario. pp. 183-192.

Iowa Department of Transportation. 1990. Integrated Roadside Vegetation Management Plan. Office of Local Systems, Iowa Department of Transportation. Ames

Jacobson. R., N. Albrecht and K. Bolin. 1990. Wildflower routes: Benefits of a management program for Minnesota right-of-way prairies. *In* D. D. Smith and C. A. Jacobs (eds.) Proceedings of the Twelfth North American Prairie Conference, Recapturing a Vanishing Heritage. University of Northern Iowa. pp. 153-158.

Effects of Post-planting Mowing on Prairie Reconstructions

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Abstract. We planted a diverse prairie seed mixture and found that regular mowing of weedy vegetation in the first year and occasional mowing in the second season increased overall species diversity and enhanced the survival of individuals throughout the planting. This paper compares plantings of prairie species where such mowing is used with plantings where mowing has not been used.

Key words: Mowing and Species Diversity

Introduction

My first small garden-size planting of prairie plants in 1975 consisted of a number of warm-season grasses in a field that had been in corn in 1974. I was advised not to mow it or control the weeds. By late summer of that year, I could find no evidence of establishing grasses and believe that they failed to establish because of intense competition from foxtail, a weedy annual grass. The density of the foxtail population probably was more than 100 plants per sq f, and they eventually grew to a height of 4 to 5 feet. Perhaps the grass seedlings were still there, but obviously the weeds had won.

In June of 1976, my second attempt consisted of 3 acres of a pre-existing corn field planted to mixed warm-season grasses and a variety of hand-collected forbs. When the weeds developed, I was determined to keep them under control and began an intense mowing campaign, first using a rotary lawn mower and later a sickle mower. Mowing was continued during the summer and by early September, I was able to find establishing warm-season plants. By the second season, I had a somewhat weedy, but well established, stand of prairie grasses. By the third season, it was nearly weed free, and I was beginning to see the scattered forbs. This stand is now in its 17th growing season and has provided a prototype for all future plantings. Its problems are related largely to a lack of species diversity.

In 1988, we hand-collected seeds of more than 30 species of forbs and supplemented them with little bluestem and side-oats grama seeds. We planted them in mid-June of 1988. Even though it was a drought year, the weeds grew well. We kept the area mowed throughout the season to a height of about 3 inches. At the end of summer, bare soil was visible everywhere. Although the 1989 growing season was nearly as dry as 1988, we again kept the area mowed throughout the season, gradually raising the cutting height to about 6 inches in mid-August when we began to see a predominance of side-oats grama. By midsummer of 1990, a wide variety of plants was established nearly everywhere. In 1991, the planting was nearly weed free and contained about 35 forb and grass species equally distributed. They were well enough established for the stand to be harvested as a seed crop in the fall of 1991, the fourth growing season.

The use of a sickle type mower speeds up mowing, although it lays down a layer of green vegetation. However, this will dry and wither in about 24 hours and in 3 to 5 days likely will not have any impact on the emerging plants. One must be careful not to bunch up mowed material when turning corners because heavy piles of it can smother small seedlings.

Robert Betz, (1986), Northeastern Illinois University states - Continuous observation of the emerging prairie on the seeded plots over the past decade has shown that relatively few prairie species are able to survive the intense competition of weedy vegetation. Even though large amounts of seed are used, many prairie species do not survive when sown directly onto plowed and disked soil+.

This seems to be the result that is obtained most frequently in prairie reconstructions. Planting a prairie in two stages is often recommended. First, a prairie matrix of tolerant species that can survive weedy competition is planted, followed by a second seeding containing species that have narrow growing tolerances and cannot compete with weedy competition. The second group should be seeded after the first stage is well established.

For a summer planting, our post-planting mowing begins when annual weed growth is 12 to 15 inches in height. If the seeds are fall planted, mowing usually is started in early or mid-June. Summer weed pressure will likely consist of lamb+s quarters *Chenopodium album*, velvet-leaf or buttonweed *Abutilon theophrasti*, pigweed *Amaranthus sp.*, yellow and giant foxtail *Setaria sp.*, common and giant ragweed *Ambrosia sp.*, nightshade *Solanum sp.*, and smartweed *Polygonum sp.* Mowing is continued at about 3-week intervals depending on rainfall. When plants reach 12 inches in height, they are mowed to a 3 inch height. This height is maintained for the first month to 6 weeks. The cut height is raised to 6 inches when the weed pressure subsides, usually in late August or early September.

Second-year mowing consists of two cuttings at a height of about 10 to 12 inches. The first is in early June to control the seed formation of curly dock *Rumex crispus*. The second cutting is in late June to control yellow sweet clover *Melilotus officinalis* and white sweet clover *Melilotus alba*.

If rainfall is adequate, emerging plants of purple prairie clover, gray-headed coneflower, and compass plant will be 2 to 3 inches in height in 6 to 8 weeks. Grasses also will begin to be visible and will be 4 to 6 inches in height. We have found 6-inch tall compass-plants in early June from fall seeding in early November.

Our latest plantings contain 65 species (Table 1). They were planted at one time or 6 months apart in a fall and a spring planting. Of this number, 10 species are abundant (9 plants per sq m), 20 species are common (1 per sq m), 21 species are infrequent (1 plant per 3 sq m), and 22 species are rare (plants are isolated).

Post-planting mowing apparently has helped to give all plants an equal start. Those that will grow easily in very low levels of sunlight seem to compete with those that have narrow tolerances for germination and growth. A few plants appear as isolated individuals, but most species appear equally distributed throughout the planting, depending on their moisture requirements. Each species is represented, not by dozens, but by hundreds, thousands, or tens of thousands of individuals.

Table 1.

Scientific Name	Common Name	Frequency
Andropogon geradii	Big Bluestem	Abundant
Aster laevis	Smooth Aster	Abundant
Bouteloua curtipendula	Side-Oats Grama	Abundant
Dalea purpureum	Purple Prairie Clover	Abundant
Gentiana alba	White Gentian	Abundant
Helianthus grosseserratus	Saw-tooth Sunflower	Abundant
Heliopsis helianthoides	Ox-eye Sunflower	Abundant
Ratibida pinnata	Gray-Headed Coneflower	Abundant
Solidago rigida	Rigid Goldenrod	Abundant
Zizia aurea	Golden Alexanders	Abundant
Aster ericoides	Heath Aster	Common
Aster novae-angliae	New England Aster	Common
Aster pilosus	Frost Aster	Common
Desmodium illinoense	Showy Tick-trefoil	Common
Echinacea pallida	Pale Purple Coneflower	Common
Elymus canadensis	Canada Wild-Rye	Common
Erigeron annus	Daisy Fleabane	Common
Liatris pynostachya	Tall Blazing-Star	Common
Monarda fistulosa	Wild Bergamot	Common
Potentilla arguta	Tall Cinquefoil	Common
Pycnanthemum virginianum	Mountain Mint	Common
Rudbeckia hirta	Black-eyed Susans	Common
Schizachyrium scoparium	Little Bluestem	Common
Silphium laciniatum	Compass-plant	Common
Solidago canadensis	Canada Goldenrod	Common
Epilobium adenocaulon	Willow Herb	Common-swale
Lycopus americanus	Cut-Leaved Water-Horehound	Common-swale
Lythrum alatum	Wing-angled Loosestrife	Common-swale
Solidago riddellii	Riddell's Goldenrod	Common-swale
Typha latifolia	Common Cattail	Common-swale-pond
Anemone cylindrica	Long-Headed Thimbleweed	Infrequent
Baptisa leucantha	Wild White Indigo	Infrequent
Cirsium altissimum	Tall Thistle	Infrequent
Eryngium yuccifolium	Rattlesnake-Masters	Infrequent
Helenium autumnale	Sneezeweed	Infrequent
Liatris aspera	Rough Blazing-Star	Infrequent
Panicum virgatum	Switch Grass	Infrequent
Petalostemum candidum	White Prairie Clover	Infrequent
Physalis virginiana	Ground Cherry	Infrequent
Silphium integrifolium	Rosinweed	Infrequent
Stipa spartea	Porcupine Grass	Infrequent
Verbina stricta	Woolly Vervain	Infrequent
Alisma triviale	Water-Plantain	Infrequent-Pond
Nuphar variegatum	Bullhead-lily	Infrequent-pond
Nymphaea odorata	Fragrant Water-lily	Infrequent-pond
Sagittaria latifolia	Broad-leaved Arrowhead	Infrequent-pond
Cicuta maculata	Water Hemlock	Infrequent-swale
Iris shrevei	Blueflag Iris	Infrequent-swale
Lysimachia quadriflora	Prairie Loosestrife	Infrequent-swale
Scirpus atrovirens	Green Bulrush	Infrequent-swale
Spartina Pectinata	*Prairie* Cord Grass	Infrequent-swale
Achillea lanulosa	Western Yarrow	Rare
Artemisia ludoviciana	White Sage	Rare
Asclepias syriaca	Common Milkweed	Rare
Astragalus canadensis	Milk-vetch	Rare
Dodecatheon media	Prairie Shooting-Star	Rare
Helianthus giganteus	Giant Sunflower	Rare
Koeleria cristata	Junegrass	Rare
Kuhnia eupatorioides	False Boneset	Rare
Lespedeza capitata	Round-headed Bush-clover	Rare
Lobelia spicata	Pale-spike Lobelia	Rare
Rosa sp.	Wild Rose	Rare
Silphium perfoliatum	Cup-plant	Rare
Thalictrum dioicum	Meadow Rue	Rare
Tradescantia virginicana	Prairie Spiderwort	Rare
Verbena hastata	Swamp Vervain	Rare
Viola Papilionacea	Western Ironweed	Rare
Vitis sp.	Wild Grape	Rare
Scutellaria lateriflora	Mad-dog Skullcap	Rare-pond edge
Asclepias incarnata	Swamp Milkweed	Rare-swale
Gentiana andrewsii	Bottle Gentian	Rare-swale
Veronicastrum virginicum	Culver's-Root	Rare-swale

In one side-by-side comparison Roger Maddux and Cindy Hildebrand of Ames, Iowa compared mowed to unmowed plantings. After the third growing season, the unmowed tract had only 8 species, whereas a mowed area had 27 species. They also observed that the good effects of mowing can be augmented by a burn early in the second year. The native plants seemed to grow more vigorously on burned areas even though they had started growing before the burn and were burned off. Maddux and Hildebrand also observed that mowing doesn+t necessarily eliminate competitive nonnative perennials and may even give short species like black medic and plantain a temporary advantage.

Without mowing to control weedy competition, easily established species as big bluestem, black-eyed Susans, big-tooth sunflowers, and gray-headed coneflowers eventually may dominate a planting creating a plant community with low species diversity and long-term instability. Mowing encourages higher species diversity, fills more spaces, and results in a more stable plant community.

Literature Cited

Betz, Robert F. (1986). One decade of research in prairie restoration at the Fermi National Accelerator Labratory (Fermilab), Batavia, Illinois. Proceedings of the Ninth North American Prairie Conference. Edited by Clambey, Gary K. and Richard H. Pemble. Moorhead, Minnesota.

Hildebrand, Cindy and Roger Maddux. (1993). Response to fire and mowing on prairie reconstructions. Personal Communication.

Schramm, Peter. (1990). Prairie Restoration: A twenty-five year perspective on establishment and management. Proceedings of the Twelfth North American Prairie Conference. Edited by Smith, Daryl and Carol A. Jacobs. Cedar Falls, Iowa.

Landscape Prairie Restoration: A Mixed-Grass Prairie Perspective

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Abstract. Last Mountain Lake National Wildlife Area (Saskatchewan, Canada) consists of 15,000 hectares (ha) of upland and wetland habitats. The upland habitat is fragmented into a patchwork of native and exotic vegetation communities and a mixture of both. The Mixed-Grass Prairie Habitat Restoration Project was initiated in 1992. The main goal of the project is to develop techniques appropriate to the mixed-grass prairie for collecting, processing, and planting of native grasses, forbs, and shrubs. Long-term fire management and prairie restoration plans have been developed for the Wildlife Area. Seventy species of graminoids and forbs were collected in 1992, 58 species in 1993, and 62 in 1994 from the native prairie in the Wildlife Area. A diverse native planting was installed on a 9 ha site in spring 1994, and a similar installation is planned for the adjacent 9 ha in spring 1995. Herbicide wicking (see text for details) is a method being developed for the control of *Bromus inermis*. Seven prescribed burns were performed in 1993 and three large burns in 1994; plans have been drafted for implementing controlled burning on numerous other sites in the next few years, including follow-up repeat burns. Flowering and seeding phenology is being monitored for numerous graminoids and forbs. Species composition before fire management has been determined for three native communities through transect analysis of species presence in 225 quadrats/site. Production plots were established in 1993 for *Gaillardia aristata* and *Ratibida columnifera* and in 1994 for *Agropyron dasystachyum* and *A. smithii* in 1994. The establishment of nursery production plots of many of the important grasses and forbs, particulary legumes, is planned.

Key words: prairie restoration, landscape restoration, habitat restoration, mixed-grass prairie, prescribed burning, exotic species control, native prairie plantings

Introduction

The Mixed-Grass Prairie Habitat Restoration Project (MGPHRP) was established in 1992 under the North American Waterfowl Management Plan within the Prairie Habitat Joint Venture region. The project was initiated at Last Mountain Lake National Wildlife Area (LML NWA), Saskatchewan, Canada (51° 22'N, 105° 12'W) (Fig. 1). The main purpose of the project is to restore habitat suitable for the nesting and propagation of waterfowl, but also habitat that would support a greater diversity of the native prairie flora and fauna. Because of past agricultural activities before the establishment of the NWA, the remaining native habitat is fragmented and isolated (Nernberg, 1993). This situation is not unlike that facing the entire prairie ecosystem (Trottier, 1992; Rowe, 1987; Coupland, 1987). Without the enlargement and connection of isolated remnants, these small prairies are susceptible to the loss of species (Betz, 1992) and the invasion of exotic species from an increased perimeter-to-area ratio (Bossard, 1992). Much of the remnant prairie habitat has become degraded from the exclusion of natural perturbations, fire and grazing in particular. Overprotection and the lack of appropriate management can cause a significant decline in the native grasses and forbs (Anonymous, 1992). In light of the necessary ecological restoration (Jordan III et al., 1988), the MGPHRP goals are to:

1) develop techniques appropriate to the mixed-grass prairie for collecting, handling, processing, cleaning, storing, and planting of native grasses, forbs, and shrubs;
2) reduce habitat fragmentation through prairie restoration;
3) rehabilitate native prairie habitat by re-introduction of fire, grazing, and other sustainable management techniques; and
4) control problem, exotic, plant species.

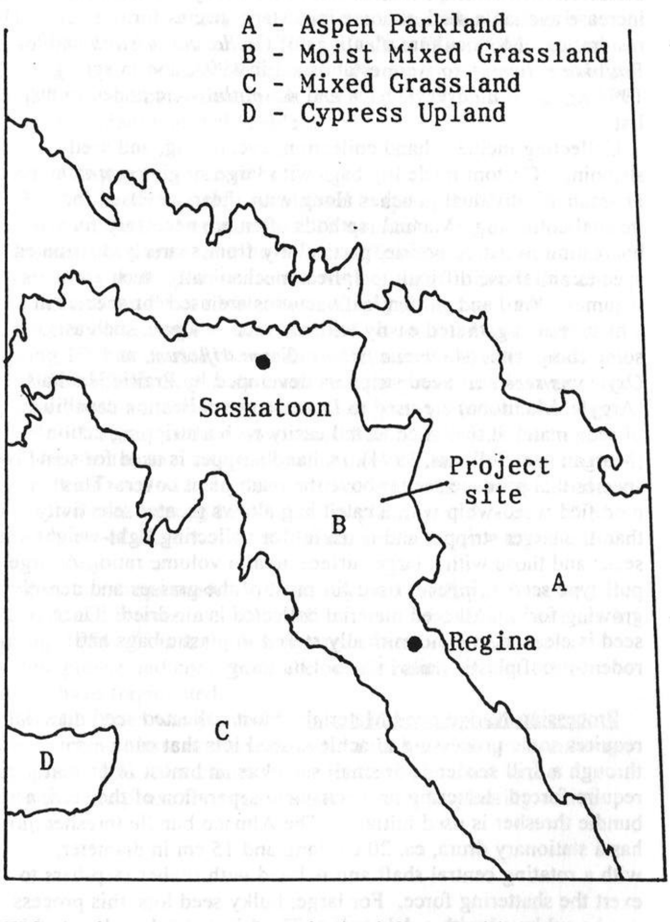

FIG. 1. Geographic location of Mixed-Grass Prairie Habitat Restoration Project at Last Mountain Lake National Wildlife Area. It is located at the north end of Last Mountain Lake in Saskatchewan, Canada, at the ecotone of the mixed-grass prairie and aspen parkland. Map derived from "Ecoregions of Saskatchewan" (Padbury and Acton, 1994).

The main activities of the project include the collection of seed material from selected native grasses and forbs on the native prairie within the NWA. Drying and processing this seed material are accomplished with on-site facilities. Prepared sites are planted with seed mixtures from this locally collected material. Prescribed burning is used to rejuvenate the remnant native prairie, to increase seed production, and to suppress exotic plant species. In some situations, exotic plants also are controlled with chemical herbicide. Long-term restoration and fire management plans have been developed for the NWA (Nernberg, 1993, 1994b).

Methods

Prairie Restoration

Collecting Native Seed Material. Seed material of selected native grasses and forbs is collected within the NWA. Collection sites for each species have been mapped on the NWA baseline vegetation maps. These sites are assessed each year for seed production potential. To facilitate collection from species difficult to re-locate after flowering, individuals or patches of plants are flagged during their peak flowering period with stakes. To aid timing of site assessments, flagging, and seed collecting, data on flowering and seeding phenology of each species are collected each year. A seed production nursery is planned to increase available seed of some important species for use in restoration. Monoculture plantings of *Gaillardia aristata* and *Ratibida columnifera* were established in 1993, and in spring 1994 *Agropyron dasystachyum* and *A. smithii* were added to the list.

Collecting includes hand collection, vacuuming, and seed stripping. Custom-made hip bags with large single compartments or smaller individual pouches along with shears are used for manual collecting. Manual methods often are necessary for wild harvesting in native prairie, particularly from sparsely distributed species and those difficult to collect mechanically, such as legumes. Yard and garden leaf vacuums are used for species in which seed is gathered easily with air suction alone, such as some composites, *Anemone patens*, *Geum triflorum*, and *Oxytropis sericea*. Seed strippers developed by Prairie Habitats (Argyle, Manitoba) are used to increase our collection capability of seed material that is collected easily with a stripping action (Morgan and Collicutt, 1994). A hand stripper is used for some species that produce seeds above the main plant cover. This modified weed-whip with a catch bag allows greater selectivity than the larger stripper and is useful for collecting light-weight seeds and those with a large surface area to volume ratio. A large pull-type seed stripper is used for most of the grasses and densely growing forbs. All seed material collected is air-dried. Once seed is cleaned, it is hermitically stored in plastic bags and rodent-proof plastic pails in a cool building.

Processing Native Seed Material. Most collected seed material requires some processing to achieve seed lots that can pass through a drill seeder. For small seed lots and most forbs that require forced shattering or mechanical separation of the seed, a bundle thresher is used initially. The Almaco bundle thresher has a stationary drum, ca. 20 cm long and 15 cm in diameter, with a rotating central shaft and is lined with rubber rasp-bars to exert the shattering force. For large, bulky seed lots, this process can be achieved with a debearder. The Clipper debearder used is ca. 150 cm long and 50 cm in diameter. Unlike the bundle thresher, this debearder uses thick metal arms, stationary on the interior side of the drum and rotating on the central shaft, to exert the shattering or rubbing force necessary, particularly for deawning the major grass species, *Stipa curtiseta* and *S. comata*.

Once seed has been freed physically from the fruit or inflorescence or has been deawned, the seed lot is ready to be cleaned. A Clipper fanning mill with different sized cleaning screens is used to clean by size and weight and an Almaco air blast seed cleaner is used to separate material by weight.

Prairie Restoration Plantings. To connect or expand the prairie remnants, intervening exotic plant communities are to be removed and replaced with native vegetation by planting locally collected, native, seed material. The exotic vegetation, mostly tame hay on previously cultivated land, is eliminated with a combination of fire, to remove litter and stress plants, and chemical herbicides (glyphosate and dicamba). The exotic vegetation consists of various amounts of *Bromus inermis*, *Agropyron cristatum*, and *Medicago sativa*. Unlike most other restoration projects and native plantings, which till and pack the soil prior to planting, no-till methods of site preparation are used here to preserve the soil structure and mycorrhizal component that has developed over 25-30 years since the land was last cultivated.

Site preparation requires at least two years to achieve satisfactory mortality in the exotic plant community. Late summer or early fall applications of herbicide are crucial for killing efficacy. Spraying at these times eliminates growth for the rest of the growing season and reduces energy reserves, thus making surviving plants more susceptible to winter kill. Anderson (1994) also found that fall glyphosate treatments on *Bromus inermis* were the most effective.

If native seed material cannot be planted immediately after the site has been prepared, native grass cultivars are planted to provide a vegetation cover, reduce weed growth, and maintain soil mycorrhizae. Cultivars of *Agropyron trachycaulum*, *A. dasystachyum*, and *A. smithii* are used. This cultivar grass community can be killed chemically with one application when a native mixture is ready for planting on the site. Mowing or haying is used in the first year and, if necessary, the second year after planting to reduce the influence of weed competition on the establishing prairie seedlings (Howell and Kline, 1994).

Seed mixtures are determined by examining the species composition of adjacent native communities and seed availability and by making adjustments to include a greater proportion of early successional species than may be found in a mature prairie. Knowledge of seed lot germination rates and species seed unit weights aids in determining the appropriate species seed composition of mixtures. Mixtures also are developed to reflect differences in topography, soil type, and moisture availability. This approach reflects field research completed at LML NWA (Nernberg, 1994a) and is used by Ducks Unlimited Canada (Jacobson et al., 1994).

Prairie Rehabilitation

Prescribed Burning. Different timing and types of prescribed burns have been used to achieve desired goals (Higgins et al., 1989). Early spring burns (April) are used to remove litter, rejuvenate growth and flowering, and/or prepare a site for herbicide wicking of *Bromus inermis*. Late spring growing-season burns (late May to early June) are used to stress shrubs and exotic grasses, particularly *Bromus inermis* and *Poa pratensis*, and release suppressed warm-season natives. Late spring is the only period in which significant changes to plant composition by burning have been observed (Henderson, 1991). Growing-season burns are recommended for maintaining and improving plant species diversity (Bragg, 1991). Late summer (mid-August to mid-Sept) and fall (October) burns also have been used, although spring burns are less detrimental to the native grasses and have more suppressive effect on the exotic grasses

(Grilz, 1992). Backburns are used whenever conditions and time allow. Otherwise, headburns and flankburns are used (Higgins et al., 1989).

Permanent vegetation transects have been established to determine community species composition and monitor changes over time with different fire regimes and other management techniques. Species presence in at least 225 quadrats (.25 x .5 m) is used to establish community species composition. Two transects have been established in each of two dominant prairie communities, including *Stipa curtiseta* and *Festuca hallii*. Preburn data have been collected from three transects. One community was burned in fall 1993 and another in spring 1994. Only minor analysis has been completed on the preburn data set from the first transect.

Control of Exotic Species. Although a systematic ranking of the exotic species present in LML NWA, as described by Hiebert and Stubbendieck (1993), has not yet been undertaken, *Bromus inermis*, *Agropyron repens*, *Poa pratensis*, *Melilotus* sp., *Linaria vulgaris*, and *Carduus nutans* have been identified as the problematic exotic species in the NWA . Elimination of these species is unlikely, although control may be achieved with different techniques dependent on the target species.

1. Appropriately timed controlled burns can reduce plant reserves and eliminate seed production.
2. Mowing also can be used to reduce plant reserves and eliminate seed production, particularly for *Melilotus* sp. and *Carduus nutans*.
3. For perennial species with growth habits conducive to selective herbicide application or in sites where overspraying is not a problem, chemicals such as glyphosate and/or 2-4-D can be used for control or complete elimination. For species such as *Poa pratensis*, which has a filamentous growth habit interwoven closely within the native vegetation, nonchemical stressors like grazing and fire must be used.
4. Grazing probably will be re-introduced as a stressor on exotic species in 1995. This method will be used primarily in the spring on *Bromus inermis*, but will likely have an effect on other exotic species, such as *Poa pratensis* and *Melilotus* sp.. Simultaneously, grazing will aid rehabilita tion of the prairie habitat by reducing excessive litter, stimulating native regrowth, and thinning shrub cover.

Prescribed burning is being used as a measure for controlling the growth of *Bromus inermis, Poa pratensis*, and *Linaria vulgaris*. Fire also is being used to eliminate seed production of *Melilotus* sp. and *L. vulgaris*.

Mowing has been used on *M. officinalis* and *L. vulgaris* and will be attempted on *Carduus nutans* as a method of eliminating the seed production of this large biennial species.

Spot spraying with glyphosate has been tried only on a few clonal islands of *Bromus inermis*, but a larger-scale herbicide application (2-4-D) was attempted on the regrowth of *L. vulgaris* after mowing in 1994 to reduce energy reserves and eliminate seed production of this problem perennial species.

'Wicking' of chemical herbicides onto problem exotic species is in its infancy at the NWA. Herbicide wicking is the process of directly applying chemical to a vegetation type or species. This can be accomplished by moving a boom with herbicide-filled sponges or ropes through vegetation at a height that would permit contact with only the taller target plants. Wicking of glyphosate, especially after a spring burn, has significantly reduced the growth of *Bromus inermis* (Grilz, 1992).

Three wicking systems have been developed using chemical reservoirs and including booms with suspended ropes for conducting herbicide. A 5 m PVC pipe boom can be mounted in the front of a tractor and a 1.5 m boom can be mounted on an all-terrain quad. Both systems are attached to pressurized chemical reservoir tanks and include wand spraying applicators to permit spot spraying where necessary. These systems will allow large-scale, selective, herbicide application on the landscape scale. The wider system can be used for large application sites on more even terrain, whereas the narrower system is ideal for smaller areas and more uneven terrain. "Hockey stick" applicators are useful for small, isolated, application jobs. These manual applicators have a reservoir shaped like a hockey stick with a suspended herbicide-conducting rope on the lower horizontal portion. These are ideal for very small applications and more selective targeting of individual isolated plants. A 33% glyphosate solution probably will be used for wicking applications. Attempts will be made to establish the rate of application and number of applications necessary for the best kill.

Results

Collections of Native Seed

Seed was collected from 70 species in 1992, 58 species in 1993, and 62 species in 1994 from the native prairie in the NWA. The species from which seed has been collected are listed in Table 1. The nomenclature follows Budd's Flora (Looman and Best, 1979). Seed unit weights and germination rates were used to provide an approximate pure live seed (PLS) number per given weight of plant material (Table 2).

Prairie Restoration Plantings

Half of an 18 ha field was planted in spring 1994 with a diverse native seed mixture (ca. 70 species). Three distinct plant communities were seeded to reflect differences in moisture availability with distance from a wetland basin. Establishment results will not be available for another year or two. The adjacent 9 ha along the same wetland basin will be planted in spring 1995 at double the seeding rate used for the other half.

A 38 ha field, across the road from the previous site, was planted with a mixture of native wheatgrass cultivars in spring 1994. This intermediate cover established well, and the field will be planted to a diverse local native mixture in sections over time, the size of which will depend on amounts of native seed collected each year and available for planting at this site. The restoration of these two sites will connect a larger native prairie community.

Two lure crops to attract migratory bird totalling 36 ha were retired, and the area was planted to native wheatgrass cultivars in spring 1994. This is the initial stage of restoring these sites to native prairie and connecting the prairie remnants that these fields have fragmented.

A 65 ha field was planted to four, 16 ha seed production plots (three monoculture and one mixed) of native wheatgrass cultivars in spring 1993. Seed from these fields will be used in the intermediate phase for site preparation prior to planting native prairie.

Table 1. Species at Last Mountain Lake National Wildlife Area, Saskatchewan from which seed has been collected under the Mixed-Grass Prairie Habitat Restoration Project.

Forbs
Achillea millefolium (yarrow)
Agoseris glauca (false dandelion)
Allium stellatum (pink onion)
A. textile (prairie onion)
Anemone multifida (cut-leaved anemone)
A. patens (crocus)
Artemisia ludoviciana (prairie sage)
Aster ericoides (many-flowered aster)
A. falcatus (white prairie aster)
A. hesperius (western willow aster)
Astragalus bisulcatus (two-grooved milk-vetch)
A. canadensis (Canada milk-vetch)
A. crassicarpus (groundplum)
A. danicus (purple milk-vetch)
A. flexuosus (slender milk-vetch)
A. missouriensis (Missouri milk-vetch)
A. pectinatus (narrow-leaved milk-vetch)
A. striatus (ascending purple milk-vetch)
Campanula rotundifolia (harebells)
Chrysopsis villosa (hairy-golden aster)
Cleome serrulata (spiderflower)
Dodecatheon pulchellum (saline shooting star)
Erigeron caespitosus (tufted fleabane)
Gaillardia aristata (gaillardia)
Gaura coccinea (scarlet gaura)
Gentiana affinis (oblong-leaved gentian)
G. amarella (northern gentian)
G. crinita (fringed gentian)
Geum triflorum (three-flowered aven)
Glycyrrhiza lepidota (wild licorice)
Gutierrezia sarothrae (broomweed)
Helianthus nuttallii (tuberous-rooted sunflower)
H. subrhomboideus (rhombic-leaved sunflower)
Heuchera richardsonii (alumroot)
Liatris ligulistylis (meadow blazingstar)
L. punctata (dotted blazingstar)
Linum lewisii (wild blue flax)
L. rigidum (yellow flax)
Lomatogonium rotatum (marsh felwort)
Oenothera biennis (yellow evening primrose)
O. nuttallii (white evening primrose)
Orthocarpus luteus (owl's clover)
Oxytropis monticola (early-yellow locoweed)
O. sericea (late-yellow locoweed)
O. splendens (showy locoweed)
Penstemon gracilis (lilac-flowered beardtongue)
P. nitidus (smooth blue beardtongue)
P. procerus (slender blue beardtongue)
Petalostemon candidum (white prairie clover)
P. purpureum (purple prairie clover)
Potentilla arguta (white cinquefoil)
P. gracilis (graceful cinquefoil)
P. pensylvanica (prairie cinquefoil)
Ratibida columnifera (prairie coneflower)
Sisyrinchium montanum (blue-eyed grass)
Smilacina stellata (false Solomon's seal)
Solidago missouriensis (low goldenrod)
S. rigida (stiff goldenrod)
Thermopsis rhombifolia (goldenbean)
Vicia americana (wild vetch)
Zizia aptera (heart-leaved alexander)
Zygadenus elegans (smooth camas)

Graminoids
Agropyron albicans (awned northern wheatgrass)
A. dasystachyum(northern wheatgrass)
A. smithii (western wheatgrass)
A. trachycaulum (slender wheatgrass)
Andropogon scoparium (little bluestem)
Bouteloua gracilis (blue grama)
Bromus ciliatus (fringed brome)
Calamagrostis inexpansa (marsh reed grass)
Calamovilfa longifolia (sand reed grass)
Elymus canadensis (Canada wildrye)
Festuca hallii (plains rough fescue)
Hierochloe odorata (sweet grass)
Koeleria gracilis (June grass)
Muhlenbergia richardsonis (mat muhly)
Poa canbyi (Canby's bluegrass)
P. cusickii (early bluegrass)
P. palustris (fowl bluegrass)
Sporobolus cryptandrus (sand dropseed)
Stipa comata (needle-and-thread grass)
S. curtiseta (porcupine grass)
S. viridula (green needle grass)

Table 2. Seed unit weights, unit pure live seeds, and germination rates for seed material collected at Last Mountain Lake National Wildlife Area in 1992.[1]

Grasses	**#Seeds/g**	**Germination Rate (%)**	**Pure Live Seed/g**
Agropyron dasystachyum	315.8	65	205.3
A. smithii (estimate)	400	75	300
A. trachycaulum	513.5	23	118.1
Andropogon scoparius	570	6	34.2
Calamagrostis inexpansa	2,222	5	111.1
Festuca hallii	837.5	89	745.4
Koeleria gracilis	3,125	54	1,687.5
Muhlenbergia richardsonis	12,500	16	2,000.0
Poa canbyi	2,222	68	1,511.0
P. cusickii	1,583	42	664.9
Stipa comata	74.2	61	45.3
S. curtiseta[2]	28.8	12	3.5
S. viridula[2]	-	53	

Forbs	**#Seeds/g**	**Germination Rate (%)**	**Pure Live Seed/g**
Achillea millefolium	4,591	95	4,361.5
Allium cernuum (estimate)	500	50	250
A. textile	590	59	348.1
Anemone multifida	-	>50	-
A. patens	275	0	0
Artemisia ludoviciana	-	low (<10)	-
Aster ericoides (estimate)	500	50	250
A. falcatus	500(est)[3]	28	140(est)
A. hesperius	500(est)	>50	250(est)
Astragalus canadensis (est)	250	50	125
A. crassicarpus (est)	200	75	150
A. danicus (est)	750	75	563
A. flexuosus	680	98	666.4
A. pectinatus	250	37	92.5
A. striatus	1,000	67	670.0
Chrysopsis villosa	113	54	61.0
Gaillardia aristata	586	43	252.0
Gentiana amarella	11,475	0.3	34.4
Geum triflorum	465	70	325.5
Helianthus subrhomboideus	-	29	-
Heuchera richardsonis	16,071	88	14,142.5
Linum lewisii	667	77	513.6
L. rigidum	761	88	669.7
Orthocarpus luteus	8,571	1.0	85.7
Oxytropis monticola	1,918	97	1,860.5
O. splendens	1,000	97	970.0
Penstemon gracilis	11,915	84	10,008.6
Petalostemon purpureum	458	69	316.0
Potentilla arguta	4,667	78	3,640.3
P. gracilis	3,864	45	1,738.8
P. pensylvanica	6,667	75	5,000.3
Ratibida columnifera	1,600	48	768.0
Solidago missouriensis	800	24	192.0
S. rigida	734	60	440.4
Zizia aptera	1,014	68	689.5

1 - Seed weights may be variable because not all lots were totally clean seed only.
2 - Germination rates should be higher, see Nernberg, 1994a.
3 - Estimate

Table 3. 1992 Preburn percent species composition of a *Stipa curtiseta/ Agropyron* vegetation community at Last Mountain Lake National Wildlife Area, Saskatchewan as determined by species presence in 225 - .5 x .25 m quadrats.

Graminoids	%	**Forbs**	%
Agropyron dasystachyum	87.0	*Achillea millefolium*	1.1
A. smithii	49.1	*Androsace septentrionalis*	9.1
A. trachycaulum	0.4	*Anemone patens*	27.4
Bouteloua gracilis	0.7	*Artemisia frigida*	12.6
Bromus inermis	0.7	*Astragalus danicus*	9.8
Carex eleocharis	24.6	*A. flexuosus*	1.4
Carex sp.	22.5	*A. pectinatus*	0.4
Carex sp.	0.7	*Carduus nutans*	0.7
Distichlis stricta	0.7	*Cerastium arvense*	3.9
Koeleria gracilis	0.4	*Descurainia richardsonii*	4.2
Muhlenbergia richardsonis	0.4	*Epilobium angustifolium*	0.4
Poa canbyi	22.8	*Galium boreale*	0.4
P. cusickii	11.9	*Phlox hoodii*	1.4
P. pratensis	4.9	*Potentilla pensylvanica*	0.4
Stipa comata	7.4	*Psoralea argophylla*	0.4
S. curtiseta	40.7	*Rosa arkansana*	2.8
S. viridula	6.0	*R. woodsii*	1.4
		Sisymbrium altissimum	9.5
		Sonchus arvensis	2.1
		Solidago canadensis	1.1
		S. missouriensis	0.7
		S. sp.	1.1
		Stellaria longipes	0.4
		Symphoricarpos occidentalis	14.4
		Thermopsis rhombifolia	9.1
		Tragapogon dubius	1.4
		Unidentified	13.0
		Urtica dioica	2.1
		Vicia americana	22.5

Prescribed Burning

Seven prescribed growing-season burns were performed in 1993 during May to early June and late August. These burns totalled approximately 225 ha. Most of these fires were timed to stress exotic grasses (*Bromus inermis* and *Poa pratensis*), and qualitative results obtained from the spring burns were very positive. These exotics, particularly *B. inermis,* were greatly suppressed, whereas regrowth of the native grasses was relatively greater. This was comparable to other burn results (Bragg, 1991 and Henderson, 1991). Spring growing-season burns on a *Festuca-Stipa* grassland have been beneficial for the native grasses and caused a resurgence in forb growth for at least three years after the burn (Bailey and Anderson, 1978).

Considerable numbers and growth of warm-season and late-season species became evident after the spring burns stressed the cool-season growth. Large patches of *Calamovilfa longifolia* and *Bouteloua gracilis*, and many thousands of *Liatris punctata* appeared following an early growing-season burn (June 7, 1993). Prior to this burn, these species had not been observed in this site during the entire six year period that the author has been acquainted with the area. All three species flowered and produced seed, but none of the seeds were filled. I suspect the growth of these late-season species had been suppressed by the cool-season natives for many years because of the absence of fire. Seed in all of these species was produced and filled in 1994. This pattern of seed fill between the two years was not observed in any other species.

Three burns were completed in 1994 from late April to early May totalling approximately 300 ha. Two burns were performed to clear litter and stimulate early, productive, growth of *Bromus inermis* exposing it for possible herbicide wicking. Because of dry spring conditions, vegetation growth was not conducive to wicking. The largest burn of ca. 200 ha served to remove thickly accumulated thatch and thin the shrub canopy. Plans for using fire management in the next few years have been drafted for numerous other sites, including follow-up repeat burns.

Species-presence data from 225 quadrats along a preburn vegetation transect in a *Stipa curtiseta/Agropyron* community are listed in Table 3.

Control of Exotic Species

Large-scale control of exotic species with herbicides will be contingent on results from smaller-scale experimentation with wicking. Positive results have been obtained from mowing *Melilotus* sp., which is a biennial, eliminating seed production and preventing restocking of the soil seed bank. Appropriate grazing also is a very effective method for eliminating *Melilotus* sp. (Marilyn Latta, pers. comm.). Successful suppression of *Bromus inermis* has been obtained with late-spring prescribed burns. This would be predicted by results of Henderson (1991) and Bragg (1991). Wicking of *B. inermis*, which has had mixed results because of technical problems, has proven successful (Grilz, 1992) and should continue. Mowing of *Melilotus* sp. proved beneficial to eliminate seed production and should be expanded.

Discussion

Work on the Mixed-Grass Prairie Habitat Restoration Project (MGPHRP) is progressing rapidly. The qualitative results from the early phases of the experimental research are very encouraging and will aid the implementation of the restoration work and the management of native prairie. Many of the activities undertaken by this project are comparable to those used or prescribed by other restoration practitioners (Collicutt and Morgan, 1990; Rock, 1981; Duebbert et al., 1981). The concerns and methods for collecting, processing, and storing seeds as expressed by Lippit et al. (1994) are equivalent to those used in this project. The restoration program at Walnut Creek National Wildlife Refuge (Drobney, 1994), because of its size, goals, and landscape approach, is very similar to the program at LML NWA, and I consider it a 'sister' project to the MGPHRP. Once both projects progress past the incipient stages, comparisons of restoration successes will be possible. One difference between the MGPHRP and the other projects, besides the obvious species differences, is the no-till site preparation and planting method used at LML NWA to preserve decades of uncultivated soil development.

The small budget and labour force greatly limit the research that can be accomplished; however, the positive qualitative and quantitative results obtained each year provide encouragement that given enough time we should have a much better idea of how to restore and manage native prairie on a large-scale. A new development that holds encouraging promise is the selection of LML NWA as the first and possible only Ecological Monitoring and Assessment Network (EMAN) site in Saskatchewan for Canada. This may signal more restoration research and data collection. We have our fingers crossed.

Literature Cited

Anderson, B. 1994. Converting smooth brome pasture to warm-season grasses. *In* R.G. Wickett, P.D. Lewis, A. Woodliffe, and P. Pratt (eds.). Proceedings of the Thirteenth North American Prairie Conference. Preney Print and Litho Inc. Windsor, Ontario. pp. 157-160.

Anonymous. 1992. Long term rest does not help plant diversity. Native Plant Society of Texas News 10(3):3.

Bailey, A.W. and M.L. Anderson. 1978. Prescribed burning of a *Festuca-Stipa* grassland. Journal of Range Management 31(6):446-49.

Betz, R.F. 1992. The tallgrass prairie. Restoration and Management Notes 10(1): 33-35.

Bossard, C.C. 1992. Factors leading to invasiveness and invasibility. *In* Abstracts from the 6th Annual Meeting of the Society for Conservation Biology. The Society for Conservation Biology-The Wildlife Society. Virginia. pp. 1.

Bragg, T.B. 1991. Implications for long-term prairie management from seasonal burning of loess hill and tallgrass prairies. *In* S.C. Nodvin and T.A. Waldrop (eds.). Proceedings of an International Symposium on Fire and the Environment: Ecological and Cultural Perspectives. U.S. Forest Service Southeastern Forest Experiment Station. North Carolina. pp. 34-44.

Collicutt, D.R. and J.P. Morgan. 1990. Tall grass prairie restoration project 1990 report. Prairie Habitats. Argyle, Manitoba. 72p.

Coupland, R.T. 1987. Endangered prairie habitats: The mixed prairie. *In* G.L. Holroyd, W.B. McGillivray, P.H.R. Stepney, D.M. Ealey, G.C. Trottier, and K.E. Eberhart (eds.). Proceedings of the Workshop on Endangered Species in the Prairie Provinces. Provincial Museum of Alberta Natural History Occasional Paper No. 9. Alberta Culture Historical Resources Division. Edmonton, Alberta. pp. 35-42.

Duebbert, H.F., E.T. Jacobson, K.F. Higgins, and E.B. Podoll. 1981. Establishment of seeded grasslands for wildlife habitat in the prairie pothole region. US Dept. of the Interior, Fish and Wildlife Service, Special Scientific Report, Wildlife No. 234, Washington, DC..

Drobney, P.M. 1994. Iowa prairie rebirth: Rediscovering natural heritage at Walnut Creek National Wildlife Refuge. Restoration and Management Notes 12(1):16-22.

Grilz, P.L. 1992. Ecological Relations of *Bromus inermis* and *Festuca altaica* subsp. *hallii*. M.Sc. thesis, Dept of Crop Science and Plant Ecology, University of Saskatchewan, Saskatoon. 130p.

Henderson, R.A. 1991. Ten year response of a Wisconsin prairie remnant to seasonal timing of fire. *In* D.D. Smith and C.A. Jacobs (eds.). Proceedings of the Twelfth North American Prairie Conference. University of Northern Iowa, Cedar Falls. pp. 121-125.

Hiebert, R.D. and J. Stubbendieck. 1993. Handbook for ranking exotic plants for management and control. U.S. Dept. of the Interior, National Park Service, Natural Resources Publication Office. Denver, Colorado. 29p.

Higgins, K.F., A.D. Kruse, J.L. Piehl. 1989. Prescribed burning guidelines in the Northern Great Plains. U.S. Fish and Wildlife Service and Cooperative Extension Service, South Dakota State University, U.S. Dept. of Agriculture.

Howell, E.A. and V.M. Kline. 1994. The role of competition in the successful establishment of selected prairie species. *In* R.G. Wickett, P.D. Lewis, A. Woodliffe, and P. Pratt (eds.). Proceedings of the Thirteenth North American Prairie Conference. Preney Print and Litho Inc. Windsor, Ontario. pp. 193-198.

Jacobson, E.T., D.B. Wark, R.G. Arnott, R.J. Haas, and D.A. Tober. 1994. Restoration and Management Notes 12(1): 46-50.

Jordan III, W.R., R.L Peters II, and E.B. Allen. 1988. Ecological restoration as a strategy for conserving biological diversity. Environmental Management 12(1):55-72.

Lippitt, L., M.W. Fidelibus, and D.A. Bainbridge. 1994. Native seed collection, processing, and storage for revegetation projects in the western United States. Restoration Ecology 2(2):120-131.

Looman, J. and K.F. Best. 1979. Budd's Flora of the Canadian Prairie Provinces. Agriculture Canada Publication 1662, Supply and Services, Ottawa.

Morgan, J.P. and D.R. Collicutt. 1994. Seed stripper harvesters: Efficient tools for prairie restoration. Restoration and Management Notes 12(1): 51-54.

Nernberg, D. 1994a. Germination, survivorship, productivity, and competitive ability of six native grass species from the northern mixed-grass prairie for use in prairie vegetation restoration. M.Sc. thesis, Dept. of Botany, University of Alberta, Edmonton. 433p.

Nernberg, D. 1994b. Prairie restoration and vegetation management for the Prairie Habitat Joint Venture region: Annual report 1993-1994. Wildlife Habitat Canada. Ottawa.

Nernberg, D. 1993. Prairie restoration and vegetation management for the Prairie Habitat Joint Venture region: Annual report 1992-1993. Wildlife Habitat Canada. Ottawa.

Padbury, G.A. and D.F. Acton. 1994. Ecoregions of Saskatchewan. Map compiled by Agriculture Canada. Central Mapping and Surveys, Regina, Saskatchewan.

Rowe, J.S. 1987. Status of the aspen parkland in the prairie provinces. *In* G.L. Holroyd, W.B. McGillivray, P.H.R. Stepney, D.M. Ealey, G.C. Trottier, and K.E. Eberhart (eds.). Proceedings of the Workshop on Endangered Species in the Prairie Provinces. Provincial Museum of Alberta Natural History Occasional Paper No. 9. Alberta Culture Historical Resources Division. Edmonton, Alberta. pp. 27-33.

Rock, H.W. 1981. Prairie propagation handbook. Wehr Nature Center, Dept. of Parks, Recreation and Culture. Milwaukee County, Wisconsin. 74p.

Trottier, G.C. 1992. Conservation of Canadian prairie grasslands: A landowner's guide. Canadian Wildlife Service, Edmonton, Alberta. p. 92.

Growth and Seed Yield of Three Grassland Perennials in Monocultures and Mixtures

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Abstract. The Land Institute is working to develop a sustainable agriculture, modeled on the prairie ecosystem, that features mixtures of grain-producing perennials. Since 1991, we have monitored growth and seed yield in monocultures and mixed plots of three perennial grain candidates: eastern gamagrass (*Tripsacum dactyloides*, Poacae); wildrye (*Leymus racemosus*, Poacae); and Illinois bundleflower (*Desmanthus illinoensis*, Mimosaceae). Six cropping-system treatments were established as 7.32 m x 9.75 m plots in both a favorable and a less favorable growing environment (n=36 plots). Each species showed a unique pattern of growth and seed yield among treatments. Eastern gamagrass, a warm-season species, yielded and grew best when grown with wildrye, whereas wildrye, a cool-season grass, yielded best in monoculture. Both grasses yielded better in the more favorable growing environment. In a dry year, Illinois bundleflower yielded and grew better in the more favorable environment, but in moist years, bundleflower seed yield and growth were similar across treatments and sites. Mixed plots overyielded in 1992 and 1993, and overyielding increased from 1992 to 1993. The study has demonstrated some effects of neighborhood and soil type on growth and reproduction in these species. Such information, gathered over many growing seasons, is necessary for the design of stable mixtures that maximize beneficial interactions between species.

Key words: competition, facilitation, overyielding, perennial grains, seed yield, sustainable agriculture

Introduction

The North American prairie landscape today consists mainly of vast monocultures of high-yielding annuals, a far cry from the highly diverse assemblage of perennial grasses and wildflowers found in unplowed prairie. This schism between agriculture and nature is at the root of many of the problems in agriculture, including soil erosion and dependence on off-farm-derived inputs to maintain fertility and control pests (Jackson 1980, Jackson and Piper 1989). The Land Institute envisions a reformed agriculture that integrates ecology, by looking to the prairie ecosystem as the basis for a sustainable, grain-producing, agriculture (Soule and Piper 1992).

If we look to the prairie for guidance in designing a sustainable agriculture that embodies long-term stability, two features stand out: perennialism and species diversity. Soils planted to perennial crops would be less susceptible to erosion than those planted to annual crops, because the ground would not be tilled every year and would be protected by a canopy. Perennials also have a large underground biomass, which helps build soil organic matter through root turnover (Anderson and Coleman 1985, Buyansovsky *et al.* 1987). Mixtures comprising species that differ morphologically or phenologically can achieve more complete utilization of soil nutrients, water, and light. Facilitation of one species' growth by another and reduction of pest problems in a mixture relative to a monoculture are other benefits. Many traditional mixed-crop systems show greater yield, even overyielding relative to monocultures of the same plants (Vandermeer 1989). We hope to incorporate these advantages into mixed-perennial cropping systems.

The predominant functional groups of plants on Kansas prairie are warm-season (C_4) grasses, cool-season (C_3) grasses, nitrogen-fixing legumes, and composites (Piper 1993). The species used in this study, eastern gamagrass (*Tripsacum dactyloides* (L.) L.), wildrye (*Leymus racemosus* (Lam.) Tselev), and Illinois bundleflower (*Desmanthus illinoensis* (Michx.) MacM.), are a warm-season grass, a cool-season grass, and a legume, respectively.

To build a knowledge base on which to develop perennial mixtures of these and other plants, we are examining how these species affect one another in established plots. Because we hope that perennial polycultures will yield well for 5 to 10 years, we need to study how these plant interactions change with time. Thus, we are monitoring seed yield and plant size over several successive growing seasons. Because the environment can influence both direction and intensity of interspecific interactions, we set up this study in two environments: a relatively fertile plain and an eroded slope. The experiment is designed to compare how each species and overall plot performs in a mixture relative to a monoculture and to consider the effect of growing environment.

We asked two main questions. Because yield and growth are good measures of plant performance, first, how do seed yield and plant size differ between monoculture and mixture? Second, in which mixtures and environments do these polycultures overyield?

Methods

Descriptions of species and study sites

Work at The Land Institute to domesticate perennial grains began in 1978 with an inventory of nearly 300 species for their suitability to the environment of central Kansas and promise of high seed yield. A second inventory studied the agronomic potential of 4300 collections of perennial grass species within six cool-season genera from around the world. From these inventories, a handful of perennial species was chosen for potential crop development. This study used three of these species.

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Eastern gamagrass is a large warm-season (C_4) bunchgrass. Its range extends throughout the southeastern United States and south to Bolivia and Paraguay (Great Plains Flora Association 1986). Wildrye is a rhizomatous cool-season (C_3) grass native to the grasslands of southeastern Europe and western Asia. Illinois bundleflower is a native nitrogen-fixing legume (Kulakow *et al.* 1990) that forms deep taproots. Its range extends east to Florida, west to New Mexico, south into Texas, and north to Minnesota (Great Plains Flora Association 1986). For more detailed descriptions of these species, see Piper (1993).

The experiment was established in March 1991 at two sites at The Land Institute, Salina, Kansas. Site 1 is a level Cozad silt loam, previously in a continuous wheat (*Triticum aestivum* L.) rotation until 1990, when it was planted to alfalfa (*Medicago sativa* L.). Site 2 is a south-facing eroded hillside, Kipson-Clime Complex soil. It was planted to native grasses (primarily big bluestem (*Andropogon gerardii* Vitman), switchgrass (*Panicum virgatum* L.), and Indiangrass (*Sorghastrum nutans* (L.) Nash)) in 1982, but had been cropped continually prior to 1982. Some key soil nutrients (NO_3, total N, K) and percent organic matter were higher at Site 1 than Site 2 at the onset of the experiment (Piper *et al.* 1991).

At both sites, there were six cropping system treatments, each replicated three times (n=six treatments x three replicates x two sites = 36 plots). The treatments included monocultures of eastern gamagrass, wildrye, and Illinois bundleflower; bicultures of bundleflower/gamagrass and gamagrass/wildrye in a 1:1 ratio of alternating plants; and a triculture of the three species randomly arrayed in a 1:1:1 ratio. Plots were 7.32 m x 9.75 m, with plants 0.75 m apart within rows and rows 0.91 m apart (96 plants per plot). The outer two rows were left unmeasured and unharvested to eliminate border effects.

Data collection and analysis

We collected yield and size data from 1991 to 1993. Bundleflower flowered and set seed in all 3 years, whereas wildrye and gamagrass generally do not flower in the establishment year. Wildrye was harvested in late June in 1992 and 1993, air-dried in a greenhouse, and threshed using a Hege single plot thresher before weighing. Eastern gamagrass harvests in 1992 and 1993 were from mid-July to early August . These were air-dried in a greenhouse, and the entire spikelet was weighed. Actual seed mass is approximately 27% of spikelet mass (Piper and Towne 1988). Illinois bundleflower was harvested from mid-August to early September in 1991-1993. After drying, seed bundles were threshed, and seed was cleaned using a Clipper office-size cleaner before weighing. Yields are reported as g/m^2.

Size was estimated in several ways. Total reproductive tiller length (cm) and number were recorded for wildrye, basal circumference of the crown (cm) for eastern gamagrass, and total basal stem area (mm^2) for Illinois bundleflower. These measures correlate well with aboveground biomass measurements of 3-year-old plants: wildrye tiller number vs. biomass r=0.68, gamagrass basal area vs. biomass r=0.71, and bundleflower basal stem area vs. biomass r=0.91 (all $P<0.0001$; Piper, unpublished). For each year, differences among sites and treatments were examined using two-way analysis of variance followed by the Student-Newman-Keuls Procedure (SigmaStat, Jandel Corporation, San Rafael, CA). Significance was established as $P<0.05$.

We evaluated overyielding for each mixture by calculating its Land Equivalent Ratio (LER) (Mead and Willey 1980). The LER represents the equivalent amount of land that would have to be planted to monocultures to match the yield found in a given mixture. First, the relative yield (RY), the ratio of the monoculture plot yield to the mixture plot yield, is calculated for each species. For example, if the relative yield of biculture/monoculture is 0.5, then the yield is no different between monocultures and bicultures. The relative yields of each species in a mixture then are summed to give the LER. If the LER>1, plots are overyielding.

Results and Discussion

Seed yield and plant size

The establishment year, 1991, was dry (60.6 cm annual precipitation vs. 73.5 cm normal), whereas 1992 and 1993 were wetter than normal (1992: 92.7 cm, 1993: 147.5 cm). Yield and growth differences have occurred among treatments, years, and environments.

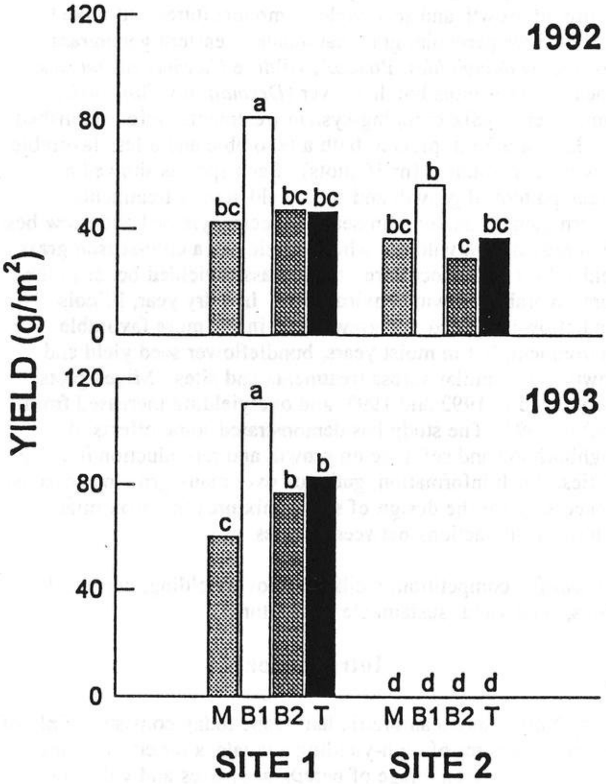

FIG. 1. Mean seed yield of eastern gamagrass in four cropping systems at two sites over 2 years. In 1993, mammal predation of reproductive tillers prevented gamagrass seed harvest. For each year, bars with the same letter do not differ at $P<0.05$ (ANOVA, S-N-K Test). Key: M=monoculture, B1=biculture with wildrye, B2=biculture with Illinois bundleflower, T=triculture.

Eastern gamagrass yielded best in mixtures with wildrye in both 1992 (F=14.48, d.f.=3,16, $P<0.0001$) and 1993 (F=23.10, d.f.=3,16, $P<0.0001$), though yields were somewhat lower at Site 2 in 1992 (F=14.51, d.f.=1,16, $P<0.01$). At Site 1 in 1993, its lowest yield was in monoculture (Fig. 1). Size data concur with yield data; gamagrass plants were larger at Site 1 (1991: F=24.90, d.f.=1,16, $P<0.0001$; 1992: F=34.82, d.f.=1,16, $P<0.0001$; 1993: F=22.44, d.f.=1,16, $P<0.0001$) and, at both sites, the largest plants were found in mixtures with wildrye (1991: F=4.07, d.f.=3,16, $P<0.05$; 1992: F=15.45, d.f.=3,16, $P<0.0001$; 1993: F=11.35, d.f.=3,16, $P<0.001$) (Fig. 2). Heavy and unusual grazing of reproductive tillers prevented harvest at Site 2 in 1993. Prairie voles (*Microtus ochrogaster* Wagner) are likely culprits based on how the stalks were chewed (Bee *et al.* 1981). Tiller grazing has not been observed in previous years, but future work should consider how to minimize the potential for this type of loss. Site 2 is surrounded by native prairie grasses, unlike Site 1, which is surrounded by agricultural land. Surrounding prairie grass may support troublesome populations of these small mammals. However, size data for 1993 followed the trend of best gamagrass performance in a mixture with wildrye (Fig. 2).

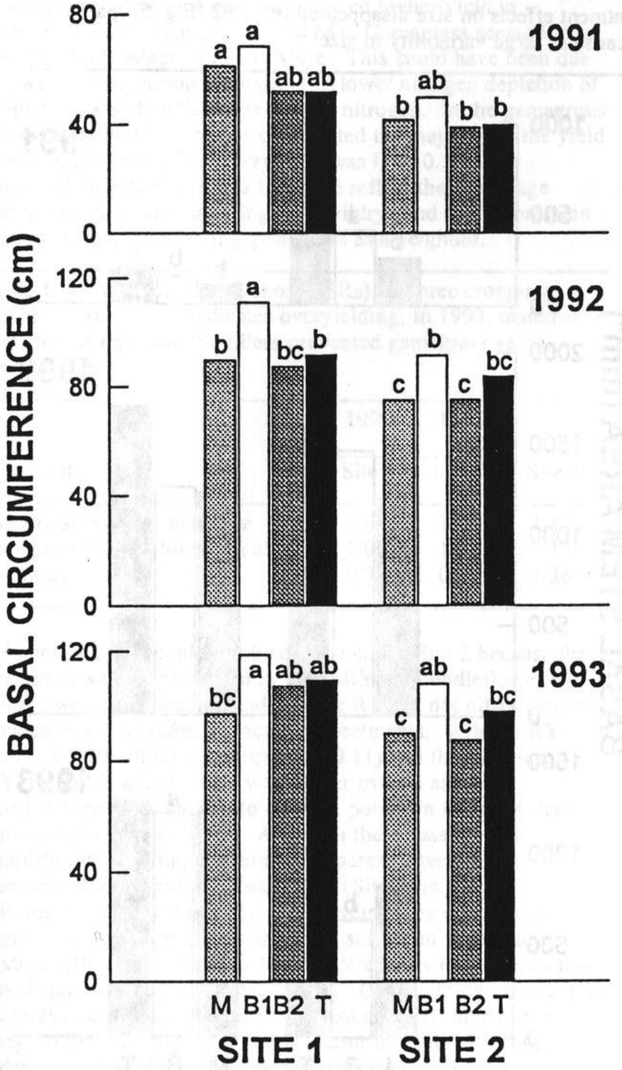

FIG. 2. Mean size, estimated as basal circumference, of eastern gamagrass in four cropping systems at two sites over 3 years. For each year, bars with the same letter do not differ at $P<0.05$ (ANOVA, S-N-K Test). Key as in Fig. 1.

High yield and large size of gamagrass growing with wildrye may be explained by small size of wildrye in these plots, thus giving each gamagrass plant more light and space. Higher yield in the other mixtures relative to monoculture for 1993 indicates that eastern gamagrass experiences greater intraspecific competition for space or other resources than interspecific competition in mixtures. It also may benefit from planting with another species, such as the N-fixing Illinois bundleflower.

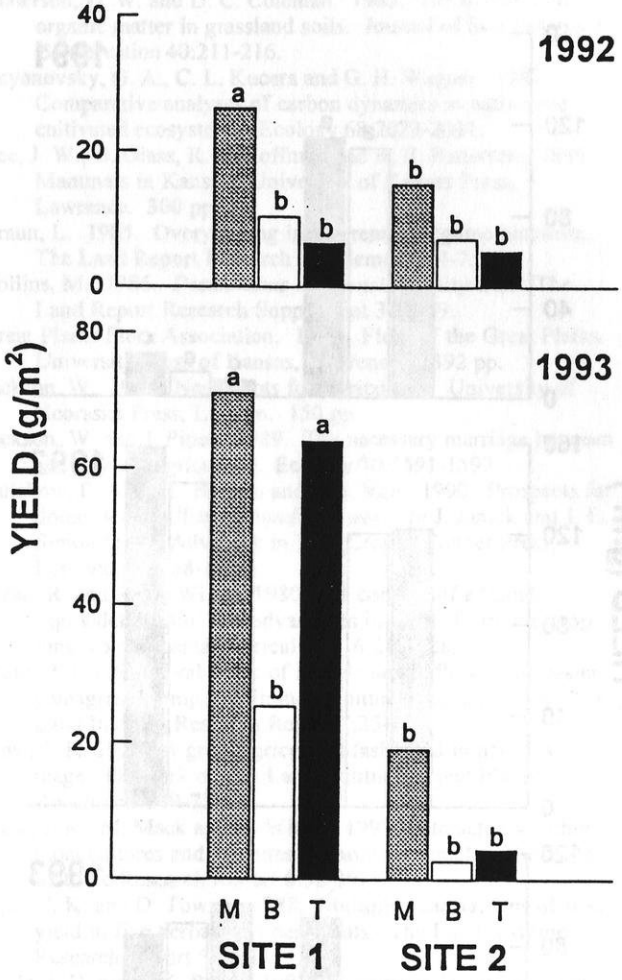

FIG. 3. Mean seed yield of wildrye in three cropping systems at two sites over 2 years. For each year, bars with the same letter do not differ at $P<0.05$ (ANOVA, S-N-K Test). Key: M=monoculture, B=biculture with gamagrass, T=triculture.

In contrast to eastern gamagrass, wildrye seed yield was highest in monoculture at both sites in 1992 (F=20.58, d.f.=2,12, $P<0.0001$) and 1993 (F=15.18, d.f.=2,12, $P<0.001$), although wildrye yield in the triculture did not differ significantly from monoculture yield at Site 1 in 1993 (Fig. 3). Yield in the eastern gamagrass/wildrye mixture was low; eastern gamagrass apparently reduced wildrye growth, possibly because of its large size coupled with the relatively slow establishment of wildrye. Overall, Site 1 yields were higher than yields at Site 2 (1992: F=6.58, d.f.=1,12, $P<0.05$; 1993: F=91.60, d.f.=1,12, $P<0.0001$), though treatment means followed the same general pattern. Wildrye may have higher available N requirements in order to yield well, as is generally true for other cool-season perennial grasses (Tilman 1990). Also, some wildrye flowering tillers were grazed by deer, another factor that reduced yield at Site 2. Size data (not shown) mirrored the yield data.

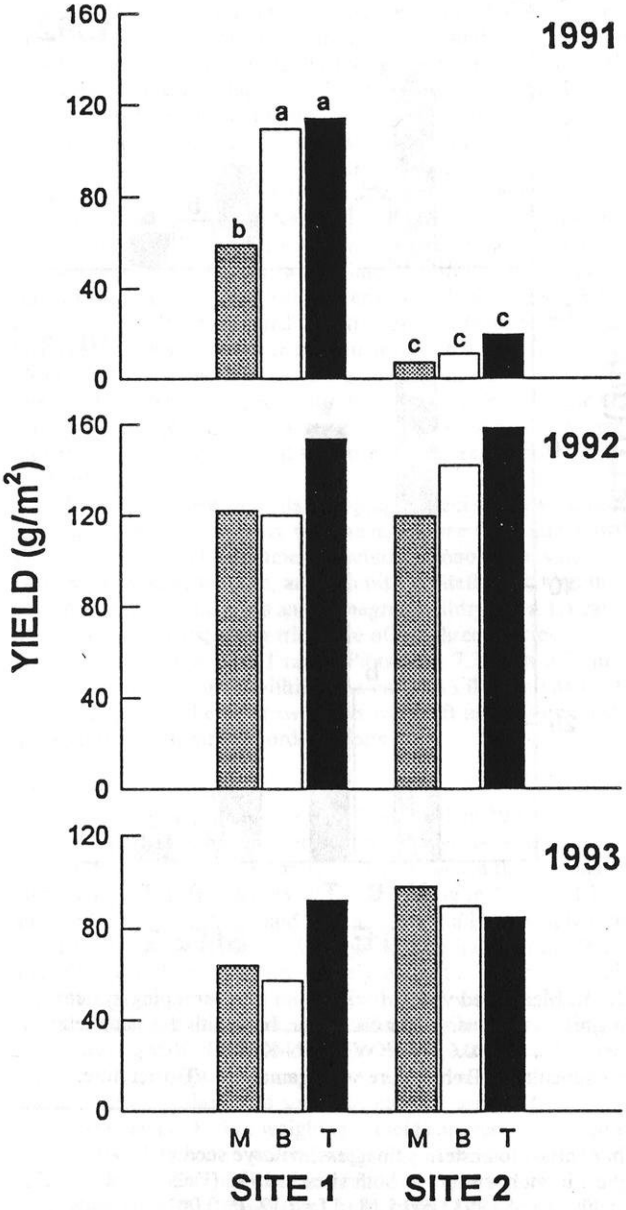

FIG. 4. Mean seed yield of Illinois bundleflower in three cropping systems at two sites over 3 years. For each year, bars with by the same letter do not differ at p<0.05 (ANOVA, S-N-K Test). Key as in Fig. 3.

In 1991, the dry establishment year, Illinois bundleflower yielded better in mixtures than monoculture at Site 1 (F=6.84, d.f.=2,12, P<0.05); no treatment effects occurred at Site 2 (Fig. 4). Overall, this species performed much better at Site 1 in 1991 (F=108.11, d.f.=1,12, P<0.0001). In 1992, bundleflower again generally yielded better in mixtures than in monoculture (F=4.80, d.f.=2,12, P<0.05). Site differences largely disappeared, however, suggesting that, when soil water is not limiting, this legume can compensate for low soil N without reducing seed yield. In 1993, bundleflower yield did not differ significantly among treatments or between sites. Bundleflower yield is relatively density-independent, so the species may be plastic enough to perform evenly with different-sized plants surrounding it (Collins 1986). Another observation is that some bundleflower plants at Site 1 had died or were very small, whereas the vigor of bundleflower plants at Site 2 was more even and survivorship was high. These observations have not been addressed formally, but seem to be site-dependent in some way. A root disease may be afflicting the poorly performing plants at Site 1. Initially, trends in size were similar to yield trends (site: F=42.68, d.f.=1,12, P<0.0001; treatment: F=5.61, d.f.=2,12, P<0.05), but treatment effects on size disappeared by 1992 (Fig. 5), partly because of large variability in size.

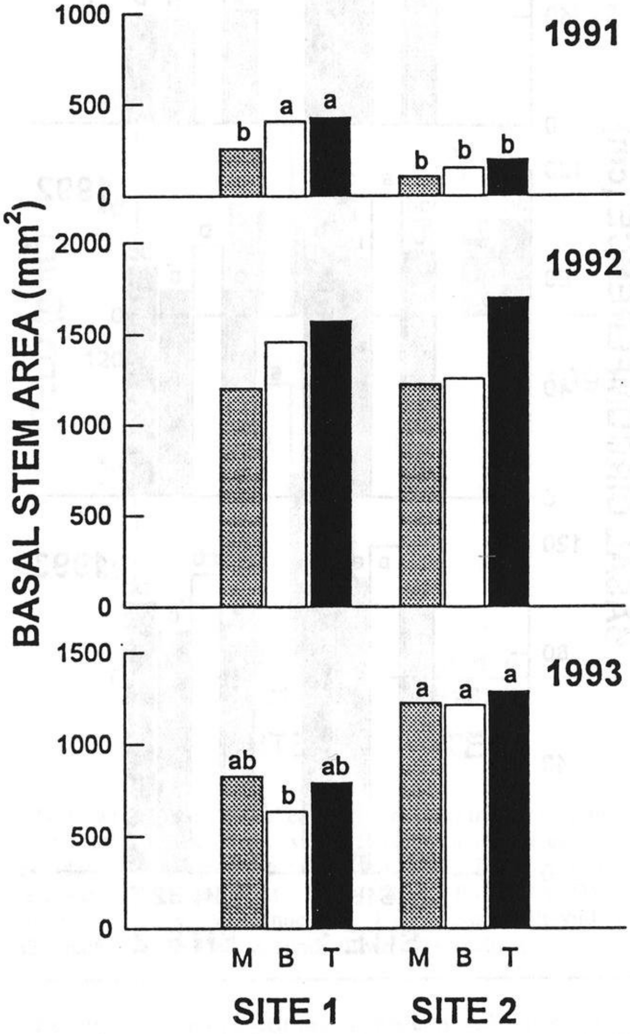

FIG. 5. Mean size, estimated as total basal stem area, of Illinois bundleflower in three cropping systems at two sites over 3 years. For each year, bars with the same letter do not differ at p<0.05 (ANOVA, S-N-K Test). Key as in Fig. 3.

Both grasses appeared to yield better in 1993 than in 1992. The plants may have responded positively to the very high precipitation in 1993 or may have simply yielded better as they grew larger. In contrast, bundleflower yields peaked in 1992.

Overyielding

Slight overyielding effects were observed in 1992 for the bicultures at both sites (Table 1). The tricultures did not overyield in 1992. In 1993, at Site 1, all mixtures overyielded. Unlike 1992, the triculture overyielded by 26%, and all three species yielded as well or better in this mixture than in their respective monocultures (i.e. RY≥0.33). Both bicultures also overyielded. In the bundleflower/gamagrass biculture, bundleflower yield was comparable between biculture and monoculture, whereas gamagrass showed higher yield in biculture than monoculture (RY=0.64). Gamagrass seemed to have some advantage in this mixture. This could have been due to lowered competition or possibly to lower nitrogen depletion of the plot because bundleflower can fix nitrogen. In the gamagrass/wildrye biculture, gamagrass contributed the majority of the yield (RY=0.92), whereas the wildrye RY was low (0.18). Overyielding patterns in this biculture reflect the advantage gamagrass gains from growing with wildrye and the suppression wildrye suffers from having gamagrass as a neighbor.

Table 1. Land Equivalent Ratios (LERs) for three cropping mixtures. An LER>1 indicates overyielding. In 1993, mammal predation of reproductive tillers prevented gamagrass seed harvest.

	1992		1993
Treatment	Site 1	Site 2	Site 1
Gamagrass/wildrye biculture	1.06	1.03	1.10
Gamagrass/bundleflower biculture	1.05	1.01	1.13
Triculture	0.78	0.91	1.26

Although LERs could not be calculated for Site 2 because the gamagrass was not harvested in 1993, RYs of bundleflower and wildrye were examined. Bundleflower RY did not differ among monoculture, biculture, or triculture treatments. Wildrye RYs were low for both the biculture (RY=0.11) and the triculture (RY=0.12). Wildrye yields were lower overall at Site 2, and wildrye also seemed to perform poorer in mixtures than monocultures than at Site 1. Although these data are not complete, overyielding advantages apparently were more pronounced at the more favorable site (Site 1) in 1993.

In future years of this study, overyielding may continue to improve, as has been observed in past studies of perennial mixtures (Braun 1985, Muto 1990). Perennials in mixtures also may display steady yields year-to-year. Overyielding in perennial mixtures over successive growing seasons has received little study, so forthcoming results should contribute much to our understanding of the long-term performance of perennial mixtures.

In conclusion, these perennials benefited from mixed planting arrangements. Gamagrass and bundleflower yield and grow better in mixture, and some mixtures overyielded. This study begins to show that the diverse nature of the prairie holds promise for a sustainable agriculture using perennials such as these to produce grain, while building the soil that sustains agriculture.

Literature Cited

Anderson, D. W. and D. C. Coleman. 1985. The dynamics of organic matter in grassland soils. Journal of Soil and Water Conservation 40:211-216.

Buyanovsky, G. A., C. L. Kucera and G. H. Wagner. 1987. Comparative analyses of carbon dynamics in native and cultivated ecosystems. Ecology 68:2023-2031.

Bee, J. W., G. Glass, R. S. Hoffman and R. R. Patterson. 1981. Mammals in Kansas. University of Kansas Press, Lawrence. 300 pp.

Braun, L. 1985. Overyielding in a perennial legume biculture. The Land Report Research Supplement 2:4-7.

Collins, M. 1986. *Desmanthus illinoensis* density trial. The Land Report Research Supplement 3:18-19.

Great Plains Flora Association. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence. 1392 pp.

Jackson, W. 1980. New Roots for Agriculture. University of Nebraska Press, Lincoln. 150 pp.

Jackson, W. and J. Piper. 1989. The necessary marriage between ecology and agriculture. Ecology 70:1591-1593.

Kulakow, P. A., L. L. Benson and J. G. Vail. 1990. Prospects for domesticating *Illinois bundle flower*. *In* J. Janick and J. E. Simon (eds.) Advances in New Crops. Timber Press, Portland, pp 168-171.

Mead, R. and R. W. Willey. 1980. The concept of a 'Land Equivalent Ratio' and advantages in yields from intercropping. Experimental Agriculture 16:217-228.

Muto, P. J. 1990. Evaluation of Illinois bundleflower and eastern gamagrass germplasm in monocultures and bicultures. The Land Institute Research Report 7:25-28.

Piper, J. K. 1993. A grain agriculture fashioned in nature's mage: the work of The Land Institute. Great Plains Research 3:249-72.

Piper, J. K., M. Mack and V. Wittig. 1991. Interactions within monocultures and mixtures of three perennials. The Land Institute Research Report 8:35-39.

Piper, J. K. and D. Towne. 1988. Multiple year patterns of seed yield in five herbaceous perennials. The Land Institute Research Report 5:14-18.

Soule, J. D. and J. K. Piper. 1992. Farming in Nature's Image. Island Press, Washington, DC. 286 pp.

Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58:3-15.

Vandermeer, J. 1989. The Ecology of Intercropping. Cambridge University Press, Cambridge. 237 pp.

The Prairie as a Model for the Sunshine Farm

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Abstract. During the past 15 years, agricultural research at The Land Institute has used nature as a standard. Because prairies are sustainable ecosystems, The Land Institute is using the prairie as a model for the Sunshine Farm. The main goal of the project is to conduct year-round accounting of energy, materials, and labor. The aims are to examine if the Sunshine Farm can provide its fuel and fertility and to determine how much industrial energy society must provide from sunlight to manufacture the farm facilities, equipment, and inputs. Prairies are characterized by species diversity, perennial plants, energy flows based on sunlight, and internal control of fertility and pest damage. Hence, the Sunshine Farm contains a diverse array of renewable energy technologies and innovative farming practices applied to conventional crops and animals. Import of nutrients is minimal, and some candidates from The Land Institute's perennial grain polyculture research are included.

Key words: energy integrated farm; sustainable agriculture; prairie ecosystem; community structure

Introduction

In our search for sustainability during the past 15 years, agricultural research at The Land Institute has used nature as a standard. Natural ecosystems such as the prairie can inform us how to develop sustainable agricultural systems that avoid the environmental problems now encountered by conventional agriculture. As fossil fuels are depleted, sustainable agriculture will require tighter nutrient cycles and energy flows driven by the sun, as in natural ecosystems (Crews *et al.* 1991). The structural pattern of prairie vegetation suggests that sustainable agriculture should include soil-conserving perennial plants and species diversity instead of annual monocultures.

The Land Institute has recently initiated a 10-year project, the Sunshine Farm, to establish a Great Plains farm that includes these features. The main goal is to explore options for reducing the dependence of modern agriculture on fossil fuels. A 1-year feasibility study was conducted to design the farm and to select renewable energy technologies and innovative farming practices (Bender and Craft 1992). The main research objective is year-round accounting of energy, materials, and labor in every task on the Sunshine Farm, which is accumulated in a computer database. Our aims are to examine to what extent a sustainable farm can provide its fuel and fertility and to determine how much industrial energy society must provide from sunlight to manufacture farm facilities, equipment, and inputs.

Another objective is component research to develop and integrate the renewable energy technologies and sustainable farming practices. This includes annual and seasonal assessments of soil quality based on chemical, physical, and biological soil properties. The component research is set up as guided, multi-year, intern experiments requiring graduate-level statistical analyses for eventual peer-reviewed publication. The components include several 5-year crop rotations, narrow strip cropping of annuals and perennials, soil quality, portable hen house and broiler pen, and short-duration cattle grazing.

Shifting Philosophies

The application of the concept of ecological sustainabilityinto agriculture requires a fundamental shift from the economic perspective that has guided scientific agriculture for the past 100 years or more. Economic efficiency has focused on maximum crop and animal yields, with the soil being a medium for conveying applied chemicals to crops. In contrast, if sustainability of the ecological resource base is the goal, then soil is regarded as the prime determinant of an agroecosystem's productivity and becomes the focus of research and stewardship (Doran *et al.* 1994). Under the goal of sustainability, higher priority would be placed on yield stability, environmental quality, and internal control of fertility and pest damage (Altieri 1987).

A long-term perspective and holism are central in the use of the prairie as a model for the Sunshine Farm. Studies of ecological systems generally require long time scales (Pimm 1991). Many changes in nature require decades to complete, such as recovery of prairie following drought. Because soil loss and pollution must accumulate a long time to affect yields appreciably, short-term economics are unlikely to address such ecological problems inherent in conventional farming (Faeth *et al.* 1991). Sustainable farming must preserve the land for many generations, rather than depleting it for some short-term profit.

Following the perspective of economic efficiency, scientific agriculture has used a reductionistic approach in studying agroecosystems by taking them apart and conducting short-term studies of cause-and-effect relationships; that is, by simplifying agroecosystems and ignoring many factors (Loomis and Connor 1992). In contrast, ecological systems contain complexity that includes interactions and boundaries between biological and physical components that can be very difficult to unravel (O'Neill *et al.* 1986). Thus, discovery of complex patterns requires an examination of the whole system, often on a long time frame. In other words, by looking for overall patterns that work, a holistic approach attempts to incorporate complex natural relationships into agriculture without first taking them apart and looking for causal relationships. In using the prairie as model for the Sunshine Farm, the reductionistic approach would not be abandoned but would be subservient to the holistic perspective.

Ecological Insights into Sustainability

To use prairie as a model, we must appreciate some important ways in which conventional agriculture differs from mature natural ecosystems in terms of sustainability. Conventional agroecosystems based on large monocultures of annual crops without livestock function as ecosystems arrested in early succession. Thus, they do not benefit from the many processes that stabilize and maintain mature ecosystems. As immature, frequently disturbed ecosystems, they do not display such natural features as efficient nutrient cycling, high species diversity, resistance to pest and disease outbreaks, and resilience to disturbance (Crossley *et al.* 1984). Immature ecosystems have low amounts of organic matter, small organisms with broad niches and short life cycles, open mineral cycles, an undeveloped detritus community, poor nutrient conservation, and linear food webs (Soule and Piper 1992). Frequent cultivation disrupts many members of the soil community, which are the foundation for healthy ecosystem function (Doran and Werner 1990).

Although natural ecosystems receive their energy from the sun, conventional agriculture is more productive than natural ecosystems because of inputs based on nonrenewable fossil fuels. On uplands, which constitute more than 85% of U.S. cropland, the annual, per-hectare, aboveground, net, primary production of conventional agriculture generally can be as high as 20-30 tonne, whereas that for native grassland ranges from 2.2 to 14 tonne (Mitchell 1984). [The productivity of naturally nutrient-subsidized lowland sites, such as marshes and floodplain forests, approaches that of conventional agriculture.] Progressively larger amounts of fossil fuel-based inputs have increased typical per-hectare corn production in the U.S. from 1.9 tonne in 1910 to 7.4 tonne in 1985 (Pimentel *et al.* 1990). However, because of the inputs, the energy ratio (usually defined as ratio of the gross energy content of the crop and/or animal products to the direct and indirect energy in the inputs, including the food/feed energy metabolized during human and draft animal labor) decreased from 5.8 to 2.9 during that time.

Much of this increase in productivity has required large nutrient inputs, because conventional agriculture simplifies agroecosystems and decouples many of the links between organisms, soil, and physical environment that serve to regulate energy and nutrient flow and accumulation in natural communities (Woodmansee 1984). First, in natural communities, remobilization and translocation of nutrients within perennial plants reduces yearly plant nutrient requirements from the soil and sequesters nutrients so that they are not lost via leaching or erosion. These properties and benefits are not as evident in conventional agriculture, which relies on annual crops that do not have perennial roots where nutrients can be tranlocated for winter storage and later release in spring.

Second, plant and microbial activities in natural ecosystems are synchronized so that, when water and temperature are favorable for biotic activity, perennial plants are ready to take up nutrients released by the microorganisms (Woodmansee 1984). In contrast, in cultivated systems, considerable periods exist during which plant growth conditions are favorable and microorganisms are active and mineralizing nutrients, but no crops are in the ground. This leaves the ecosystem vulnerable to loss of nutrients through leaching or erosion.

Third, plants in natural ecosystems have a variety of root structures and depths, which allows efficient exploitation of nutrients throughout an entire soil volume with different water regimes (Woodmansee 1984). In comparison, cultivated systems tend to have a single type of rooting system, usually shallow, that may not effectively remove nutrients from deeper depths, thus exposing them to loss by leaching.

Fourth, large nutrient inputs are required in conventional agroecosystems, because they lack the degree of nutrient cycling evident in mature ecosystems. Crucial minerals are conserved in mature ecosystems, so that outputs approximately equal inputs in a dynamic equilibrium or steady state. Although natural nutrient inputs and outputs are low (Waring and Schlesinger 1985, Clark *et al.* 1978, Duvigneaud and Denaeyer-De Smet 1975), the productivity of natural ecosystems is maintained, because most of the plant uptake of nutrients is offset by the return of detritus and leached nutrients (throughfall and stemflow) to the soil; in other words, nutrient cycling. For example, generally 70-90% of plant uptake of mineral elements is returned annually to the soil in deciduous and coniferous forests (Cole and Rapp 1981, Duvigneaud and Denaeyer-De Smet 1975, Harrison 1985, Waring and Schlesinger 1985) and in shrub ecosystems (Harrison 1985, Schlesinger 1991), with the remainder sequestered as wood. This ratio of return to uptake can approach 100% in grassland (Harrison 1985) and in herbaceous old fields (Stinner *et al.* 1984), because very little woody increment occurs in these ecosystems.

Return of nutrients from on-farm crops and pasture can occur via crop residues, use of manure, droppings on grazed areas, seed saved for sowing, and recycling of food wastes and human excrement. The ratios of nitrogen, phosphorus, and potassium return to plant uptake were computed from a large data set representing approximately 40 farms (Frissel 1978). Conventional agriculture based on large annual monocultures with or without return of crop residues had the lowest ratios, generally 20-60%.

The highest ratios were for farms that sold only livestock meat and/or dairy products. Whether the products came from pasture and/or crops with return of manure, the ratios were within those for mature forests and grasslands. This was true for intensive production systems (large inputs) as well as extensive ones (few or no inputs), because nutrients were recycled in the intensive systems (the ratio considers only nutrient transfers internal to the farm, not inputs and outputs). However, with regard to sustainability, the amount of inputs and outputs must be considered in addition to nutrient cycling. It is clear that the large nutrient requirements of intensive systems and concomitant nutrient losses such as volatilization, denitrification, and leaching are less sustainable than those for extensive systems.

The ratios for farms that sold both crop and livestock products, ranging from 40-90%, generally fell between those for conventional systems and those for livestock systems, as one would expect with recycled manure. This extensive system is one of the most prevalent on earth and often relies on transfer of nutrients from nonarable land to arable land or gardens (Frissel 1978). For example, in mixed crop/livestock farms of northwestern Europe, manure from sheep on clover pastures is gathered from stalls and applied to cropland. Also, a common practice on organic farms is to feed three-fourths of the crops by returning the manure (MacRae *et al.* 1990).

This comparison of conventional agriculture with mature ecosystems makes evident the ecological reasons for environmental problems of conventional agriculture and the need for an ecosystem perspective in moving toward a sustainable agriculture. Natural mature ecosystems provide the best models for the structural patterns necessary to achieve the tight nutrient cycling and solar-driven energy flow that are crucial to agricultural sustainability. Natural communities have been tailored by climatic and evolutionary forces to accommodate local environments and to endure. Mature communities are shifting mosaics of differing vegetation mixes shaped by periodic, local, natural disturbances. These mosaics contribute to species diversity and resilience in ecosystems.

Nature as a Structural Model

The use of nature as a standard, model, or analogy for agriculture is a difficult notion to articulate. Nature's model can be regarded as a package of a natural ecosystem's vegetation structure and the stabilizing processes woven into it. If an ecosystem is not too fragile or too harsh for agriculture, then the ecosystem can be examined to understand what makes it work sustainably in its particular landscape.

The single problem/single solution approaches typical of agricultural science have been process-oriented. The process model usually involves transplanting one or a few ecological processes into an otherwise fairly conventional agriculture. Although narrow solutions solve some agricultural problems, they obscure other problems, including fundamental ones.

What is proposed here is the use of a mostly unexplored structural model. The structural approach is more holistic than the process model, because it imitates a working community, so that a multitude of beneficial ecological processes would be incorporated into agroecosystems. When the system is imitated, certain emergent properties that are expressed only at the ecosystem level can appear in agroecosystems. In this holistic approach, the aim is to mimic the general structure of a natural community, not to reproduce every detail. One can start with an initial structure and note the concomitant functional attributes. Then, this structure can be modified until other desired attributes are attained. It should not be necessary to know in great detail how each minute particular of the system works.

Simple successional crop systems that mimicked the physiognomic structure of successional tropical vegetation have been studied by various researchers. Hart (1980) measured only one functional attribute, weed suppression, whereas Ewel *et al.* (1981, 1991) and Berish and Ewel (1988) monitored soil fertility, seed bank, and soil CO_2 evolution. Nabhan *et al.* (1990) examined the structure of desert vegetation needed to raise chiltipene peppers (*Capsicum annum*) without the diseases they have in intensive monocultural production. The Land Institute has used the prairie as a structural model for the design of perennial grain polycultures (Soule and Piper 1992; Barker and Piper, this volume), including soil fertility (Piper 1993b), weeds (Piper 1993a), insect pests and plant pathogens (both in progress).

Various agroecosystems already exist that incorporate crops as structural mimics, and thereby functional analogs, of wild species in natural vegetative structure. Examples are the agriculture of the Kumeyaay and Papago Indians in southwestern North America, the shifting agriculture in tropical forests and of native Americans in eastern North America, and some agroforestry systems. These systems are associated with indigenous agriculture, but some are being used in newly designed farming systems.

The Kumeyaay Indians once interplanted wild native species in many econiches, which gave a more stable food supply in the erratic California environment than the fluctuating yields from a few highly productive domesticates (Shipek 1989). They planted trees (*Prosopis* spp., *Quercus* spp.); shrubs (*Prunus* spp., *Arctostaphylos* spp., *Ceanothus* spp.); and various herbaceous species (*Artemisia* spp., *Salvia* spp., *Opuntia* spp.) in econiches ranging from coastal ecosystems eastward across mountains to desert valleys. As an analogy of arroyo vegetation in the Sonoran desert, the Papago practiced runoff farming with domesticates, semidomesticates, and wild species, which evolved or were selected to grow quickly, root deeply, and disperse heat loads (Nabhan 1979, 1984). Semi-domesticates and wild species included devil's claw (*Proboscidea parviflora*), coyote melon (*Cucurbita digitata*), mesquite (*Prosopis velutina*), mescal (*Agave palmeri*), and amaranth greens (*Amaranthus palmeri*).

Shifting agriculture was a common practice in late prehistoric, eastern North America (Ford 1985) and currently is used in the tropics (Dommen 1988). The timing of slash and burn mimics the temporal pattern evident in the shifting mosaic structure of regional forest vegetation. That is, trees are girdled and eventually burned, with the ashes scattered amongst hoe-cultivated annual and perennial domesticates, for less than a decade. This is followed by a fallow period of one or more decades, during which the land is allowed to revert to forest as a way of accumulating nutrients in the woody vegetation, which are released upon the next slash and burn. Agroforestry systems based on shifting agriculture include tropical home gardens (Gliessman 1990) and systems in which desired tree species are planted during fallow periods, sometimes including livestock grazing (Dover and Talbot 1987).

Agroforestry systems that are more permanent than shifting agriculture include silvopastoral systems and alley farming. An example of ecologically beneficial alley farming in western Australia is rows of trees (*Chamaecytisus palmensis*, *Eucalyptus* spp., *Pinus radiata*, *Acacia saligna*) with crops and pasture in between (Francis 1992). These trees perform the same function that the original bush vegetation did, which is to draw down the water table to reduce surface waterlogging and salinity that hinders crops. Similar to alley farming are the tropical coffee (*Coffea arabica*) and cacao (*Theobroma cacao*) plantations with herbaceous crop understories such as maize or cowpeas (Beer 1988). These leguminous trees fix nitrogen, reduce nutrient leaching, and extract nutrients from deep soil.

Energy ratios have been determined for various shifting agricultural systems, but not within North America, because very few of these systems remain as a result of the conquest and settlement by Europeans and their descendants. For such tropical systems, ratios range roughly from 10 to 40 (Cox and Atkins 1979), which are much greater than the ratios cited above for U.S. corn production during this century. These ratios are large because of the small inputs, mainly food energy metabolized during human labor and energy required to manufacture axes and hoes.

Prairie as Model for Sunshine Farm

The remnants of intact prairie in North America can serve as a model for sustainable agriculture in the Great Plains. Prairie plants have adapted successfully to fluctuating climate, grazing, and frequent fires on the Great Plains. Moreover, because humans are primarily grass-seed eaters, and secondarily, legume-seed eaters, it is most useful to look to prairie with dominant grasses as the model for a sustainable grain agriculture.

The prairie has many structural features for enduring in a region of climatic extremes. An important one is a diversity of species with a variety of strategies for coping with environmental changes, which provides resilience in prairies. For example, some species are adapted to endure climatic extremes, such as grasses with warm-season C_4 photosynthesis and drought-hardy forbs, whereas others avoid summer drought, such as grasses and forbs with cool-season C_3 photosynthesis (Martin *et al.* 1991). Prairie species also differ in their root systems, such as tap-rooted forbs and C_4 grasses with coarse roots compared to C_3 grasses with fine roots. Moreover, species with thick or coarse roots are dependent upon mycorrhizae for efficient nutrient uptake, whereas cool-season species with fine roots are not mycorrhizal because fungi are less metabolically active during spring and fall (Hetrick *et al.* 1988).

Internal control of fertility is another sustainable feature of the prairie. Tight nutrient cycling is a result of nutrients being tied up in living biomass and soil organic matter, so that they are not vulnerable to leaching or erosion loss. Perennial plants and litter also provide a cover that protects the soil. For example, on grazed western grasslands in the U.S. International Biological Program, total annual losses of nitrogen through natural processes and harvested beef were 2 g/m^2 or less (Woodmansee 1978). In contrast, standing crops of nitrogen were roughly 20-35 g/m^2 in plants, less than 3 g/m^2 in vertebrates and invertebrates, 3-10 g/m^2 in microorganisms, and 300-1200 g/m^2 in soil organic matter (Coupland and Van Dyne 1979, Woodmansee *et al.* 1981, Risser and Parton 1982).

The prairie is characterized by tightly coupled plant and animal interactions, which provide internal control of fertility and pest damage. Belowground/aboveground relationships are coupled by activities of herbivores and the decomposer community. For example, intermediate levels of grazing by ungulates can increase the degree of root turnover, thereby increasing the densities of root-feeding arthropods (Seastedt *et al.* 1988). In turn, this can raise rates of nutrient cycling.

These functional attributes make the prairie an appropriate structural model for the Sunshine Farm, in terms of achieving tight nutrient cycling and solar-driven energy flows. This research farm consists of 20 ha of crops and 40 ha of pasture, mostly native grasses. This farm is intended to be representative of Great Plains agriculture by using mostly conventional crops and animals but raised by innovative practices.

In the feasibility study, determination of the acreage for each crop was based on requirements for animal feed, oilseeds for oil as tractor fuel, and approximate crop demand for nitrogen from symbiotic fixation in legumes. Oilseeds and forage legumes for nitrogen each require roughly one-fourth of the crop acreage, with feed grains on the remaining half. To mimic the species diversity of the prairie, these requirements are provided by a mix of two 5-year crop rotations: 1) grain sorghum, soybeans, oats or wheat, sunflowers, and sweetclover green manure, and 2) grain sorghum, soybeans, oats or wheat, alfalfa, and alfalfa again. The crops are in 120 4-meter-wide strips (four rows) that progress through the rotations and provide edges between crops that should lead to higher yields as a result of polyculture effects. The strip-cropping and rotation, which mimic the spatial and temporal diversity of the prairie, should help control pests and plant pathogens, because no pesticides are used on the Sunshine Farm.

As in the prairie, perennial crops and crop residues will provide a cover that protects the soil. The perennials are alfalfa and some of the candidates from the perennial polyculture research at The Land Institute (Soule and Piper 1992). Eastern gama grass (*Tripsacum dactyloides*), Illinois bundleflower (*Desmanthus illinoensis*), and mammoth wild rye (*Leymus racemosus*) currently are being grown in one of the Sunshine Farm strips to determine if the perennial candidates can be strip-cropped with annual crops.

Eventually, with the practice of ridge-till on the Sunshine Farm, crop residues will be retained on the soil surface through the winter and incorporated into the soil during planting to reduce soil erosion and runoff (Thompson *et al.* 1994). This is a recent form of conservation tillage that allows weed control by cultivation that is as efficient as ridge-till with herbicides (Thompson *et al.* 1990, Jurik 1993). However, it is known that ridge-till causes vertical stratification of phosphorus and potassium in the soil (Robbins and Voss 1991). Because of this positional unavailability of nutrients, more research will be needed to determine if ridge-till will be an appropriate method for organic crop production, including farms with little or no nutrient import.

To provide species diversity in animals, there are 50 Rhode Island Red layer hens and 75 Cornish Cross broilers, both in portable shelters, and 9 Texas Longhorn cows with rented bull for a cow-calf herd in a rotational grazing system. In regard to the concept of farm enterprises requiring low inputs, longhorns are the most appropriate domestic beef cattle for the Great Plains, because they have been in this region for 5 centuries. The pasture fence has been built to accommodate bison, but an eventual switch to bison will require strong handling facilities for vaccination, isolation of sick animals, and relocation of bison prior to burning of pasture. We decided against pastured hog production to avoid problems with residential neighbors.

Just as the prairie is powered by the sun, some renewableenergy technologies are being used to run the Sunshine Farm on sunlight. For acceptance in the feasibility study of this farm, each technology had to: 1) have a positive energy balance to be renewable; 2) show promise of eventually being developed into a reliable source; and 3) be developed on the farm or at a farmers' cooperative to retain money within the local economy (Bender and Craft 1992). Note that the third criterion applies to fuel sources, not devices in which the fuels would be used. This is because these devices require various metallic ores for which geologic deposits of sufficient grade and quantity are limited in geographic distribution (Cameron 1986). Thus, commercial-scale mining and processing of ores are required at limited locations to produce enough supplies for national demand.

The renewable sources for traction are draft horses and a tractor operating on biodiesel (chemically processed vegetable oil). This mix of traction is used rather than draft horses alone because timeliness is important in field operations, especially regarding small farm families, which is why labor is part of the detailed accounting on this farm. We are recording the fossil fuels consumed on the Sunshine Farm with the assumption that these would be replaced by renewable energy technologies in a post-fossil-fuel era. Although the tractor will be operated on purchased biodiesel, we will continue to used gasoline in the trucks on this farm.

In the future, guaranteed-quality biodiesel would be produced more economically with a more positive energy balance by farmers' cooperatives than on-farm (Gavett and Van Dyne 1992). Nevertheless, we will attempt on-farm production with an oilseed press and may investigate small-scale chemical processing of the oil into biodiesel (Peterson *et al.* 1994).

Draft horses have an advantage over tractors in that they can consume a wide variety of feeds on a diversified farm, whereas the few fuel crops for a tractor could be vulnerable to drought or pest losses. If pasture area is not counted, given that most farms have land that cannot be cropped but can be used for horse pasture, detailed calculations based on numerous early bulletins from the U.S. Department of Agriculture and state agricultural experiment stations show that draft horses require no more cropland for feed than tractors do for biodiesel on a net energy basis (Bender and Craft 1992).

Electricity for workshop tools, water pumping, fence chargers, and grain drying are being provided by a 12x38-foot, 4.5-kilowatt, photovoltaic array. This system is connected to the utility grid, because there may be times of the year when the power load is greater than what is produced. The future dependence of sunlight-powered farms on fuel cooperatives and utility grids demonstrates that renewable energy technologies are not for self-sufficiency but for reducing the use of fossil fuels.

Nutrient and Energy Aspects of the Sunshine Farm

Analogous to grazing in prairies, nutrient recycling on the Sunshine Farm is achieved by returning manure from the feeding of on-farm grain sorghum, oats, alfalfa, and eventually soybean and sunflower meal cakes left over from the oilseed press. Although this conserves nutrients by reducing the amount sold off the farm, it does not replace the nutrients that are sold.

There are various ways to replace nutrients sold from the farm. Current organic farms are able to match average yields for conventional practices, if they replace many of the sold nutrients by on-farm transfer of nutrients from nonarable land to cropland (see above) or by import of commercial fertilizer, manure, feed, or other organic material, with the remaining sold nutrients compensated by processes discussed below for the Sunshine Farm. Although the former practice will be a common method of maintaining productivity in a post-fossil fuel era, it is not energetically efficient for the Sunshine Farm, because the pasture is 2.5 km from the cropland. This illustrates the importance of land ownership conforming to landscape in terms of efficient transfer of nutrients. The latter practice is not being used, with the exception of a small amount of animal feed, because the Sunshine Farm is being modeled after the prairie, which has small nutrient inputs. Moreover, this will be the case for many farms in a post-fossil-fuel era, because conservation of nutrients on farms will make it more difficult to find external sources of nutrients such as manure and straw.

A third practice that was prevalent in traditional Asian agriculture is recycling human wastes (King 1911). However, efficient recycling of wastes will require very long-term societal change to achieve decentralization of populations and appropriate management of human sewage and food processing wastes.

Because manure is returned on the Sunshine Farm, the amount of nutrients sold through crop and animals products is low enough that crop yields during the decade should remain near county averages, even though the above three practices are not used. Beyond this decade, nitrogen (N) would not be the limiting major nutrient because the N sold off the farm is replaced mainly by symbiotic fixation in the legumes (alfalfa, sweetclover, and soybeans). Studies of total ^{15}N recovery (crops and soils) indicate that, over periods of several years, similar amounts of legume N and fertilizer N are lost to the environment, contrary to the common belief that the former is less susceptible to losses than the latter (Harris *et al.* 1994). However, compared to fertilizer N, legume N contributes more to long-term soil fertility through buildup of organic N reserves (Harris *et al.* 1994). Research has shown that microbial populations in legume-based systems are larger (Harris *et al.* 1994), which has been suggested to lead to greater soil N-supplying capacities that can compensate for lower use efficiency of legume N by crops (Bolton *et al.* 1985).

Supplying N through legumes can require an amount of energy that is less or not much more than the indirect energy in N fertilizer. A total of 5,810 MJ (149 liters of diesel) are used to plow, plant, mow, and plow-under 1 hectare of sweetclover providing 168 kg N, whereas 7,042 MJ are required to manufacture fertilizer supplying 140 kg N/ha (Pimentel *et al.* 1983). Foregoing a cut of alfalfa and plowing it down as green manure can provide a net surplus of 53 kg N/ha (Heichel and Barnes 1984), although some believe that this surplus could be greater (Voss and Shrader 1984). The energy cost for providing this N would be the energy needed to replace the cut that was foregone. As one of three or four cuts, this would represent that fraction of the annual energy inputs for alfalfa, or slightly more than 3,000 MJ/ha, or 57 MJ/kg of N, which makes it slightly more energy-intensive than the fertilizer mentioned above (Pimentel and Pimentel 1979, Heichel and Martin 1980).

With N provided by legumes, the sold phosphorus (P) and potassium (K) must be offset by inputs through weathering of soil parent material and through dry and wet deposition, which sum to roughly 5.6 kg/ha (5 lbs/acre) or more for each nutrient (Likens *et al.* 1967, Likens *et al.* 1977, Cole and Rapp 1981, Papendick and Elliott 1984, Waring and Schlesinger 1985, Granstedt 1991). The use of deep-rooted crops, such as alfalfa and sweetclover, reduces nutrient leaching so that these inputs end up in crops.

In the case of the Sunshine Farm, K is the limiting nutrient because the forage crops and oilseeds, constituting half the crop acreage, have a much greater content of K than P (Crampton and Harris 1969). This is reflected in the sold P and K. If the K content of each crop is weighted by the respective fraction of total crop yield for each crop and by the fraction of crop K retained in sold crop and/or animal products for each crop, then the 5.6 kg K or more per hectare of cropland will support grain yields of at least 2020 kg/ha (30 bu/acre).

The calculations for this yield assume that all the forage crops and meal from the oilseeds and half the feed grains are fed to the animals on the Sunshine Farm, with the remaining half of the feed grains sold off the farm. This represents the common organic practice of selling only one-fourth of the crops and feeding the remainder on-farm (MacRae *et al.* 1990). They are also based on the fact that an average 15% of the K in animal feed is retained in livestock, with the remainder in manure, as reported in a review of 12 livestock systems by Salter and Schollenberger (1939). Moreover, if the manure is kept in a covered shed, additional losses of P and K are negligible (Aldrich 1980, p. 58).

Because the projected yield is only 15% less than average wheat yields in Kansas (U.S. Department of Agriculture 1991), long-term crop yields on the Sunshine Farm should remain respectable. This calculation also was confirmed by a careful review of long-term cropping experiments with no nutrient imports, in which modern grain yields were roughly 1685 kg/ha (25 bu/acre) in semi-arid regions and 2350 kg/ha (35 bu/acre) in humid areas (Bender 1993).

On the Sunshine Farm, detailed accounting is being done on the direct and indirect energy, materials, and human labor in every farm transaction, including construction, town trips, field operations, animal care, and farm planning. The indirect energy to mine, process, and fabricate an input is estimated from the product of its weight and an energy conversion factor selected from the literature. For each raw material recycled in society, the energy conversion factor is prorated for a mix of virgin and recycled materials according to: 1) the estimated recycled portion of that material in a solar future; 2) the reduced energy to reuse recycled materials; and 3) the increased energy to mine lower grades of metal ores or materials. Much literature is available on the former two considerations, and the latter was based mainly on Goeller and Weinberg (1976).

Although the energy analysis of the first 2 years of the Sunshine Farm is still in the preliminary stage, other studies provide some information on the energetics of recent low-input agriculture. A comparison of Amish and English farms in three states found that the former had higher energy ratios, 0.9-1.6, than the latter, 0.3-0.7 (Johnson *et al.* 1977). A case study in North Dakota found that crop yields per unit of energy consumed on sustainable farms were nearly double those on conventional farms (Northwest Area Foundation 1994). The energy ratio for a ridge-till system with manure, cover crop, and crop rotation was 7.0, whereas those for conventional tillage and no-till were 3.3 and 3.6, respectively (Pimentel 1989).

Implications for Sustainable Agriculture

The Sunshine Farm Project will determine a more accurate ecological cost for our food, which is currently the product of a national policy of cheap food and fuel. Because the current economic system does not reflect the ecological costs that will be important in a post-fossil-fuel era, the present profitability of the Sunshine Farm is not pertinent. Expenses and income are parts of the detailed accounting, but analysis of the economics will be left to other researchers. Energetics is the most important factor in this project.

By the end of 10 years, an accumulated database and analyses will be available for the Sunshine Farm, which would be included in a book on sunlight-powered agriculture to raise the questions and issues that will need to be addressed by farmers, researchers, and society. Exploration of these problems will lead to much more effective national policies on directing the transition to an agriculture based on renewable energy technologies, sustainable practices, and an enduring soil.

Literature Cited

Aldrich, S. 1980. Nitrogen: In Relation to Food, Environment, and Energy. Illinois Agricultural Experiment Station Special Publication No. 61. Champaign-Urbana.Altieri, M.A. 1987. Agroecology: The Scientific Basis of Alternative Agriculture. Westview Press, Boulder, CO. 227 pp.

Barker, A.A. and J.K. Piper. 1995. Growth and seed yield of three grassland perennials in monocultures and mixtures. Proceedings of the Fourteenth North American Prairie Conference, Prairie Diversity: from Molecule to Landscapes, from the Past to the Future. Kansas State University. pp. ___-___.

Beer, J. 1988. Litter production and nutrient cycling in coffee (*Coffea arabica*) and cacao (*Theobroma cacao*) plantations with shade trees. Agroforestry Systems 7:103-114.

Bender, M. 1993. Agricultural productivity in a post-fossil fuel era. Land Report No. 47:11-16.

Bender, M. and J. Craft. 1992. Sunshine Farm Feasibility Study. The Land Institute, Salina, Kansas. 121 pp.

Berish, C.W. and J.J. Ewel. 1988. Root development in simple and complex tropical successional ecosystems. Plant and Soil 106:73-84.

Bolton, H., Jr., L.F. Elliot, R.I. Papendick and D.F. Bezdicek. 1985. Soil microbial biomass and selected soil enzyme activities: Effect of fertilization and cropping practices. Soil Biology and Biochemistry 17:297-302.

Cameron, E.N. 1986. At the Crossroads: The Mineral Problem of the United States. John Wiley, New York.

Clark, F.E., C.V. Cole and R.A. Brown. 1978. Nutrient cycling. In A.I. Breymeyer and G.M. Van Dyne (eds.). Grasslands, Systems Analysis, and Man. Cambridge University Press, New York, pp 659-712.

Cole, D.W. and M. Rapp. 1981. Elemental cyling in forest ecosystems. In D.E. Reichle (ed.). Dynamic Properties of Forest Ecosystems. Cambridge University Press, New York, pp 341-409.

Coupland, R.T. and G.M. Van Dyne. 1979. Systems synthesis. In R.T. Coupland (ed.). Grassland Ecosystems of the World: Analysis of Grasslands and their Uses. Cambridge University Press, Cambridge, U.K., pp 97-106.

Cox, G.W. and M.D. Atkins. 1979. Agricultural Ecology: An Analysis of World Food Production Systems. W.H. Freeman, San Francisco. 721 pp.

Crampton, E.W. and L.E. Harris. 1969. Applied Animal Nutrition, 2nd edition. W.H. Freeman, San Francisco. 753 pp.

Crews, T.E., C.L. Mohler and A.G. Power. 1991. Energetics and ecosystem integrity: The defining principles of sustainable agriculture. American Journal of Alternative Agriculture 6:146-149.

Crossley Jr., D.A., G.J. House, R.M. Snider, R.J. Snider and B.J. Stinner. 1984. The positive interactions in agroecosystems. In R. Lowrance, B.J. Stinner and G.J. House (eds.). Agricultural Ecosystems: Unifying Concepts. John Wiley, New York, pp 73-81.

Dommen, A.J. 1988. Innovation in African Agriculture. Westview Press, Boulder, CO. 140 pp.

Doran, J.W., D.C. Coleman, D.F. Bezdicek and B.A. Stewart (eds.). 1994. Defining Soil Quality for a Sustainable Environment. SSSA Special Publication Number 35. Soil Science Society of America, Madison, WI. 244 pp.

Doran, J.W. and M.R. Werner. 1990. Management and soil biology. In C.A. Francis, C.B. Flora and L.D. King (eds.). Sustainable Agriculture in Temperate Zones. John Wiley, New York, pp 205-229.

Dover, M. and L.M. Talbot. 1987. To Feed the Earth: Agroecology for Sustainable Development. World Resources Institute, Washington, DC. 88 pp.

Duvigneaud, P. and S. Denaeyer-De Smet. 1975. Mineral cycling in terrestrial ecosystems. In: Productivity of World Ecosystems. Proceedings of symposium sponsored by U.S. National Committee for the International Biological Program, Seattle, WA. National Academy of Sciences, Washington, DC, pp 133-154.

Ewel, J., C. Berish, B. Brown, N. Price and J. Raich. 1981. Slash and burn impacts on a Costa Rican wet forest site. Ecology 62:816-829.

Ewel, J., M.J. Mazzarino and C.W. Berish. 1991. Tropical soil fertility changes under monocultures and successional communities of different structure. Ecological Applications 1:289-302.

Faeth, P., R. Repetto, K. Kroll, Q. Dai and G. Helmers. 1991. Paying the Farm Bill: U.S. Agricultural Policy and the Transition to Sustainable Agriculture. World Resources Institute, Washington, DC. 70 pp.

Ford, R. (ed.). 1985. Prehistoric Food Production in North America. University of Michigan, Museum of Anthropology Anthropological Papers 75, Ann Arbor.

Francis, Patrick. 1992. Alley farming challenge for sustainable cropping. Australian Farm Journal (October): 64-67.

Frissel, M.J. (ed.). 1978. Cycling of Mineral Nutrients in Agricultural Ecosystems. Elsevier Scientific Publishing, New York. 354 pp.

Gavett, E.E. and D.L. Van Dyne. 1992. The economic feasibility of biodiesel. 1992 ASAE International Summer Meeting, Charlotte, NC. Paper No. 926027. American Society of Agricultural Engineers, St. Joseph, MI.

Gliessman, S.R. 1990. Integrating trees into agriculture: The home garden agroecosystem as an example of agroforestry in the tropics. In S.R. Gliessman (ed.). Agroecology: Researching the Ecological Basis for Sustainable Agriculture. Springer-Verlag, New York, pp 160-168.

Goeller, H.E. and A.M. Weinberg. 1976. The age of substitutability. Science 191:683-689.

Granstedt, A. 1991. The potential for Swedish farms to eliminate use of artificial fertilizers. American Journal of Alternative Agriculture 6:122-131.

Harris, G.H., O.B. Hesterman, E.A. Paul, S.E. Peters and R.R. Janke. 1994. Fate of legume and fertilizer nitrogen-15 in a long-term cropping systems experiment. Agronomy Journal 86:910-915.

Harrison, A.F. 1985. Effects of environment and management on phosphorus cycling in terrestrial ecosystems. Journal of Environmental Management 20:163-179.

Hart, R.D. 1980. A natural ecosystem analog approach to the design of a successional crop system for tropical forest environments. Biotropica 12:73-82.

Heichel, G.H. and D.K. Barnes. 1984. Opportunities for meeting crop nitrogen needs for symbiotic nitrogen fixation. In D.F. Bezdicek and J.F. Power (eds.). Organic Farming: Current Technology and Its Role in a Sustainable Agriculture. American Society of Agronomy, Madison, WI, pp. 49-59.

Heichel, G.H. and N.P. Martin. 1980. Alfalfa. In D. Pimentel (ed.). Handbook of Energy Utilization in Agriculture. CRC Press, Boca Raton, FL, pp 155-161.

Hetrick, B.A.D., D.G. Kitt, and G.T. Wilson. 1988. Mycorrhizal dependence and growth habit of warm-season and cool-season tallgrass prairie plants. Canadian Journal of Botany 66:1376-1380.

Johnson, W.A., V. Stoltzfus and P. Craumer. 1977. Energy conservation in Amish agriculture. Science 198:373-378.

Jurik, T.W. 1993. Weed population dynamics in ridge-tilled soybeans with and without herbicides. In: Leopold Center Progress Report, Volume 2. Leopold Center for Sustainable Agriculture, Ames, IA, pp 41-44.

King, F.H. 1911. Farmers of Forty Centuries. Rodale Press, Emmaus, PA.

Likens, G.E., F.H. Bormann, R.S. Pierce, J.S. Eaton and N.M. Johnson. 1977. Biogeochemistry of a Forested Ecosystem. Springer-Verlag, New York.

Likens, G.E., F.H. Bormann, N.M. Johnson and R.S. Pierce. 1967. The calcium, magnesium, potassium, and sodium budgets for a small forested ecosystem. Ecology 48:772-785.

Loomis, R.S. and D.J. Connor. 1992. Crop Ecology: Productivity and Management in Agricultural Systems. Cambridge University Press, Cambridge, U.K. 538 pp.

MacRae, R.J., S.B. Hill, G.R. Mehuys and J. Henning. 1990. Farm-scale agronomic and economic conversion from conventional to sustainable agriculture. Advances in Agronomy 43:155-198.

Martin, C.E., F.S. Harris and F.J. Norman. 1991. Ecophysiological responses of C_3 forbs and C_4 grasses to drought and rain on a tallgrass prairie in northeastern Kansas. Botanical Gazette 152:257-262.

Mitchell, R. 1984. The ecological basis for comparative primary production. In R. Lowrance, B.R. Stinner and G.J. House (eds.). Agricultural Ecosystems: Unifying Concepts. John Wiley, New York, pp 13-53.

Nabhan, G.P. 1979. The ecology of floodwater farming in southwestern North America. Agro-Ecosystems 5:245-255.

Nabhan, G.P. 1984. Replenishing desert agriculture with native plants and their symbionts. In W. Jackson, W. Berry and B. Colman (eds.). Meeting the Expectations of the Land. North Point Press, San Francisco, pp 172-182.

Nabhan, G.P., M. Slater and L. Yarger. 1990. New crops for small farmers in marginal lands?: Wild chiles as a case study. In M. Altieri and S. Hecht (eds.). Agroecology and Small Farm Development. CRC Press, Sarasota, FL, pp 17-23.

Northwest Area Foundation. 1994. A Better Row to Hoe: The Economic, Environmental, and Social Impact of Sustainable Agriculture. Northwest Area Foundation, St. Paul, MN.

O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen. 1986. A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton. 253 pp.

Papendick, R.I. and L.F. Elliott. 1984. Tillage and cropping systems for erosion control and efficient nutrient utilization. Pp. 69-81 in: Organic Farming: Current Technology and Its Role in a Sustainable Agriculture. American Society of Agronomy, Madison, WI. 192 pp.

Peterson, C.L., D.L. Reece, B.J. Hammond, J. Thompson and S.M. Beck. 1994. Processing, characterization and performance of eight fuels from liquids. 1994 ASAE International Winter Meeting, Atlanta, GA. Paper No. 946531. American Society of Agricultural Engineers, St. Joseph, MI.

Pimentel, D. 1989. Agriculture and ecotechnology. In W.J. Mitsch and S.E. Jorgensen (eds.). Ecological Engineering: An Introduction to Ecotechnology. John Wiley, New York, pp 103-125.

Pimentel,D., G. Berardi and S. Fast. 1983. Energy efficiency of farming systems: Organic and conventional agriculture. Agriculture, Ecosystems and Environment 9:359-372.

Pimentel, D., W. Dazhong and M. Giampietro. 1990. Technological changes in energy use in U.S. agricultural production. In S.R. Gliessman (ed.). Agroecology: Researching the Ecological Basis for Sustainable Agriculture. Springer-Verlag, New York, pp 305-321.

Pimentel, D. and M. Pimentel. 1979. Food, Energy and Society. John Wiley, New York.

Pimm, S. L. 1991. The Balance of Nature?: Ecological Issues in the Conservation of Species and Communities. University of Chicago Press, Chicago, IL. 434 pp.

Piper, J.K. 1993a. Neighborhood effects on growth, seed yield, and weed biomass for three perennial grains in polyculture. Journal of Sustainable Agriculture 4(2):11-31.

Piper, J.K. 1993b. Soil water and nutrient change in stands of three perennial crops. Soil Science Society of America Journal 57:497-505.

Risser, P.G. and W.J. Parton. 1982. Ecosystem analysis of the tallgrass prairie: Nitrogen cycle. Ecology 63:1342-1351.

Robbins, S.G. and R.D. Voss. 1991. Phosphorus and potassium stratification in conservation tillage systems. Journal of Soil and Water Conservation 46:298-300.

Salter, R.M. and C.J. Schollenberger. 1939. Farm manure. Ohio Agricultural Experiment Station Bulletin No. 605. Wooster.

Schlesinger, W.H. 1991. Biogeochemistry: An Analysis of Global Change. Academic Press, New York.

Seastedt, T.R., R.A. Ramundo and D.C. Hayes. 1988. Maximization of densities of soil animals by foliage herbivory: Empirical evidence, graphical and conceptual models. Oikos 51:243-248.

Shipek, F.C. 1989. An example of intensive plant husbandry: The Kumeyaay of southern California. In D.R. Harris and G.C. Hillman (eds.). Foraging and Farming: The Evolution of Plant Exploitation. Unwin Hyman, London, pp 159-170.

Soule, J.D. and J.K. Piper. 1992. Farming in Nature's Image. Island Press, Washington, DC. 286 pp.

Stinner, B.J., D.A. Crossley Jr., E.P. Odum and R.L. Todd. 1984. Nutrient budgets and internal cycling of N, P, K, Ca and Mg in conventional tillage, no-tillage, and old-field ecosystems on the Georgia Piedmont. Ecology 65:354-369.

Thompson, R., S. Thompson and D. Exner. 1990. Case study: A resource-efficient farm with livestock. In C.A. Francis, C.B. Flora and L.D. King (eds.). Sustainable Agriculture in Temperate Zones. John Wiley, New York, pp 263-280.

Thompson, R., S. Thompson and R. Thompson. 1994. Thompson On-Farm Research with Wallace Institute, 1994 Report. Thompson On-Farm Research, Boone, IA.

U.S. Department of Agriculture. 1991. Agricultural Statistics. U.S. Government Printing Office, Washington, DC.

Voss, R.D. and W.D. Shrader. 1984. Rotation effects and legume sources of nitrogen for corn. In D.F. Bezdicek and J.F. Power (eds.). Organic Farming: Current Technology and Its Role in a Sustainable Agriculture. American Society of Agronomy, Madison, WI, pp 61-68.

Waring, R.H. and W.H. Schlesinger. 1985. Forest Ecosystems: Concepts and Management. Academic Press, New York. 325 pp.

Woodmansee, R.G. 1978. Additions and losses of nitrogen in grassland ecosystems. Bioscience 28:448-453.

Woodmansee, R.G. 1984. Comparative nutrient cycles of natural and agricultural ecosystems: A step toward principles. In R. Lowrance, B.R. Stinner and G.J. House (eds.). Agricultural Ecosystems: Unifying Concepts. John Wiley, New York, pp 145-156.

Woodmansee, R.G., I. Vallis and J.J. Mott. 1981. Grassland nitrogen. In F.E. Clark and T. Rosswall (eds.). Terrestrial Nitrogen Cycles. Ecological Bulletin, Stockholm. Vol 33, pp 443-462.

A New Look at Prairie Plant Germplasm

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Abstract. In 1988, data describing the prairie plant germplasm maintained by the U.S. National Plant Germplasm System (NPGS) were surveyed, and the results were reported to the Eleventh North American Prairie Conference. During the 6 years since that initial survey, the taxonomic database of the Germplasm Resources Information Network (GRIN), the primary database for the NPGS, has been improved substantially, and additional germplasm has been added to the NPGS and made available for distribution. Because of this progress, NPGS holdings were surveyed anew, and demand for these holdings also was examined. In 1988, 295 of 862 prairie taxa identified from a search of midwestern floras were included in the GRIN database. By 1994, this number had increased by 33% to 393. In 1988, only 146 of these taxa were actually maintained by NPGS, but now 184 taxa are maintained, with 92 currently available to researchers. All taxa held by NPGS that were not included in the initial survey report are listed along with addresses for maintenance sites. Trends in usage relative to other germplasm holdings also are discussed.

Key words: genetic resources, National Plant Germplasm System, seed sources, species introduction

Introduction

The Agricultural Research Service of the U.S. Department of Agriculture coordinates a national network for maintaining germplasm of agronomic and horticultural crop plants and their relatives. This network, 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 (White *et al.*, 1989). Samples of these collections are provided freely by the NPGS for scientific research. As a result, these germplasm collections are used widely in research by scientists worldwide.

Nevertheless, many workers studying prairies and other North American plant communities may be unaware of the NPGS and its resources. A survey of NPGS collections of prairie plant germplasm, conducted in 1988, was presented to the Eleventh North American Prairie Conference (Widrlechner, 1989) to publicize the availability of these collections. During the 6 years since that initial survey, the taxonomic database of the Germplasm Resources Information Network (GRIN), the primary database for the NPGS (Mowder and Stoner, 1989), has been expanded, and additional germplasm has been acquired and made available for distribution. This progress is documented by a new survey conducted with the GRIN database early in 1994, with the hope that this update will inform more potential users about prairie plant germplasm. This survey also examines demand for this germplasm by analyzing germplasm distributions for 1989-1993, to document recent levels of prairie plant germplasm utilization in comparison with overall germplasm demand.

Table 1. Taxa available for distribution in 1994 that were not listed as available by Widrlechner (1989).

Taxon[1]	Site[2]	Number available[3]
Allium cernuum	W-6	1
Amaranthus graecizans	NC-7	1
Asclepias syriaca	S-9	7
Astragalus nuttallianus	W-6	1
Bouteloua curtipendula	S-9	47
Bouteloua gracilis	S-9	2
Chamaecrista fasciculata	S-9	24
Chamaecrista nictitans	S-9	5
Elymus lanceolatus	W-6	17
Euphorbia marginata	NC-7	1
Helianthus occidentalis subsp. *plantagineus*	NC-7	8
Helianthus pauciflorus	NC-7	10
Hilaria *jamesii*	S-9	1
Indigofera miniata var. *leptosepala*	S-9	2
Ipomoea leptophylla	S-9	1
Koeleria macrantha	W-6	2
Lesquerella auriculata	W-6	1
Linum lewisii	NC-7	2
Lotus unifoliolatus	NC-7	2
Monarda fistulosa	NC-7	5
Pascopyrum smithii	W-6	19
Poa secunda	W-6	15
Prunus besseyi	CDAV	4
Prunus munsoniana	CDAV	1
Pseudoroegneria spicata	W-6	76
Pycnanthemum tenuifolium	CCOR	9
Pycnanthemum virginianum	CCOR	6
Ratibida columnifera	W-6	1
Rhus glabra	NC-7	10
Salvia azurea var. *grandiflora*	W-6	1
Schedonnardus paniculatus	NC-7	1
Sporobolus airoides	W-6	1
Stachys tenuifolia	NC-7	1
Strophostyles leiosperma	S-9	2
Verbena halei	NC-7	1

[1] Taxonomy follows GRIN database.
[2] For explanation of site abbreviations see Table 2.
[3] Accessions of U.S. or Canadian origin.

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Methods

The master list of 862 prairie taxa from the 1988 survey (Widrlechner, 1989) was rechecked against the taxonomy records of the GRIN database in early 1994. Taxa included in GRIN were then checked for accession, inventory, and order records. The accessions' availability and origins were noted, as well as the locations of the NPGS sites maintaining these accessions.

Order records for 1989-1993 from the GRIN database were reviewed for all available accessions. Those orders representing distributions to requestors for evaluation, plant breeding, or other research applications (as opposed to internal orders related to managerial activity) then were tabulated by accession, taxon, and supply site.

Results and Discussion

Of the 862 prairie taxa from the master list, 393 were included in the GRIN database, an increase of 33% over the 295 taxa noted in 1988 (Widrlechner, 1989). Of the 393 taxa included in the new survey, 351 were listed as valid names, whereas the other 42 were listed in taxonomic synonomy. Although this increase reflects substantial additions to the database during the last 6 years, the continued omission of over 450 prairie taxa probably reflects a bias in the NPGS towards crop plants and closely related species.

The 351 valid taxa, plus the names for the 42 synonyms in GRIN, were checked against pertinent accession and inventory records to identify accessions maintained by, and available from, the NPGS. In 1988, only 146 taxa with populations of U.S. or Canadian origin were represented in the GRIN database (Widrlechner, 1989). By 1994, this number had increased by 26% to 184 taxa. Of these, 931 accessions representing 92 of 184 taxa were noted as available for distribution.

Table 2. Addresses for NPGS sites with prairie plant germplasm.

Plant Introduction Stations:
NC-7 - North Central Regional Plant Introduction Station
Iowa State University
Ames, IA 50011
NE-9 - Northeastern Regional Plant Introduction Station
New York State Agricultural Experiment Station
Geneva, NY 14456
S-9 - Southern Regional Plant Introduction Station
1109 Experiment
Griffin, GA 30223-1797
W-6 - Western Regional Plant Introduction Station
Washington State University
59 Johnson Hall
Pullman, WA 99164-6402

Clonal Germplasm Repositories:
CCOR - National Clonal Germplasm Repository
33447 SE Peoria Road
Corvallis, OR 97333
CDAV - National Clonal Germplasm Repository
University of California - Davis
Davis, CA 95616

Other Sites:
NSGC - National Small Grains Collection
P.O. Box 307
Aberdeen, ID 83210
NSSL - National Seed Storage Laboratory
1111 South Mason Street
Fort Collins, CO 80521-4500

Table 1 lists those taxa currently available for distribution that were unavailable in the initial survey (Widrlechner, 1989) and includes the number of available accessions and the site from which they can be obtained. (Addresses for these sites are listed in Table 2.) Of the 35 taxa listed in Table 1, 17 are new to this survey, 13 were reported as unavailable by Widrlechner (1989), and five reflect changes in taxonomic treatment. Nearly half of the taxa and over 75% of the accessions in Table 1 are grasses or legumes.

Table 3 presents other taxa being maintained but not now available for distribution, which were not listed previously (Widrlechner, 1989). Seven of 10 taxa from Table 3, held by the National Seed Storage Laboratory (NSSL), result from a cooperative project between NSSL and the Center for Plant Conservation, a consortium of U.S. botanical gardens (Thibodeau and Falk, 1984). The NSSL provides long-term seed storage for rare and endangered plants curated by the member institutions of the Center (McMahan and Falk, 1989).

Table 3. Additions to NPGS holdings, not available for distibution in 1994.

Taxon[1]	Site[2]
Agalinis auriculata	NSSL
Anemone canadensis	NC-7
Anemone riparia	NC-7
Artemisia ludoviciana	W-6
Astragalus purshii	W-6
Baptisia bracteata var. *laevicaulis*	NC-7
Besseya bullii	NSSL
Carex lasiocarpa	W-6
Cerastium arvense	NSSL
Cirsium hillii	NSSL
Coreopsis grandiflora	NSSL
Cyperus esculentus	W-6
Desmodium canadense	S-9
Desmodium obtusum	S-9
Echinacea atrorubens	NC-7
Erysimum asperum	NC-7
Erysimum inconspicuum	NC-7
Helictotrichon hookeri	NSGC
Heliopsis helianthoides	NC-7
Ipomoea pandurata	S-9
Lespedeza leptostachya	NSSL
Oenothera caespitosa	NSSL
Oenothera triloba	NSSL
Pediomelum argophyllum	S-9
Potentilla norvegica	NC-7
Potentilla simplex	NC-7
Pulsatilla patens	NC-7
Silene regia	NSSL
Sphaeralcea coccinea	NC-7
Sporobolus asper	W-6
Symphoricarpos occidentalis	NC-7
Talinum rugospermum	NSSL
Thermopsis rhombifolia	W-6

[1] Taxonomy follows GRIN database.

[2] For explanation of site abbreviations see Table 2.

Samples of prairie plant germplasm were provided to requestors 1490 times from 1989 to 1993, making the mean distribution rate (**D**) for all available accessions 0.41 distributions accessions^{-1} year^{-1}. The mean, mode (0.0), and median (0.2) distribution rates seem low, partly as a consequence of 426 accessions not being distributed during this period. In contrast, the 505 accessions that were distributed represented 82 of 92 available taxa, and 9 accessions were highly requested (**D** > 2.0; Table 4).

Table 4. Highly requested prairie plant accessions.

Taxon	Accession number	**D**[1]
Allium cernuum	PI 372503	3.4
Amaranthus graecizans	PI 553079	4.2
Amelanchier alnifolia	PI 495876	2.8
Astragalus bisulcatus	PI 372510	2.8
Astragalus racemosus	PI 315671	3.0
Buchloe dactyloides	PI 476988	2.2
Helianthus pauciflorus	PI 435869	5.0
Helianthus pauciflorus	PI 451979	4.6
Lupinus argenteus	PI 477930	2.2

[1] Mean distribution rate (distributions accessions^{-1} year^{-1}).

These distribution rates can be compared to those based on broader samples of germplasm. Nearly all (1459) of the 1490 distributions were supplied by only four NPGS sites: CCOR, NC-7, S-9, and W-6 (see Table 2). A comparison of demand for prairie plant germplasm and for the entire holdings of those four NPGS sites in 1993 (Table 5) indicates that the distribution rate for prairie plant germplasm is within the range of rates reported for all types of germplasm provided by these four NPGS sites in 1993. The proportion of prairie plant accessions actually distributed may seem higher than that of the larger holdings, but proportions based on 1 year's data are not directly comparable to those collected over 5 years. *A priori*, one would expect the proportion distributed to increase over time, as requests for diverse accessions accumulate.

Table 5. Comparative demand for prairie plant and other germplasm.

Sample	Available accessions	Years	Proportion distributed	**D**[1]
Prairie Plants	931	5	0.54	0.41
Entire CCOR collection	6,874	1	0.17	0.23
Entire NC-7 collection	20,402	1	0.51	0.97
Entire S-9 collection	55,507	1	0.25	0.31
Entire W-6 collection	42,265	1	0.31	0.48

[1] Mean distribution rate (distributions accessions^{-1} year^{-1}).

As with distribution rates for individual accessions (Table 4), certain plant families and genera of NPGS prairie plant germplasm were in disproportionately high demand. Four families: grasses (Poaceae), legumes (Fabaceae), roses (Rosaceae), and composites (Asteraceae) represent 94% of all samples distributed. The other 6% included eight other families. Similarly, six genera: bush clovers (*Lespedeza*), bluegrasses (*Poa*), strawberries (*Fragaria*), sunflowers (*Helianthus*), lupines (*Lupinus*), and wheatgrasses (*Pseudoroegneria* or *Agropyron*) comprise just over half the samples distributed, with 41 other genera found in the remainder. The top six include two legume genera used for forage, conservation plantings, and grain (*Lupinus*); two forage grass genera; two species of *Fragaria* used to varying degrees in strawberry breeding (Hancock and Luby, 1993; Sjulin and Dale, 1987); and five species of *Helianthus*, wild relatives of domesticated sunflowers (Heiser, 1978).

Although comparatively little prairie plant germplasm is held by the NPGS, the number of accessions available for research is increasing. Demand for this germplasm is uneven, with most of the recent requests focusing on native forage legumes and grasses (which may be related to provisions of federal farm legislation) and on strawberries and sunflowers, both relatively important crops. This suggests that demand for prairie plant germplasm has been driven more by economic forces and crop improvement efforts than by possible germplasm needs of taxonomists, ecologists, and prairie researchers in general.

In the absence of coordinated projects to acquire taxa of prairie plants new to the NPGS, the curators of NPGS collections do analyze past demand and unmet requests and use such analyses to prioritize germplasm regeneration and new acquisitions. Informing curators at NPGS sites holding prairie plant germplasm about your research needs and about important germplasm collections held outside of the NPGS would help the system meet future demand. Opportunities also may exist for field researchers and land managers to cooperate with NPGS curators on projects that involve curators' expertise in *ex situ* conservation with the *in situ* preservation of prairie plants. Cooperative projects on the *in situ* preservation of cranberry (*Vaccinium*), and hickory and pecan (both *Carya*) are being developed between NPGS and the USDA Forest Service and the US National Park Service (Anonymous, 1994). A similar project for sunflower species native to prairies has been discussed, but not yet implemented, by the staff at NC-7. As a broader range of scientists who study prairie plants learns more about the NPGS, I very much welcome the personal contacts and establishment of cooperative research that can lead to even more extensive use of this prairie heritage.

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Literature Cited

Anonymous. 1994. Funding shortages dominate Crop Advisory Committee deliberations. Diversity 10(2): 44-45.

Hancock, J.F. and J.J. Luby. 1993. Genetic resources at our doorsteps: The wild strawberries. BioScience 43: 141-147.

Heiser, C.B., Jr. 1978. Taxonomy of *Helianthus* and origin of domesticated sunflower. *In* J.F. Carter (ed.) Sunflower Science and Technology. American Society of Agronomy, Madison, WI, pp 31-53.

McMahan, L.R. and D.A. Falk. 1989. The Center for Plant Conservation: Collaborating with the National Plant Germplasm System to save seeds for the future. Diversity 5(2/3): 43.

Mowder, J.D. and A.K. Stoner. 1989. Information systems. Plant Breeding Reviews 7: 57-65.

Sjulin, T.M. and A. Dale. 1987. Genetic diversity of North American strawberry cultivars. Journal of the American Society for Horticultural Science 112: 375-385.

Thibodeau, F. and D. Falk. 1984. The Center for Plant Conservation Development Plan. Center for Plant Conservation, Jamaica Plain, MA. 16 pp.

White, G.A., H.L. Shands, and G.R. Lovell. 1989. History and operation of the National Plant Germplasm System. Plant Breeding Reviews 7: 5-56.

Widrlechner, M.P. 1989. Germplasm Resources Information Network and *ex situ* conservation of germplasm. *In* T.B. Bragg and J. Stubbendieck (eds.) Proceedings of the Eleventh North American Prairie Conference. University of Nebraska, Lincoln, pp 109-114.

Evaluation of Leafhoppers and Their Relatives (*Insecta: Homoptera: Auchenorrhyncha*) as Indicators of Prairie Preserve Quality.

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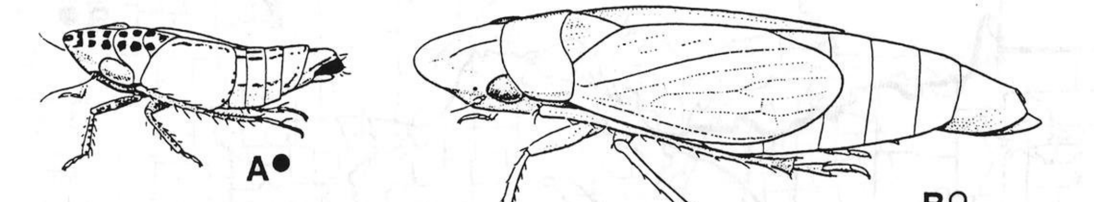
Abstract. Sampling insects in 100 northern "tallgrass" prairies and alvars yielded many Auchenorrhyncha that are unknown from other ecosystems. Those species hypothesized as endemic to prairies include 72 leafhoppers (Cicadellidae), 2 spittlebugs (Cercopidae) and 7 planthoppers (Caliscelidae) including 30 species recorded for the first time in Minnesota, 21 in Wisconsin, 14 in Manitoba, 3 each in North Dakota and Ontario, 2 in Illinois and 1 from Michigan. Spittlebugs are distributed on the prairies chiefly by habitat and apparently are affected little by prairie management practices. Their persistence in disturbed habitats makes them chiefly useful as markers of prehistorical prairie extent. The number of prairie-endemic species of leafhoppers and caliscelids can be used as a test for satisfactory faunal preservation within the study area. The presence of at least 4 of the 9 most common prairie-endemic species can provide a quick test. One-third of the "best" sites (with 9-24 prairie-endemic species) are managed only by haying and/or by infrequent use of fire. Full faunal regeneration after a fire takes at least 4 years.

Key words: Caliscelidae, Cercopidae, Cicadellidae, faunal diversity, fire management, leafhopper, planthopper, prairie, spittlebug

Introduction

Prairie preserve management strategies are based largely on easily observed effects. As a consequence, moths and butterflies are usually the only insect fauna that are considered when establishing prairie management practices. Thus, smaller prairie insects are little utilized and seldom sampled intensively.



FIGs. 1A-B. Cicadellid (leafhopper) specialists on prairie dropseed. A, *Aflexia rubranura*, male; B, *Memnonia* nr. *grandis* Shaw, female. Dots, *Aflexia* only; circles, *Memnonia* only; split circles, both species together; crosses, prairie dropseed common, but without either leafhopper species.

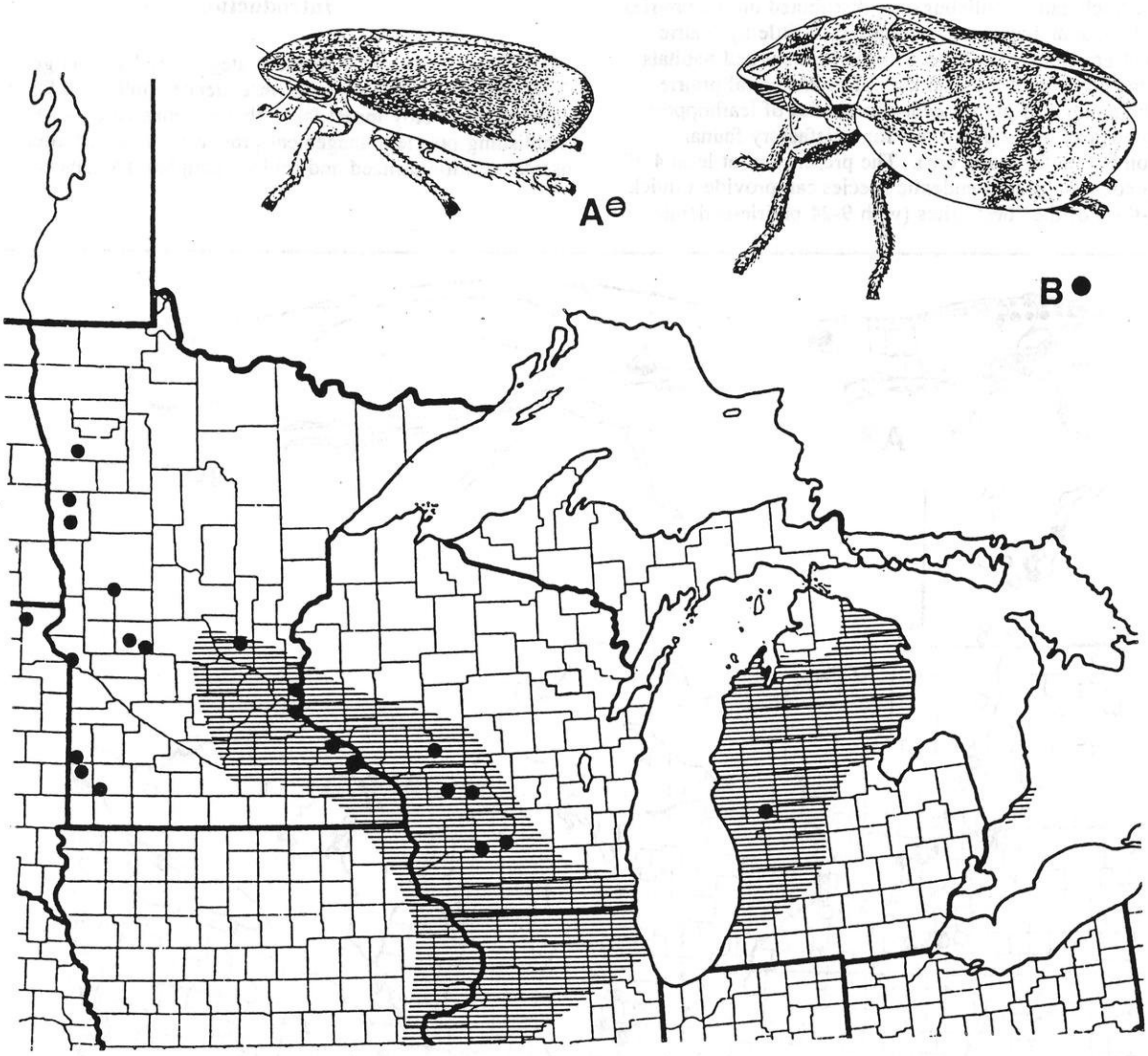
Here I report on leafhoppers (Fig. 1) and related "short-horned" bugs, the Auchenorrhyncha, of northern prairies. These are plant feeding insects of the suborder Homoptera with tiny, inconspicuous antennae. They are common in prairie situations. They include spittlebugs (Cercopoidea), cicadas (Cicadoidea), planthoppers (Fulgoroidea), and leafhoppers and treehoppers (Membracoidea). No prairie-endemic cicadas and treehoppers occur in the northeast, and most planthoppers show no such endemicity.

Although easily collected, Auchenorrhyncha are hardly ever reported from northern "tallgrass"[°] prairies (prairies east of 100°W and north of 41°N in Illinois, the vicinity of Chicago, to 43°N in South Dakota, the vicinity of Sioux Falls). Most published reports from this area are of a single prairie-endemic species per site, with the exception of Little Rock, Iowa in the southwest corner of this area (43°N 96°W), and around Chicago (DeLong 1948) and adjacent Indiana (Panzer *et al.* in press) where leafhoppers have been collected intensively.

Unreported material in collections are equally sparse. Only 1 hillside at Arena, Wisconsin (sampled in 1965 by Stannard and Smith of the Illinois Natural History Survey) yielded specimens of more than 1 prairie-endemic species. There were 3 species, each representing a different family: *Philaenarcys killa* (Cercopidae), *Bruchomorpha dorsata* (Caliscelidae), and *Laevicephalus vannus* (Cicadellidae). These 3 families are the subject of this study.

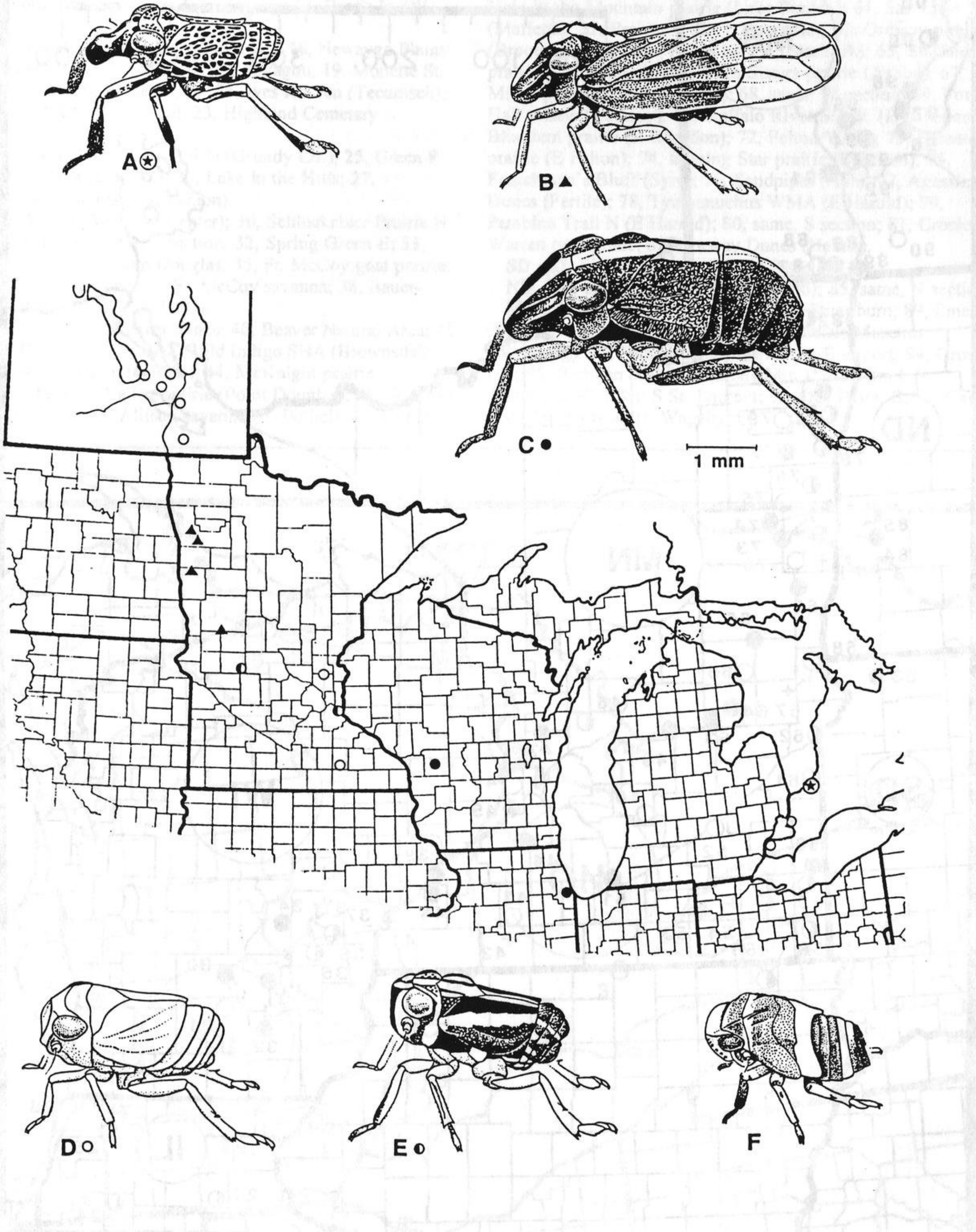
Cercopoidea: Cercopidae

Spittlebugs or froghoppers (Figs. 2 A-B) include about 50 North American species (Hamilton 1982) of which 19 occur in Michigan (Hanna and Moore 1966). These include 4 species in northern prairies, of which 3 feed on grasses; 2 appear to be prairie-endemic.

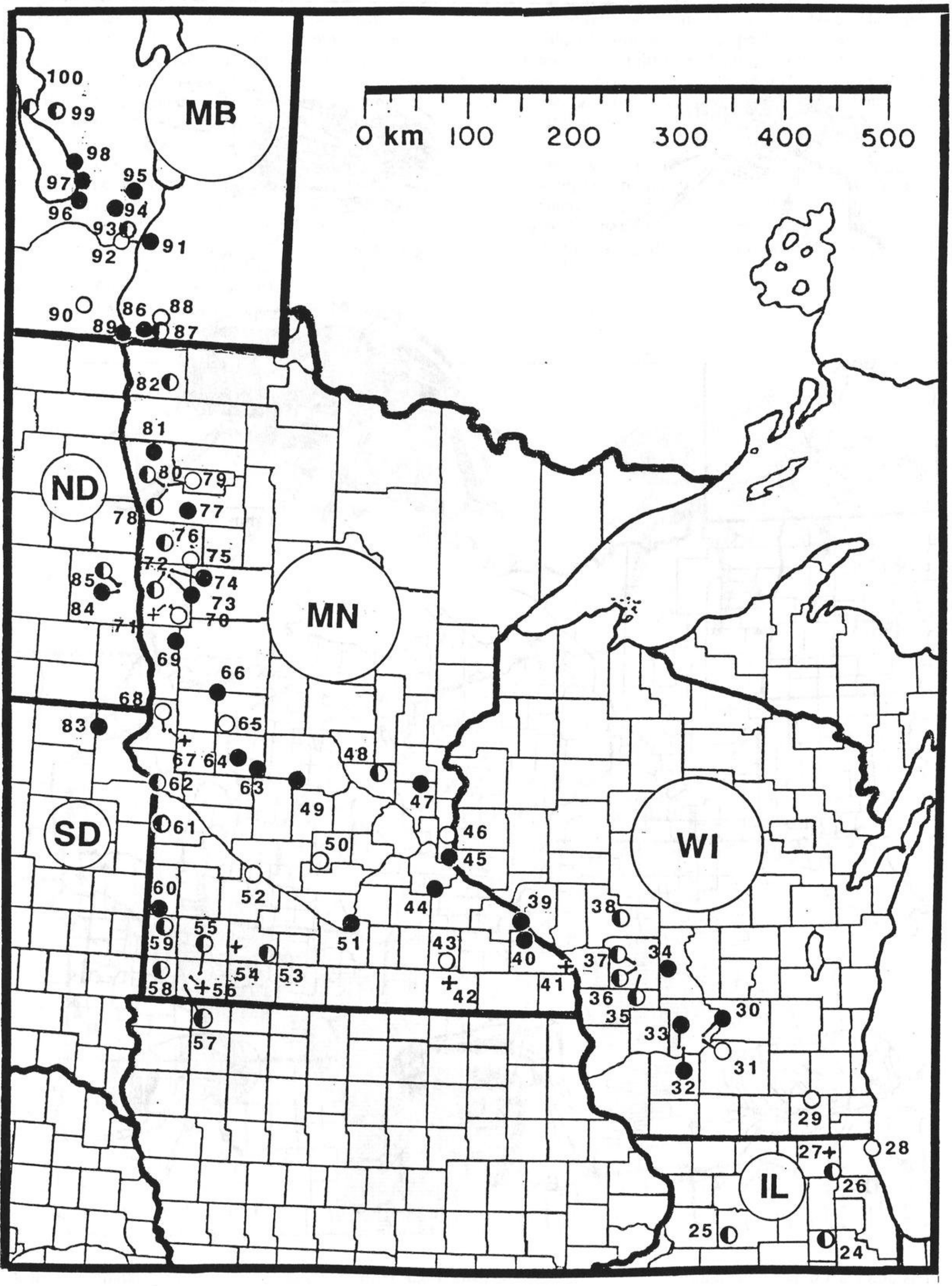


FIGs. 2A-B. Cercopidae (spittlebugs) endemic to prairies and known sites of occurrence. A, *Philaenarcys killa* Hamilton and distribution (hatched); B, *Lepyronia gibbosa* Ball and distribution (dots).

[°] "Tallgrass" in the traditional sense, being dominated by grasses that can attain heights of over 0.5 m. Within most of the study area, dominant grasses form extensive tall swards only following a fire; at other times, their growth usually is stunted.



FIGs. 3 A-F. Calisceline Fulgoroidea and known sites of occurrence. A, *Fitchiella robertsoni*, male; B, *Bruchomorpha beameri*, long-winged female; C, *B. extensa*, female; D, *Aphelonema simplex*, male; E, *Peltonotellus bivittatus*; F, same, nymph. Species A, B, C, D, and E represented by star, triangle, dot, circle, and split circle, respectively.



FIGs. 4 A-B. Prairie sites sampled in U.S.A., Ontario, and southern Manitoba; A, western half; B, eastern half. Dot: best sites (9-19 prairie-endemic cicadellid and caliscelid species); split circle: average sites (4-8 such species); circle, poor sites (1-3 such species); cross, no prairie-endemic Homoptera found.

ON - 1 Ramsay alvar (Almonte); 2, Point Anne alvar (Belleville); 3, Brantford Golf Club; 4, Matchette Road half of Ojibway Prairie (Windsor); 5, Walpole Is.; 6, Watson Nature Trail (Sarnia); 7, Prairie Point (Cape Croker I.R.); 8, Cabot Head; 9, Little La Cloche Is.; 10, Great La Cloche Is.; 11, Goat Is.; 12, Wikwemikong I.R.; 13, Barrie Is. causeway; 14, Barrie Is. (W extremity).

MI - 15, Maxton Plains (Drummond Is.); 16, Newaygo Plains (9 km E Newaygo); 17, Fennville; 18, Pokagon; 19, Monette St. fen (Cassopolis); 20, Cement City; 21, Ives Rd. fen (Tecumseh); 22, Pinckney SRA (N Chelsea); 23, Highland Cemetary (Ypsilanti).

IL - 24, Goose Lake State Prairie (Grundy Co.); 25, Green R. Conservation Area (Lee Co.); 26, Lake in the Hills; 27, Woodstock; 28, Illinois Beach (Zion).

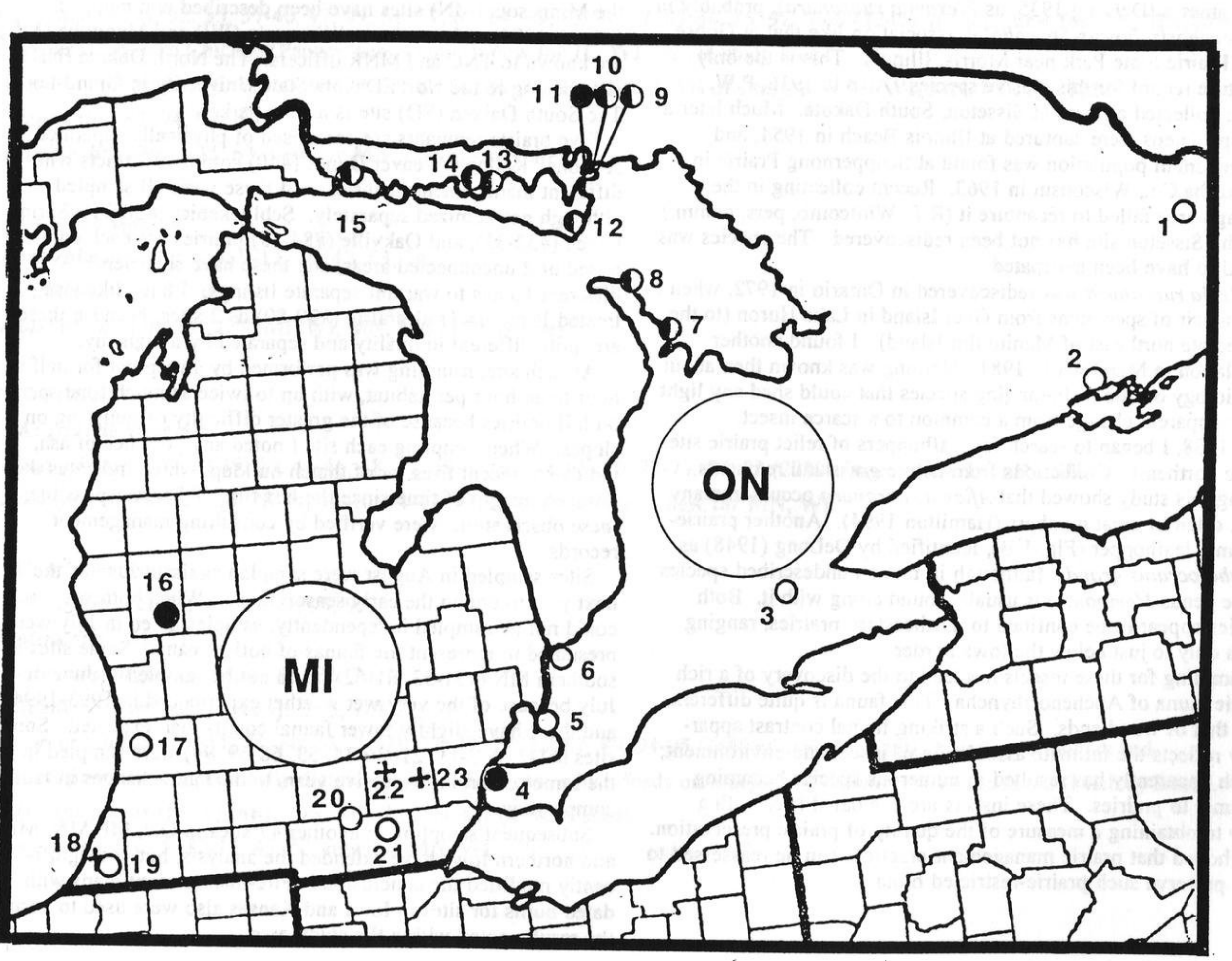
WI - 29, Lulu Lake (Troy Center); 30, Schluckebier Prairie N (Prairie du Sac); 31, same, S section; 32, Spring Green E; 33, same, W section; 34, Camp Douglas; 35, Ft. McCoy goat prairie; 36, Ft. McCoy drop zone; 37, Ft. McCoy savanna; 38, Bauer-Brockway Prairie (Black R. Falls).

MN - 39, Kellogg-Weaver dunes; 40, Beaver Natural Area; 41, King's Bluff (Winona Co.); 42, Wild Indigo SNA (Brownsdale); 43, Iron Horse prairie (Hayfield); 44, McKnight prairie (Randolph); 45, Lost Valley prairie (Point Douglas); 46, St. Croix savanna (Bayport); 47, Allison savanna (E. Bethel); 48, Uncas Dunes (Orrock); 49, Roscoe prairie; 50, Schaefer prairie (Brownton); 51, Kasota prairie (St. Peter); 52, Delhi prairie; 53, Mountain Lake; 54, Expandere WMA; 55, Lundblad prairie (Slayton); 56, 3 km W Chandler; 57, 7 km W Chandler; 58, Blue Mounds St. Pk. (Luverne); 59, Prairie Coteau (Holland); 60, Hole-in-the-Mountain prairie (Lake Benton); 61, Salt Lake WMA (Marietta); 62, Prairie WMA (Ortonville); 63, Ordway prairie (Brooten); 64, Glacial Lakes St. Pk. (Starbuck); 65, Staffanson prairie (Kensington); 66, Seven Sisters prairie (Ashby); 67, Miller prairie E (NE Dumont); 68, same, W section; 69, Town Hall prairie (Rothsay); 70, Buffalo River St. Pk. (E Glyndon); 71, Bluestem prairie (E Glyndon); 72, Felton WMA; 73, Bicentennial prairie (E Felton); 74, Blazing Star prairie (E Felton); 75, Frenchman's Bluff (Syre); 76, Sandpiper (Ada); 77, Agassiz Dunes (Fertile); 78, Tympanuchus WMA (E Harold); 79, Pembina Trail N (E Harold); 80, same, S section; 81, Crookston-Warren rwy. grade; 82, Norway Dunes (Halma).

SD - 83, Sica Hollow St. Pk. (N Sisseton).

ND - 84, Oakville Prairie S (Emerado); 85, same, N section.

MB - 86, Tolstoi; 87, Gardenton; 88, Stuartburn; 89, Emerson; 90, Myrtle; 91, Transcona; 92, Living Prairie Museum (Winnipeg); 93, Winnipeg, industrial site E airport; 94, Grosse Isle; 95, Brennan prairie (N Stony Mtn.); 96, 7 km E St. Ambroise; 97, 8 km S St.-Laurent; 98, Oak Point, B; 99, Camper; 100, The Narrows (E Wapah).



Fulgoroidea: Caliscelidae

These insects, unofficially called "piggy bugs", are usually very robust insects without obvious wings and often with a snout-like head process (Figs. 3 A-F). There are about 60 North American species in 4 genera, mostly characteristic of the southwestern plains (Doering 1940, 1941); their reported hosts are grasses. These tiny insects were placed previously in the family Issidae, but are related more closely to Dictyopharidae such as *Rhaphiophora*.

Membracoidea: Cicadellidae

Leafhoppers are abundant and diverse, with over 3000 North American species, of which 800 are associated with grasses and sedges. More than 200 of these are endemic to prairies (Hamilton & Whitcomb 1993), and there are smaller numbers of other prairie-endemic species on broadleafed hosts.

Historical

This study began as an attempt to identify prairie sites that still retain populations of a leafhopper of northeastern prairies that was thought to have been extirpated: *Aflexia rubranura*, a bug easily recognized by the bricklike spots on the head and the bright red "tail" spot on the male abdomen (Fig. 1 A). It is the only species in its genus.

This species was collected first by H.H. Ross and colleagues in 1935-1936 in the vicinity of Chicago, Illinois, where it once occurred in large numbers on wet black-soil prairie dominated by short grasses (DeLong 1935, as *Flexamia rubranura*), probably in an *Eleocharis-Juncus-Sporobolus* association like that at Goose Lake Prairie State Park near Morris, Illinois. This is the only literature record for this elusive species. Also in 1936, P.W. Oman collected a series at Sisseton, South Dakota. Much later a few specimens were captured at Illinois Beach in 1954, and another small population was found at Scuppernong Prairie in Waukesha Co., Wisconsin in 1963. Recent collecting in the Chicago area failed to recapture it (R.F. Whitcomb, pers. comm.) and the Sisseton site has not been rediscovered. The species was feared to have been extirpated.

Aflexia rubranura was rediscovered in Ontario in 1972, when I took a pair of specimens from Goat Island in Lake Huron (to the immediate northeast of Manitoulin Island). I found another population in Manitoba in 1981. Nothing was known then about the biology of this wide-ranging species that could shed any light on its apparent change from a common to a scarce insect.

In 1988, I began to search for leafhoppers of relict prairie sites in the northeast. Collections from native grassland remnants during this study showed that *Aflexia rubranura* occurs in many sites, often in great numbers (Hamilton 1994). Another prairie-endemic leafhopper (Fig. 1 B), identified by DeLong (1948) as *Parabolocratus grandis* (although in fact an undescribed species of the genus *Memnonia*) is usually found along with it. Both species appear to be confined to northeastern prairies, ranging south only to just below the Iowa border.

Sampling for these insects has lead to the discovery of a rich prairie fauna of Auchenorrhyncha. This fauna is quite different than that of woodlands. Such a striking faunal contrast apparently reflects the intimate association of insect and environment, which apparently has resulted in numerous species becoming endemic to prairies. These insects are evaluated here with a view to obtaining a measure of the quality of prairie preservation. It is hoped that prairie management practices can be reassessed to help preserve such prairie-restricted biota.

Methods

The sample area chosen extends from southern Ontario to the Red River valley of the Dakotas, northwest to Lake Manitoba (Figs. 4 A-B). This is believed to comprise the majority of northern "tallgrass" prairie areas from presettlement days and includes "prairie peninsula" relict prairies and alvars (Hamilton 1994).

Sites

Sites were deemed to be "prairie" that had stands of cordgrass (*Spartina* spp.), prairie dropseed (*Sporobolus heterolepis*), grama (*Bouteloua* spp.), June grass (*Koeleria* spp.) or porcupine grass (*Stipa spartea*). Bluestems (*Andropogon* spp.) and Indian grass (*Sorghastrum* spp.) were not used to define sites, because these prairie-dominant grasses are not limited to prairies and similar arid grasslands, being found in southeastern woodlands or invading roadsides.

One hundred sites were sampled (Figs. 4 A-B). This does not pretend to be an exhaustive survey of relict prairie sites in the study area, and the work is on-going. Sites were selected mainly on the advice of botanists at Agriculture Canada and personnel involved in prairie conservation with The Nature Conservancy (TNC) and state (DNR) or provincial (MNR) agencies. Some additional sites were discovered during collecting trips.

Grassland sites in Ontario (ON) and Michigan (MI) have been sampled and mapped recently (Hamilton 1987, 1990). Most of the Minnesota (MN) sites have been described and mapped (Wendt 1984). Most sites in Wisconsin (WI) and Manitoba (MB) are known to TNC and MNR officers. The North Dakota (ND) sites belong to the North Dakota State University in Grand Forks. The South Dakota (SD) site is a state park.

Five prairie remnants are composed of physically separated sections. Kellogg-Weaver Dunes (#40) comprise 3 tracts with different management histories, and these were all sampled although not itemized separately. Schluckebier (#30-31), Spring Green (#32-33), and Oakville (#84-85) prairies are each composed of 2 unconnected areas, and these have sufficiently different faunas to warrant separate listings. I have likewise treated Pembina Trail prairie (#79-80) as 2 sites, because these are quite different in quality and separated by a highway.

At each site, sampling was performed by sweep net for half an hour to an hour per habitat, with up to twice as much time spent on hill prairies because of the greater difficulty of sampling on slopes. When sampling each site I noted any presence of ash, indicating recent fires, or of thatch buildup, which indicates the probable length of time since the last fire. Wherever possible, these observations were verified by consulting management records.

Sites sampled in August were sampled again in June of the next year to obtain the early season fauna. When both seasons could not be sampled independently, samples taken in July were presumed to represent the faunas of both seasons. Some sites in southern MN (#51-53, 61-62) could not be sampled in June or July because of the very wet weather experienced in 1993-1994, and these have slightly lower faunal counts than expected. Some sites (#1-2, 4, 7-11, 21, 30-34, 53, 68-69, 94) were sampled in the same season in successive years to note any changes in faunal composition.

Subsequent sampling in another 47 sites in ON, MI, MN, MB and northern Iowa have extended the analysis, but not significantly modified the conclusions. Fire-management maps with dated burns for sites in Iowa and Kansas also were used to verify the results noted within the study area.

For analysis, prairie habitats were divided into 6 categories: (A) alvars (limestone plains that are wet in spring and very dry in summer); (B) bottom (wet) land (dominated by cordgrass, sedges and/or mat muhly, *Muhlenbergia richardsonis*); (C) common prairies (deep-soil mesic plains); (D) dry prairies (on sandy soil; on coteaux, moraines, or limestone ridges; "goat prairie" on steep hillsides; "dolomite prairie" on lower ridges); and (E) railway embankments and associated ditches. The last of these differs from the others in having been burned annually during the era of steam locomotives, although such practices have long been discontinued.

Fauna

Total leafhopper faunas have been recorded for Minnesota (Medler 1942), Illinois (DeLong 1948), Ontario (Beirne 1956), and Manitoba (Hamilton 1972). In particular, bugs of forested habitats in this area are well studied. Much material is deposited in the Canadian National Collection of insects, housed by Agriculture Canada in Ottawa.

Bugs sampled in prairies but not known from the forest fauna are presumed to represent prairie endemics. This is assumed to apply even if they are found occasionally in nonprairie native grasslands. For example, both forest-glade and prairie-inhabiting species may be found on native grasses on sandy sites such as beach dunes. A few species that are dominantly prairie-inhabiting may be found occasionally in other nonprairie sites. If these are encountered rarely (e.g. *Limotettix urnura* in an alkaline swale in woods), they may still be considered as prairie-endemic. However, if they are carried by wind over long distances, as is *Balclutha neglecta*, or tend to invade old meadows, as does *Stirellus bicolor*, then they are not "endemic" even if characteristic of plains.

TABLE 1 - Caliscelidae, Cercopidae, and Cicadellidae of prairie sites. Numbers refer to sites listed in Table I and located on Fig. 1 (ON=1-14, MI=15-13, IL=24-28, WI=29-38, MN=39-79, SD=80, ND=81-82, MB=83-100). Common (>12%) nonendemic taxa listed by state/province only. Records by DeLong (1948) are marked with an asterisk (*).

CALISCELIDAE

A: prairie endemics

Aphelonema simplex: 4-5, 43, 47, 86, 91, 94-95, 97-98 (10% of sites); **new for MN.**

Bruchomorpha beameri: 66, 73, 77-78; **new for MN.**

B. dorsata: 9, 21, 32, 35, 37-40, 47, 49, 51, 57, 62, 64, 69, 73-74, 77, 83-84, 86, 92, 96-97 (24% of sites); **new for ON, MN, MB.**

B. extensa: 36; also Chicago (Panzer, pers. comm.); **new for IL, WI**; rare in study area.

B. jocosa: 16, 30-31, 36, 51, 60, 63, 73, 77, 83-84, 86, 89, 94, 96-97 (16% of sites); **new for WI, MN, ND, SD, MB.**

B. keidensia: 87, 94, 97; rare.

Peltonotellus bivittatus: 45, 63; **new for MN**; rare in study area.

B: other species

Bruchomorpha oculata: 1-3, 9-13, 16, 47, 63, 74.

B. pallidipes: 16, 38; rare.

Peltonotellus histrionicus: ON, MI, WI, MN, MB (15% of sites).

CERCOPIDAE

A: prairie endemics

Lepyronia gibbosa: 16, 30-39, 40, 45-46, 48, 57, 59-60, 62-64, 66, 70, 72-73, 77, 83 (27% of sites); **new for MN, SD.**

Philaenarcys killa: 16, 25-26, 28-34, 36-40, 44-45, 48, 51 (18% of sites); **new for MN, WI.**

B: other species

Aphrophora spp.: 21-22, 37, 43, 77, 94, 97.

Clastoptera spp.: 18, 21, 33.

Lepyronia quadrangularis: 4, 18-19, 21, 70, 94.

Neophilaenus lineatus **(European)**: 3, 5, 7-9, 11, 15.

Philaenarcys bilineata: 9-11, 57, 60, 63, 70-71, 73, 75, 77, 83, 87, 89, 94-95 (16% of sites). On little bluestem on alvars and prairies; possibly subspecifically distinct from northern race which feeds on bluejoint, *Calamagrostis canadensis* (Michx.) Beauv.

Philaenus spumarius **(European)**: ON, MI, IL, MN, SD (49% of sites).

Prosapia ignipectus: 5, 32-33, 43, 62; **new for MN, WI.**

TABLE 1 contd.

CICADELLIDAE

Aceratagallia nanella: 70; **new for MN**; rare in study area.

A. n. sp. A: 40; **new for MN**; rare.

A. n. sp. B: 2, 11-14, 16, 32, 39, 47, 75 (10% of sites); **new for ON, MN, WI.**

A. n. sp. C: 7, 10-11, 15-16, 34, 48, 63, 69, 72, 81, 83, 86, 88, 90-91 (16% of sites); **new for ON, WI, MN, SD, MB.**

Aflexia rubranura: 9-14, 24, 26, 28, 30, 32, 35, 45, 49, 51, 55, 62-64, 73-74, 83, 94-98, 100 (27% of sites); **new for WI, MN, SD, MB.**

Amblysellus punctatus: 32, 38, 97, 100; **new for WI, MB.**

Athysanella attenuata: 44, 93; **new for MN.**

A. terebrans: 77, 82, 95.

Attenuipyga sp.: 94, 97-98; **new for MB**; rare.

Auridius helvus: 16, 32, 34, 38, 47; **new for WI.**

Chlorotettix brevidus: 28*; rare.

C. spatulatus: 4, 59; also reported (DeLong 1948) from 28.

Commellus colon: 32, 47, 57, 60, 62-63, 73-74, 83-84, 91, 94, 97 (13% of sites); **new for WI.**

C. comma: 16, 25, 28*, 34, 37, 39, 43-44, 51, 60, 74, 80, 83 (12% of sites); **new for WI.**

C. sexvittatus: 77, 82, 93; **new for MB.**

Cuerna sayi: 33, 36, 40, 69.

Deltocephalus n. sp.: 69; **new for MN**; unique specimen.

Dikraneura arizona: 44; **new for MN**; rare in study area.

Dorycara platyrhynchus: 34, 45, 47; **new for WI.**

D. minor: 60, 74, 77, 80, 82, 85, 89-91.

Dorydiella kansana: 4, 7, 28.

Driotura robusta: 38, 59-60, 68, 73, 75, 78, 84; **new for ND, WI**

Extrusanus oryssus: 16, 24, 26, 28, 32, 34, 45, 47, 49-50, 53, 58, 60, 63, 65, 69, 74, 76-77, 80, 82, 84-86, 89, 91-95, 97-98, 100 (33% of sites).

Flexamia abbreviata: 30, 32, 39, 47, 60, 63-64, 66, 73-74, 77 (11% of sites).

F. albida: 33, 40, 45, 51, 57-60, 62-64, 66, 83 (13% of sites); **new for WI.**

F. atlantica: 32; **new for WI**; rare in study area.

F. dakota: 69; **new for MN**; rare in study area.

F. decora: 85, 94-100.

F. delongi: 8-16, 30, 34, 36-38, 40, 94-98 (20% of sites); **new for MN.**

F. graminea: 52, 55, 73, 81, 84; **new for MN.**

F. pectinata: 26, 29, 32-33, 40, 44-45, 48, 51, 60, 63, 66 (12% of sites); **new for WI.**

F. prairiana: 21, 28*, 43, 49, 52-53, 55, 69, 72-73, 77, 78-81, 86-89, 91-92, 94, 96-97, 100 (24% of sites); **new for MI.**

F. serrata: 45, 63, 69, 84, 86-87, 94-95, 97-98; **new for MN.**

F. stylata: 25, 45, 59-60, 63; **new for IL.**

Graminella mohri: 8, 28*, 81; **new for MN.**

G. oquaka: 4-5, 28*, 47, 51; **new for MN, WI.**

G. pallidula: 4.

Gypona contana: 89, 91, 94, 96.

Gyponana vincula: 30, 33, 49, 57, 60, 62, 64, 69, 72-73, 81 (11% of sites); **new for MN.**

Hecalus viridis: 28*, 34, 39, 44, 47, 77, 83, 86, 89; recorded as *Parabolocratus* (DeLong 1948).

Hebecephalus signatifrons: 28*; rare; needs confirmation.

Laevicephalus minimus: 2-3, 26, 32-33, 35, 40, 43-45, 47, 51, 57-58, 60, 63, 66, 73, 83 (19% of sites).

L. poudris: 86, 94-97.

L. saskatchewanensis: 93; rare in study area; **new for MB.**

TABLE 1 contd.

L. unicoloratus: 4, 6-11, 13, 16, 20-21, 23-26, 28, 30-34, 36-40, 44-49, 51, 53, 55, 57-66, 68-70, 72-74, 76-83, 86-87, 89, 94-95, 97-99 (67% of sites).
L. vannus: 36, 40; rare in study area.
Limotettix elegans: 4; rare.
L. urnura: 2, 4, 7-13, 15, 28*, 43, 53, 94.
Lonatura megalopa: 44, 60, 63, 66; **new for MN**.
L. salsura: 61, 94, 97; **new for MN**.
L. teretis: 94, 97; **new for MB**; rare in study area.
Memnonia nr. *grandis*: 1, 8-11, 13-14, 30, 33, 35, 44-45, 49, 55, 57, 59-60, 62-63, 65, 69, 72-74, 76, 80-81, 83, 86-89, 94-95, 97-98 (36% of sites); **new for WI, SD, MB**.
M. n. sp.: 49, 69, 76, 84, 86, 94-95, 97-98, 100 (10% of sites); **new for MN, ND, MB**.
Mesamia ludovicia: 47, 77, 83, 89, 94; **new for MB**.
Mocuellus americanus: 9-11, 58, 74, 76, 80, 83-85, 91, 94-100 (18% of sites); **new for MN**.
Neohecalus nr. *lineatus*: 17, 19, 28*, 55, 61, 69, 72, 80-81, 97-98 (10% of sites); recorded (DeLong 1948) as Hecalus lineatus.
Orocastus perpusillus: 73, 77; **new for MN**; rare in study area.
Paraphlepsius altus: 28*, 36, 44, 60, 63, 66.
P. lobatus: 11, 15, 30, 49, 52, 64, 94; **new for MB**.
P. lupalus: 28*; rare; recorded (DeLong 1948) as *P. turpiculus*.
P. nebulosus: 55, 58; **new for MN**; rare in study area.
P. umbrosus: 33, 35, 37-38, 47, 94.
Pendarus magnus: 94, 97-98; **new for MB**.
Polyamia caperata: 16, 30, 32-33, 39-40, 44-47, 49, 51, 60, 63-64, 66, 69, 81, 83, 91, 94, 97 (22% of sites).
P. dilata: 32, 35, 40; **new for MN, WI**; rare.
P. rossi: 25, 32; **new for WI**.
Prairiana cinerea: 33, 58, 60, 82, 85, 97; **new for WI**.
P. nr. *kansana*: 32-34, 39, 47-48, 55, 60, 63-64, 86-87, 95, 99 (14% of sites).
Psammotettix knullae: 61; **new for MN**.
Rosenus cruciatus: 16, 28*, 32, 36, 39, 44, 47, 73, 75-76; reported (DeLong 1948) as *Hebecephalus*; **new for WI**.
Texananus cumulus: 28*; rare in study area.
T. marmor: 9.
Unoka gillettei: 77; **new for MN**; rare in study area.

B: other species

Aceratagallia humilis: 11, 25-26, 30, 33-34, 43, 77, 80.
A. sanguinolenta: ON, MI, WI, MN, SD, ND, MB (27% of sites)
A. n. sp. D: 2, 16, 25, 28*, 31-34, 77; recorded (DeLong 1948) as *A. sanguinolenta*.
Acinopterus sp.: 32.
Agalliopsis sp.: 28*.
Agalliota spp.: 4, 21, 28*, 43, 48, 55, 63-64, 69, 72; recorded (DeLong 1948) as *Agallia*.
Amplicephalus inimicus: ON, MI, IL, WI, MN, ND, MB (52% of sites).
Anoscopus spp. **(European)**: 59-60, 81, 94, 97.
Aphrodes spp. **(European)**: ON, MI, IL, WI, MN (16% of sites).
Athysanella acuticauda: 28*
A. longicauda: 1-3, 16.
Athysanus argentarius **(European)**: ON, MI, IL, WI, MN, ND, MB (66% of sites).
Balclutha spp.: ON, MN, SD, ND, MB (36% of sites).

TABLE 1 contd.

Chlorotettix fallax: 4; rare in study area.
C. galbanatus: 4.
C. obsenus: 28*; rare; possibly a damaged form of *C. unicolor*.
C. tergatus: 55.
C. unicolor: ON, MI, IL, WI, MN, MB (48% of sites).
Cicadula spp.: ON, MI, IL, WI, MN, MB (15% of sites).
Colladonus clitellarius: 28*.
Commellus cedilla: 34, 49, 86, 94-96, 98.
Cosmotettix spp.: 10.
Cribrus shingwauki: 28*; recorded as *Laevicephalus* (DeLong 1948).
Cuerna striata complex: 3, 47, 75, 78, 97.
Deltocephalus balli: 4, 28*, 100.
Dikraneura angustata: 30, 53.
D. hungerfordi: 91; **new for MB**.
D. mali: 2, 59, 61, 75.
D. urbana: 49.
D. variata: 94, 96.
Diplocolenus configuratus: ON, IL, WI, MN, ND, MB (44% of sites).
D. evansi: 2, 7-8, 10-11, 13-14, 93, 95.
Doratura stylata **(European)**: ON, MI, IL, WI, MN, SD, ND, MB (58% of sites).
Draeculacephala spp.: ON, MI, IL, WI, MN, MB (30% of sites).
Driotura gammaroides: ON, MI, IL, WI, MN, ND, MB (21% of sites).
Elymana sulphurella **(European)**: 1, 8.
Empoasca spp.: 2, 7, 63, 75, 82.
Erythroneura ziczac: 55.
Euscelis sp.: 28*.
Exitianus exitiosus: IL, WI, MN (17% of sites); recorded (DeLong 1948) as *E. obscurinervis*.
Flexamia inflata: 2, 4, 24, 91, 95.
F. picta: 24; rare in study area.
F. reflexa: 4, 21; **new for MI**; rare in study area.
Forcipata spp.: ON, MI, IL, WI, MN, SD, MB (21% of sites).
Graminella fitchii: 28*
G. nigrifrons: 16, 19, 22.
Graphocephala spp.: 32, 37.
Gypona melanota: ON, MI, MN (16% of sites).
Gyponana ortha: 28*; recorded as *G. conferta* (DeLong 1948).
Gyponana serpenta: 15, 92, 94, 97.
Hecalus major: 28*, 39, 41, 69, 74, 82, 84, 89, 95, 100.
H. montanus: 28*, 34, 83-84, 89-91, 93; recorded as *H. rotundus* (DeLong 1948).
Helochara communis: 53, 84.
Idiocerus spp.: 1, 11, 24, 28*, 34, 43, 81, 94.
Idiodonus sp.: 7.
Jikradia olitoria: 4, 32.
Laevicephalus sylvestris: 70.
Latalus spp.: ON, MI, IL, WI, MN, SD, MB (61% of sites).

TABLE 1 contd.

Limotettix balli: 8-9, 13, 15, 21.
  L. ferganensis: 28*, 43, 53, 97; recorded (DeLong 1948) as *L. striolus*.
  L. kryptus: 24, 69, 79.
  L. osborni: ON, MI, IL, WI, MN, MB (27% of sites).
  L. plutonius: 10, 34, 99.
  L. sphagneticus: 13, 86.
Macropsis spp.: 28*, 43.
Macrosteles spp.: ON, MI, IL, WI, MN, SD, MB (51% of sites).
Memnonia flavida: 4.
Menosoma cincta: 33; **new for WI.**
Mesamia nigridorsum: 4, 24, 28*, 38, 40, 69, 72, 81, 89, 94, 97.
Neocoelidia tumidifrons: ON, IL, WI, MN, ND, MB (20% of sites).
Neokolla hieroglyphica: ON, MI, IL, WI, MN, MB (15% of sites).
Norvellina sp.: 28*.
Paluda gladiola: 12, 69, 74, 76, 84, 86, 91, 94-95, 97.
Paraphlepsius fulvidorsum: 1, 7.
  P. irroratus: ON, MI, IL, WI, MN, SD, MB (20% of sites).
  P. solidaginis: 28*, 94, 97.
  P. truncatus: 1-2, 6-7, 9-11 13.
Pendarus punctiscriptus: 4, 15, 31, 80, 94.
Platymetopius spp.: 1, 10, 37, 46, 62, 69, 77-78, 80, 94, 96.
Polyamia apicata: 1, 8-9, 25, 28*, 32, 34, 46-47, 66.
  P. compacta: ON, IL, WI, MN (21% of sites).
  P. obtecta: 47; rare in study area.
  P. weedi: 25, 33-34.
Prescottia lobata: 28*.
Psammotettix lividellus complex: ON, MI, IL, WI, MN, ND, MB (32% of sites).
Scaphoideus spp.: 2, 4, 10, 15, 28*, 37, 47, 94.
Scaphytopius spp.: ON, MI, IL, WI, MN, SD, MB (32% of sites).
Sorhoanus spp.: ON, MI, IL, WI, MN, MN, ND, MB (20% of sites).
Stirellus bicolor: MI, WI, MN, MB (13% of sites); **new for WI.**
Texananus arctostaphylae: 1, 11, 15, 47, 92, 96.
  T. decorus: 94; **new for MB.**
Tylozygus bifidus: 4, 32.
Xerophloea major: 4, 24-25, 32.
Xestocephalus spp.: 2, 8, 15, 23, 83, 91-92, 94.

Results

Overall endemic species diversity

Total prairie-endemic species included 72 leafhoppers, 7 caliscelids, and 2 spittlebugs (Table I). This includes 30 species recorded for the first time in MN, 21 in WI, 14 in MB, 3 each in ND and ON, 2 in IL and 1 in MI. By contrast, the nonendemic fauna of these prairies is more diverse (over 100 species) but includes only 7 new state and provincial records of such leafhoppers.

Two prairie-endemic bugs have been collected on beach dunes in ON and MI (Hamilton 1990) but were not found on prairie sites during this study: the caliscelid *Fitchiella robertsoni* (Fig. 3 A) and the leafhopper *Macropsis quadrimaculata*, a reddish bug that is a specialist on sand cherry, *Prunus pumila*. These insects should be expected in northeastern prairies.

Spittlebugs

Four species of spittlebugs associated with grasslands were found in this survey. Two appear to represent prairie endemics.

The spittlebug *Philaenarcys killa* (Fig. 2 A) occurs east of the Red River valley in sandy or gravelly areas, where it feeds exclusively on little bluestem, *Andropogon scoparius*. It is usually flightless, but 5 long-winged individuals were taken at Schluckebier N (site 30).

The spittlebug *Lepyronia gibbosa* Ball (Fig. 2 B) feeds on a very wide variety of plants, both grasses and forbs, but is limited to well-drained soils. Therefore it is found on both sand plains and moraine hills east to MI. It also used to inhabit sandy areas near Boston, Massachusetts.

Leafhoppers and caliscelid bugs

The other 2 families of bugs show little bias in favor of habitat (Table I). The most commonly encountered species, *Laevicephalus unicoloratus*, a generalist on bluestem grasses, was found in fully 67% of sites sampled. This was as abundant on prairies as the most aggressive of introduced leafhoppers, *Athysanus argentarius* (in 66% of sites). Frequency of occurrence for 9 other common species are:

36% for *Memnonia* nr. *grandis* on prairie dropseed;
33% for *Extrusanus oryssus* on blunt sedge, *Carex obtusata*;
27% for *Aflexia rubranura* on prairie dropseed;
26% for *Bruchomorpha dorsata* on little bluestem;
25% for *Laevicephalus minimus* on side-oats grama, *Bouteloua curtipendula*;
24% for *F. prairiana* on big bluestem, *Andropogon gerardii*;
22% for *Polyamia caperata* on little bluestem;
20% for *Flexamia delongi* on little bluestem;
18% for *Mocuellus americanus* on slender wheatgrass, *Agropyron trachycaulum.*

The last of these leafhoppers occupies 33% of the sites in the Red River valley (sites #56-100); otherwise, it is known in the study area only from the La Cloche Islands in Lake Huron (#9-11). *Laevicephalus minimus* is common in the south of the study area, whereas *Flexamia delongi* is common in the north; these 2 species have a narrow range overlap. All of the other species may be found in each of the habitat types throughout most of the study area. All other prairie-endemics are found in 16% or fewer of the sites.

Fauna of prairie dropseed

Only the leafhoppers *Aflexia rubranura* and *Memnonia* nr. *grandis* are found on prairie dropseed. Both have been collected repeatedly on this host but only rarely on any other plant, demonstrating that they are host-specific. These 2 leafhopper species occurred together in 18 sites. Two other sites (Sisseton, SD, 1936; Scuppernong, WI, 1963) once supported *Aflexia*, but until these sites can be reinvestigated, there is no way to determine whether *Memnonia* was also present. Only 9 sites supported *Aflexia* alone, but 18 prairie sites supported *Memnonia* alone (Fig. 1 B). Many of the latter are fire-managed prairies or railway embankments.

Discussion

Diversity

Faunal diversity is rather low in alvars, "dolomite" and "goat" prairies, which have a lower floral diversity than deep-soil prairies. The richest alvar faunas are those of the La Cloche Islands (sites #9-11), with 7-9 prairie-endemic species.

Up to 10 such species may be encountered on "goat" prairies (site #40) and 12 on "dolomite" prairies (#45). Wet prairies may have 13-14 species (#69, 95), whereas xeric deep-soil prairies have 17-19 species each (#28, 32, 47, 60, 63). Mesic deep-soil prairies are more variable, with up to 15-16 species in Minnesota (#73, 97) and up to 24 in Manitoba (#94, 97).

The absence of *Aflexia rubranura* in 7 frequently burned prairies and along most railway rights-of-way, where prairie dropseed is common, points towards fire-depopulated sites. *Memnonia* nr. *grandis* on the same host is abundant even in sites that are burned repeatedly, such as Ramsay alvar (site #1), locally known as "The Burnt Lands". Panzer (pers. comm.) has found that it is much more resistent to prairie fires than *Aflexia*, recovering to full populations within a single generation. By contrast, *Aflexia* requires **4 or more generations** for full recovery (Panzer 1992), probably largely by overland migration of individuals from unburned areas with some assistance from wind. It may produce a second generation during the year, but only in the south of its range. Thus, it takes 2-4 years to recover from fire, depending on the number of its broods.

The reason for this different response to fire probably lies in the seasonality of these 2 species. *Memnonia* lays its eggs in summer; adults appear early in the spring, suggesting that nymphs hatch out before the fall. Thus, this species is active during the fall and spring when grass fires are most common and probably can escape burns by living on root crowns. By contrast, *Aflexia* apparently overwinters as eggs in exposed stems, which are highly vulnerable to fire.

It might be thought that winged females of *Aflexia* would permit this species to disperse more readily than *Memnonia*, with flightless females. Fully winged forms are usually very rare in the midsummer brood, but in Illinois, where an early summer brood also occurs, as much as 10% of females are fully winged (Panzer 1992), although males are always brachypterous. Fully winged forms occur only in unburned areas and do not appear to invade adjacent burned areas (Panzer, pers. comm.); therefore, they are probably also flightless. A burned site separated from an unburned site by a paved highway initially failed to regain its *Aflexia* population (Panzer 1992), although small populations eventually were found there (Panzer, pers. comm.), probably brought in by wind dispersal.

Both of these dropseed-specialist leafhoppers were absent or rare on high hills. Presumably these flightless insects are not active dispersers up steep slopes. By contrast, low hills (e.g., sites #45, 63, 64) had some of the heaviest populations of *Aflexia*.

Categories

The prairies sampled can be divided into 6 roughly equal portions (Table II): *depauperate*, 0-1 endemic species; *poor*, 2-3 such species; *fair*, 4-5 such species; *good*, 6-8 such species; *very good*, 9-11 such species; *excellent*, 12-24 such species. Thus, half the maximum number of species (or more) per site occur in only the top 1/6th of the sites.

No sites in the "depauperate" to "poor" categories support populations of *Aflexia rubranura*. Many of these sites have been burned heavily (e.g. railway embankments) or were burned too recently for the fauna to recover. The "fair" category shows 25% of sites that support *Aflexia*; most are alvars. Of the sites rated "good" to "very good", over 40% support *Aflexia*. For sites in the "excellent" category the comparable figure is 63%.

Similar results may be obtained by grouping prairie sites according to the 9 most common leafhoppers and caliscelids (Table III). Overall, 56% of the sites received the same rating, whereas only 4% changed by more than 1 level, and these only by 2 levels. Because of the smaller number of species considered, the groups are larger and, therefore, less accurately divided into 6ths; thus 27 received a higher rating, whereas only 17 receive a lower one. The results of such a rating compensate for regional faunal diversity, thus lowering the rating of Manitoban prairies and raising that of Ontario alvars. Such a rating system has the further advantage in being easier to apply, because only 9 target species must be sampled and identified.

Another alternative system ranks prairie sites by the presence of species considered rare in the sample area (Table IV). Only 22% of the sites sampled contained such species; these correspond fairly well with Table III except in 4 cases. This is a rather subjective method, because "rare" may refer to sampling defects rather than to actual scarcity. It also relies upon intensive collecting to disclose insects that may be very difficult to find. Nevertheless, it helps to draw attention to localities of special scientific interest, such as Zion, IL (site #28) which has by far the largest number of rare, prairie-endemic species.

Table 2. Sites (numbered as in Fig. 4) ranked by numbers of prairie endemic cicadellid and caliscelid species.

DEPAUPERATE: poorest 1/6th

0 spp. **B-22, 54; C-27, 67, 71; DG-41; DM-56; E-18, 42**

1 sp. **A-1; B-17, 19, 20; C-50; DM-23, 29; DS-3; E-6**

POOR: second 1/6th

2 spp. **B-5, 70; C-68, 79; DM-46; DS-31; E-90**

3 spp. **A-2; B-21, 52, 65; C-88, 92; DM-75; E-43**

FAIR: third 1/6th (below average)

4 spp. **A-7, 12*, 14*, 15; B-53, 61, 99; C-78; DS-25; E-93**

5 spp. **A-8; B-24*, 85; DM-26*; DS-37, 48**

GOOD: fourth 1/6th (above average)

6 spp. **A-13*; B-72; C-76, 87; DG-35*; DM-59; DS-82**

7 spp. **A-10*; C-38, 57, 62*; DD-58, 100***

8 spp. **A-9*; B-80; C-55*; DS-4, 36**

VERY GOOD: fifth 1/6th

9 spp. **A-11*; B-30*, 84, 91; C-89, 96*; DM-64*, 66; DS-34; E-81**

10 spp. **C-49*, 51*, 74; DS-16, 39**

11 spp. **DG-40; DM-33**

EXCELLENT: top 1/6th

12 spp. **DD-45*, DM-44**

13 spp. **B-95*, C-86, 98***

14 spp. **B-69, C-73*, DM-83*, DS-77**

17 spp. **DS-32*, 47**

18 spp. **DM-63*, DS-28***

19 spp. **DM-60**

24 spp. **C-97*; E-94***

* the 27 sites with *Aflexia*.

A--alvar.

B--bottom (wet) land.

C--common (mesic) prairie.

D--dry prairie: DD, "dolomite" prairie; DG, "goat" prairie; DM, moraine hill or coteau; DS, sand plain.

E--railway embankment.

Table 3 - Sites ranked according to occurrence of 9 most common prairie-endemic species: *Aflexia rubranura*, *Bruchomorpha dorsata*, *Extrusanus oryssus*, *Flexamia delongi*, *F. prairiana*, *Laevicephalus minimus*, *L. unicoloratus*, *Memnonia* nr. *grandis*, and *Polyamia caperata*.

DEPAUPERATE: poorest 1/6th

0 spp. 5, 17, 18, 19, 22, 27, 29, 41, 42, 54, 56, 67, 71, 75, 90

POOR: second 1/6th

1 sp. 1, 2, 3, **4=**, 6, 7-, 15-, 20, 23, 25-, 31, 48-, 50, 52, 61-, 68, 70, 85-, 93-, 99-

FAIR: third 1/6th (below average)

2 spp. 12, 36-, 43+, 46+, 59-, 78, 79, 82-, **84=** (ND), 88+, 92+

GOOD: fourth 1/6th (above average)

3 spp. 8+, 14+, 21, 24+, 34-, 37+, 38, 39-, 44+, 53+, 58, 65, 66-, 72, 76, 87, 100

VERY GOOD: fifth 1/6th

4 spp. 10+, 11, 13+, 16 (MI), **26++** (IL), 28-, 33, 35+, 55+, 57+, 62+, 64, 77, 80+, 81, 89, 91, 96

EXCELLENT: top 1/6th

5 spp. **9++** (ON), 30+, 40+, 47+, 51+, 60+, 74+, 86, 95, 98

6 spp. 32+ (WI), 45, 63, 69, 73 (MN), 83 (SD)

7 spp. 49+ (MN), 94

8 spp. 97 (MB)

()	best site in each state and province.
+/-	sites with different rating than in Table II.
++	sites with higher rating by 2 levels.
=	sites with lower rating by 2 levels.

Table 4 - Sites ranked according to occurrence of prairie-endemic species considered rare in the study area.

DEPAUPERATE to GOOD:

0 spp. 1-3, 5-15, 17-31, 33-34, 37, 39, 41-43, 46-54, 56-57, 59-62, 64-68, 71-72, 74-76, 78-86, 88-92, 95-96, 99-100

VERY GOOD: top 22%

1 spp. **4+++**, 16, 35, 38+, 44+, 45-, 55, 58+, 63-, **70+++**, 73-, 77, 87+, **93+++**, 98-

EXCELLENT: top 7%

2 spp. 32, **36++**, 69, 94, 97

3 spp. 40

5 spp. 28

+/-	sites in 2 top categories with different rating than in Table III.
++	sites rated "fair" in Table III
+++	sites rated "depauperate" in Table III.

Special cases

Some sites are far from uniform and present interesting contrasts in management styles.

Ojibway Prairie PNR (site #4). This is composed of 2 tracts separated by an unpaved road. The smaller, N section is largely unburned sand prairie with a mixture of prairie and southeastern leafhopper species. The S section has a wet prairie that is burned annually, with virtually no leafhopper fauna remaining.

Schluckebier (#30). This sand prairie is composed of 2 tracts, both fire-managed by TNC. The S section has dropseed on flat surfaces near a small gully (which probably survived plowing in the gully), whereas the N section has dropseed growing on a steep northwest-facing slope. *Aflexia* and other prairie endemics are limited to the northern site. Because fires do not burn as hot and close to the ground on steep slopes as on flat areas, the leafhopper might survive there.

Spring Green (#32). This TNC-managed sand prairie is extensive, with detailed fire management records dating back to 1978. The best areas had not been burned in 3 years, and only the "old field" areas were burned less than 4 years apart. Sand "blowout" areas afforded particularly fine collecting. *Aflexia* leafhopper nymphs but no adults were found; they probably were taken on clumps of dropseed near the base of the bluffs at the eastern section of the preserve, where the dense rank growth made collecting difficult by August.

Kellogg-Weaver dunes (#39). This extensive sand plain is under multiple ownership. TNC and State Natural Areas (SNA) were burned within 1-2 years before sampling (1993); McCarthy Lake State Wildlife Management Area (SWMA) is apparently unburned. Most of the TNC and SNA tracts were sampled, plus the roadside (dune) area of SWMA. The prairie leafhopper fauna was confined mostly to SWMA, or along the highway adjacent to SWMA, and in "blowout" areas in SNA where fire probably did little damage.

Iron Horse Prairie SNA (#43). The land in a triangle surrounded by the railway "wye" (3-way junction), apparently heavily burned, has strikingly different vegetation than the area south of the tracks adjacent to a cornfield. The limited fauna of prairie leafhoppers on this site occurs mostly in the latter area, which is mesic to wet and dominated by shorter grasses. Wild rye, *Elymus canadensis*, and its leafhopper specialist *Commellus comma* were confined to the roadbed.

McKnight Prairie (#44). This site has 2 moraine hills with sandy slopes. The westernmost was burned recently by Carleton College and showed limited prairie fauna; the other has its best fauna around a sand "blowout" area.

Lost Valley (#45). This is the finest "dolomite prairie" sampled. Its low vegetation is dominated by prairie dropseed, bluestems, and sideoats grama, *Bouteloua curtipendula*. This is the easternmost site for the caliscéline bug *Peltonotellus bivittatus* Ball on its host prairie muhly, *Muhlenbergia cuspidata*, on an unburned limestone ridge W of the site entrance. Many *Aflexia* also were found there and on the N tip of the access area, which was burned by DNR in the 1-2 years before sampling (1993). No prairie leafhoppers were found on a recently burned ridge N of the site entrance.

Kasota Prairie (#51). The entire site has been burned by TNC, probably in 1992. No prairie-endemic leafhoppers were found there. A small, unburned parcel of land outside the prairie boundary has a thriving population of *Aflexia* and other interesting species adjacent to a 10' high cedar.

Hole-in-the-Mountain Prairie (#60). This is a fine coteau prairie with "old field" vegetation in low areas, mostly managed by TNC using mowing. The central and eastern sections, plus hillsides outside the preserve boundary north of the site, have a rich prairie fauna. Special mention must be made of stands of hairy grama, *Bouteloua hirsuta*, and prairie muhly on "saddles" between low hills near railway tracks, which have their own fauna of prairie leafhoppers.

Town Hall Prairie SNA (#69). This wet, black-soil prairie is the best such site sampled, probably typical of the Red River Valley, and rich in floral and faunal diversity. A third was burned by TNC that spring (1993) and was without prairie insects; 1/3rd was burned a few years previously and had a limited fauna; and 1/3rd (adjacent to the preserve sign) was burned after sampling was complete. The best collecting was from the vicinity of the sign. An adjacent, unburned field is wetter and has a lower species diversity than the prairie preserve.

Bicentennial Prairie (#73). This is an extensive, deep-soil prairie on a low morainal "bench". This TNC prairie preserve is surrounded by much semiarid, unprotected land, pocked with gravel pits, and dominated by *Stipa* and little bluestem. The best collecting is outside the preserve or immediately adjacent to the preserve sign.

Blazing Star Prairie (#74). This prairie is situated adjacent to site #73. It has an access trail down the middle, which apparently serves as a burn boundary. Of the prairie endemics, only the fire-resistant *Memnonia* nr. *grandis* was dispersed generally; others were mostly, or exclusively, within 10' of the road, especially on the grass strip in its middle.

Crookston-Warren railway grade (#81). This unprotected prairie has an unusually high species diversity for a railway grade, possibly because it has a 30' wide strip of land between the railway ditches and highway that may not have been burned as frequently as the railway grade itself. The Crookston end is wider and is partly hayed. The end closest to Warren has the greatest floral and faunal diversity, including the state's most abundant population of the leafhopper *Flexamia graminea* on little bluestem.

Grosse Isle railway grade (#94). The "wye" where the Prairie Dog Express (a steam excursion train) turns on its run back to Winnipeg encloses an unprotected triangle of land that was burned twice a year until recently. There is also a 20' wide strip between the railway and the highway. Amazingly for such a small, frequently burned site, there is one of the richest prairie faunas occurs there. Flightless leafhoppers are confined to the strip along the roadside (*Attenuipyga* sp.) and to the wettest area along the return "wye" track (*Aflexia rubranura*). Perhaps these parts have been burned not so often as the verges of the main lines. Much of the area next to the highway was reduced to a mud bath when heavy construction equipment was parked on it in 1991.

Conclusions

Family differences

Spittlebugs do not correlate with prairie quality, being found on both recently burned prairie and prairie densely overgrown with European grasses and weedy plants. However, their persistence in degraded sites can show the extent of prehistoric prairie vegetation. The spittlebug *Philaenarcys killa*, usually flightless and unlikely to be wind-dispersed, is particularly good for this. Its occurrence on sand plains as far east as Ontario (Fig. 2 A) may indicate the extent of prairies during the Hypsithermal (6000-8000 years ago) when world temperatures were higher than today.

Leafhoppers and caliscelids together can be used to determine the state of faunal preservation on a site. Sampling must not be carried out until at least 3 years after burning, to allow the fauna to propagate and reach observable levels. Then sampling for the 9 most common prairie-endemic species should yield a standardized assessment of the site: at least 3 such species should be present and preferably 5 or more for well-managed sites within the study area.

Management

In sand prairies (e.g., sites #32, 39, 44), the prevalence of interesting prairie leafhoppers around sand "blowout" areas where fire would not burn completely suggests faunal degradation elsewhere from fire.

Leafhoppers are most abundant in sites where fire has been used only at wide intervals or not at all. A 4-year firing cycle seems to be the greatest frequency that will not damage their populations. In this regard, it is noteworthy that the best (least burned?) faunas are associated with wooden property signs (e.g., at sites #69, 73).

Fire is probably not highly destructive to leafhoppers on slopes and hill prairies (e.g., sites #30, 63-64, 66), because the fire goes up the slope too quickly to burn close to the ground. Hill prairies thus have some of the richest of prairie faunas. On the other hand, some flightless leafhoppers (e.g., *Aflexia*) apparently do not migrate readily up steep slopes.

Mowing seems to have little, if any, effect on prairie insects. Some of the most productive sites have been managed exclusively (site #97) or mostly (#60, 64) by mowing.

The extensive (40 km long!) prairie along the Warren-Crookston railway grade (site #81) is uniform enough and has enough prairie species to serve as a "test plot" for fire/mowing management strategies.

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Literature cited

Beirne, B.P. 1956. Leafhoppers (Homoptera: Cicadellidae) of Canada and Alaska. The Canadian Entomologist 88, suppl. 2. 180 pp.

DeLong, D.M. 1935. Some new species of deltocephaloid leafhoppers (Homoptera Cicadellidae). Annals of the Entomological Society of America 28:154-159.

DeLong, D.M. 1948. The leafhoppers, or Cicadellidae, of Illinois (Eurymelinae-Balcluthinae). State of Illinois Natural History Survey Bulletin 24 (2): 91-376.

Doering, K.C. 1940. Part III: a contribution to the taxonomy of the subfamily Issinae in America north of Mexico (Fulgoridae, Homoptera). Bulletin of the University of Kansas 51 (22). University of Kansas Science Bulletin 26: 83-167.

Doering, K.C. 1941. [Part IV:] A contribution to the taxonomy of the subfamily Issinae in America, north of Mexico (Fulgoridae, Homoptera). Bulletin of the University of Kansas 52, Pt. 1 (10). University of Kansas Science Bulletin 27: 185-233.

Hamilton, K.G.A. 1972. The Manitoban fauna of leafhoppers (Homoptera: Cicadellidae): II. The fauna of macro-leafhoppers. The Canadian Entomologist 104: 1137-1148.

Hamilton, K.G.A. 1982. The spittlebugs of Canada. Homoptera: Cercopidae. Insects and Arachnids of Canada 10. Agriculture Canada Publication 1740, Ottawa. 102 pp.

Hamilton, K.G.A. 1987. The Ojibway Prairie Provincial Nature Reserve, Ontario. Arthropods of Canadian Grasslands Newsletter 4: 2-3.

Hamilton, K.G.A. 1990. Grasslands of Ontario and surrounding areas. Arthropods of Canadian Grasslands Newsletter 5: 2-10.

Hamilton, K.G.A. 1994. Leafhopper evidence for origins of northeastern relict prairies (Insecta: Homoptera: *Cicadellidae*). Pp. 61-70 *in*: Wickett, R.G., Lewis, P.D., Woodliffe, A. and Pratt, P. [Eds.], Proceedings of the Thirteenth North American Prairie Conference. Preney Print & Litho Inc., Windsor.

Hamilton, K.G.A. and R.F. Whitcomb. 1993. Leafhopper (Insecta: Homoptera: Cicadellidae) evidence of Pleistocene prairie persistence [abstract from 4th joint meeting of the Botanical Society of America and the Canadian Botanical Association]. American Journal of Botany 80: 67.

Hanna, M. and Moore, T.E. 1966. The spittlebugs of Michigan (Homoptera: Cercopidae). Papers of the Michigan Academy of Science, Arts and Letters 51:39-73.

Medler, J.T. 1942. The leafhoppers of Minnesota. Minnesota Technical Bulletin 155: 196 pp.

Panzer, R. 1993. Recovery Research Project Progress Report (1992) [unpublished]. 8 pp.

Panzer, R., D. Stillwaugh, R. Gnaetinger and G. Derkovitz. 1995. Prevalence of remnant restriction among the prairie and savanna-inhabiting insects of the Chicago region. Natural Areas Journal 15:101-116.

Wendt, K.M. 1984. A Guide to Minnesota Prairies. Minnesota Department of Natural Resources, St. Paul. 71 pp.

Variations in Transeau's Maps of the Prairie Peninsula

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Abstract. Edgar N. Transeau published a map of the Prairie Peninsula in *Ecology* (1935) that was a modified version of a pre-1935 map. A different version of the pre-1935 map was published in J. E. Weaver's *North American Prairie* (1954). Another map, left by Transeau, with "(revised 1956)" printed on it and nearly identical to the one published in Weaver's book, is in the archives of the Natural Vegetation of Ohio Project at The Ohio State University. The map in Weaver (1954) and Transeau's Revised 1956 map were trimmed so that the western and southwestern boundaries of the Prairie Peninsula were moved about 165 km east and 160 km north, respectively, of their locations on the 1935 published map. The version of the pre-1935 map, from which the 1954 and 1956 maps were derived, may have been trimmed, perhaps on the advice of Weaver, before Transeau sent a copy to Weaver, or it may have been altered by Weaver, in which case Transeau accepted Weaver's modification of the map. The western boundary of the Prairie Peninsula on the map in Weaver (1954) and on Transeau's Revised 1956 map coincides very closely to the locations of Weaver's easternmost Tallgrass Prairie study sites in western Iowa.

Key words: E. N. Transeau, J. E. Weaver, revised maps of Prairie Peninsula, Tallgrass Prairie

Introduction

The Prairie Peninsula, an eastward peninsula-like extension of the Tallgrass Prairie into the Eastern Deciduous Forest Region long has been recognized as a distinct geographic feature of the North American Grasslands (Pound and Clements 1898). Gleason (1923) was the first individual to characterize this region floristically, but Transeau (1935) provided the name "Prairie Peninsula" and mapped its boundaries (Stuckey 1981).

Plant geographers, vegetation scientists, plant ecologists, and other students of the North American Tallgrass Prairie are well aware of Transeau's map of the Prairie Peninsula published in *Ecology* (1935). However, these same individuals apparently are unaware that more than one version exists of Transeau's map. For example, the caption for the map of the Prairie Peninsula printed in both the first and second editions of Barbour *et al.* (1980, 1987) reads "...as mapped by Transeau (1935)." However, except for deletion of county boundary lines, this map is identical to the map of the Prairie Peninsula published in Weaver (1954), which differs from Transeau's 1935 map published in *Ecology* (1935).

In this paper, five versions of Transeau's map of the Prairie Peninsula are compared, and a suggested scenario is given for the origins and relationships of these maps.

Methods

The boundaries and inclusions of prairies were compared on five versions of Transeau's map of the Prairie Peninsula: (1) map of the Prairie Peninsula prepared by Transeau, here designated as a pre-1935 map[1]; (2) modified version (Version 1) of the pre-1935 map; (3) map published in *Ecology* in 1935 (same as Version 1); (4) map published in *North American Prairie* by Weaver (1954); and (5) map left by Transeau (1956a) with "(revised 1956)" printed on it. These maps also were compared with a map showing the locations of Weaver's Tallgrass Prairie study sites (Weaver and Fitzpatrick 1934; see also Weaver 1968). In the latter comparison, particular attention was given to the location of the western boundary of the Prairie Peninsula in relation to the locations of Weaver's easternmost Tallgrass Prairie study sites. The pre-1935 map, the map used for publication in *Ecology* (1935), and the Revised 1956 map are in the archives of the Natural Vegetation of Ohio Project at The Ohio State University, under the care of Ronald L. Stuckey.

Results and Discussion

The map of the Prairie Peninsula published in Weaver (1954) and the Revised 1956 map left by Transeau (1956a) initially appear to be the same (see below), but they differ from the one published by Transeau (1935) in *Ecology* (Fig. 1). On the 1954 and 1956 maps, the western boundary of the Prairie Peninsula is shown to be about 165 km east of where it was on Transeau's 1935 published map, and the southwestern boundary is about 160 km north. Thus, the 1954 and 1956 maps do not include western Iowa, extreme western Missouri, southeastern Kansas, eastern Oklahoma, or Arkansas (except for the extreme northern tier of counties). The western boundary of the Prairie Peninsula on the revised map is a straight north-south line that passes very close to the easternmost study sites of Weaver in western Iowa (Fig. 2).

Further changes occurring on the 1954 and 1956 maps are: (1) prairie sites on these maps in Darke, Hancock, Henry, Jackson, Pickaway, Ross, Sandusky, Seneca, Van Wert, Williams, and Wyandot counties, Ohio, do not appear on the pre-1935 map or the 1935 published map; (2) a few small prairies in Champaign, Clark, Greene, Madison, and Fayette counties, Ohio, are on the 1935 published map, but not on the pre-1935, 1954, or 1956 maps; (3) prairies in Franklin, Gasconade, Maries, and Osage counties, Missouri, south of the Missouri River, are on the published 1935 map, but not on the pre-1935, 1954, or 1956 maps; and (4) sizes of prairies have been enlarged in Montgomery, St. Charles, and Warren counties, Missouri, north of the Missouri River, on the published 1935 map, but not on the pre-1935, 1954, or 1956 maps (see Fig. 3).

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[1] An earlier version of the pre-1935 map prepared by Transeau also is in the archives of the Natural Vegetation of Ohio Project. It may be Transeau's first attempt at mapping the Prairie Peninsula.

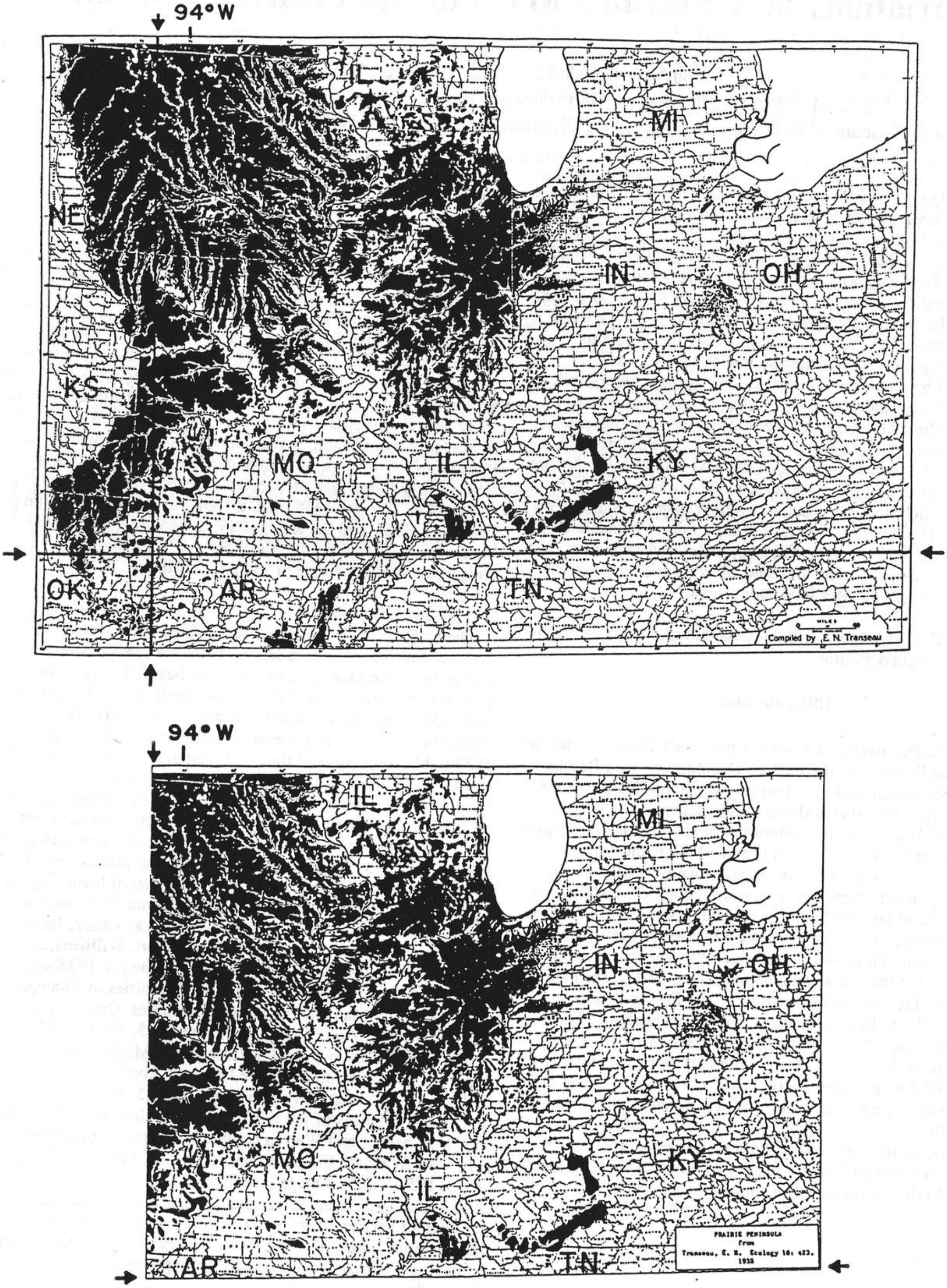

FIG. 1. (Top) Edgar N. Transeau's map of the Prairie Peninsula published in *Ecology* (1935; by permission of the Ecological Society of America) and (bottom) a modified version of Transeau's pre-1935 map of the Prairie Peninsula published in J. E. Weaver's *North American Prairie* (1954).

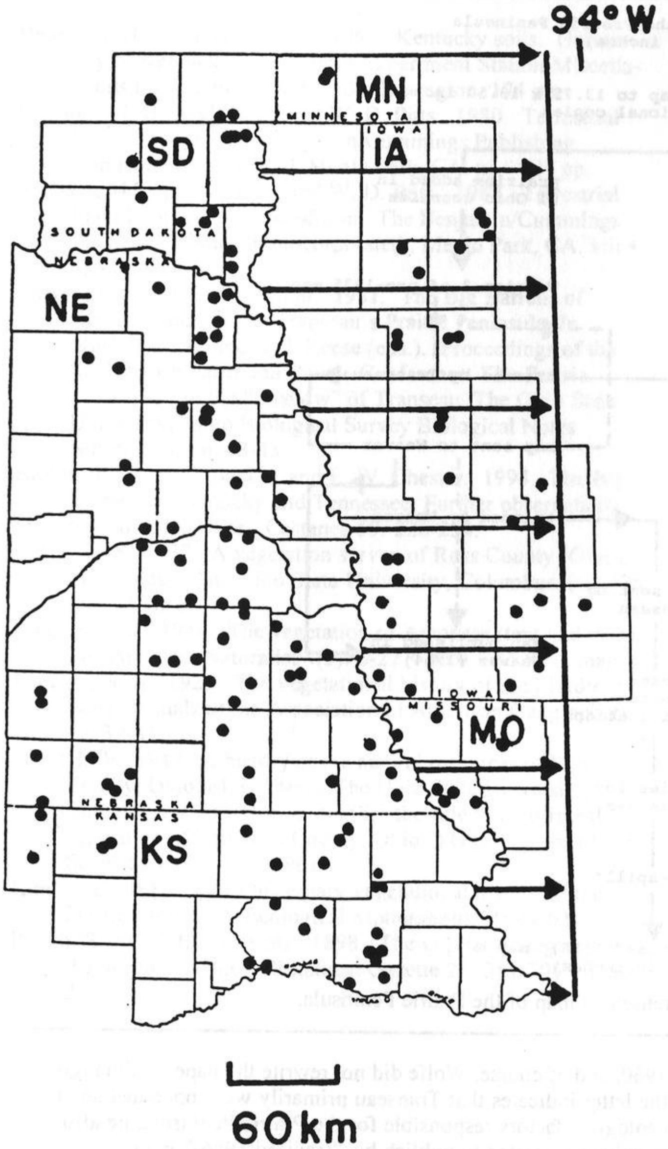

FIG. 2. Outline map showing locations (·) of J. E. Weaver's Tallgrass Prairie study sites (modified from Weaver and Fitzpatrick 1934; by permission of the Ecological Society of America). Vertical line indicates position of the western boundary of the Prairie Peninsula on the map of the Prairie Peninsula in Weaver (1954) and on the Revised 1956 map of Transeau (1956a); length of arrows shows how far the boundary was moved eastward.

The only difference between the map of the Prairie Peninsula published in Weaver (1954) and the Revised 1956 map of Transeau is a large area blackened-in with ink on the latter map. This blackened area covers portions of Carroll and Boone counties in northwestern Arkansas and adjacent parts of Stone and Taney counties in southwestern Missouri. Close examination under magnification reveals sharp black projections of ink around the edge of the blackened area, indicating that the ink flowed a bit. All other blackened areas on the map representing prairie have smooth edges. Hence, the conclusion is that the blackened area represents an accidental ink spill, and not prairie.

The ink spill occurred after the trimmed map was copied for use in plant ecology classes at The Ohio State University (Hal R. DeSelm, letter to R. Boerner, dated 28 October 1994, copy in possession of Ronald L. Stuckey). DeSelm, who obtained his Ph.D. at The Ohio State University (OSU) in 1953, has a copy of the trimmed map that he received while a student at OSU, and it lacks the ink spot.

The difference between the 1954 and 1956 maps probably is of little significance. Only one small prairie, in Carroll County, within the area covered by the ink spot is shown on the map of the natural vegetation of Arkansas by Dale (1986), and no prairies are shown on the map of the presettlement prairies of Missouri (Schroeder, 1982) in the area of the ink spot.

Transeau drew his pre-1935 map of the Prairie Peninsula on a large sheet of heavy paper that measures 26.50 x 38.25 inches (67.30 x 97.20 cm). The map is mounted on a large board covered with a mounted sheet of glass. Transeau had smaller copies printed of this large-size pre-1935 map. The smaller-size map measured 13.75 x 19.50 inches (34.90 x 48.50 cm). Before he sent it to *Ecology*, Transeau made modifications to the map in Ohio and Missouri. These changes include the addition of a few small prairies to five counties in west-central Ohio, the addition of prairies to four counties in Missouri, and the increase in sizes of prairies in three counties in Missouri (Fig. 3). Transeau made these modifications with a black-ink pen. The new blackened-in areas stand out and are more shiny than all the other black areas representing prairies on the map.

This smaller, modified, pre-1935 map (Version 1, Fig. 3) was used for making the copy of the map published in *Ecology* (1935), because on the back of the map is written in red ink "Transeau fig. 1 Reduce to 7 in " along the short side of the page. These notations were written by an editor, because the words are not in Transeau's handwriting.

It seems reasonable that Transeau sent Weaver a 13.75- x 19.50-inch (34.90- x 48.50-cm) copy-size of a modified version (Version 2, Fig. 3) of his pre-1935 map, but not of the one published in *Ecology* (1935). Several years may have elapsed between the time Version 1 of the pre-1935 map was published in *Ecology* and the time Transeau sent a copy to Weaver. In the meantime, Transeau was making changes in Ohio by adding prairie locations in other counties on another copy of the pre-1935 map. The map on which these changes were made become Version 2 (Fig. 3). This procedure would explain why the prairies in Darke, Hancock, Henry, Jackson, Pickaway, Ross, Sandusky, Seneca, Van Wert, Williams, and Wyandot counties are shown on the map in Weaver's book (1954) and on the Revised 1956 map of Transeau, but not on the map in *Ecology* (1935). The prairies added in these 11 Ohio counties probably came about as Transeau's students completed their M.S. or Ph.D. theses on the vegetation of various counties in Ohio, for example, Ross County (Crowl 1937) and Van Wert County (Good 1947). Transeau apparently took the prairie locations from their maps and added them to a 13.75- x 19.50-inch (34.90 x 48.50 cm) copy of his pre-1935 Prairie Peninsula map.

Two unanswered questions are: (1) Who was responsible for trimming the modified, pre-1935 map (Version 2 in Fig. 3) to the boundaries of the Prairie Peninsula shown on the map in Weaver (1954) and on the Revised 1956 map of Transeau (Fig. 1)?; and (2) Why was the date on Transeau's Revised 1956 map added 2 years after publication of Weaver's book? The map could have been cut off by Transeau before it was sent to Weaver, perhaps at the suggestion of Weaver, or Weaver could have trimmed it, in which case Transeau accepted Weaver's modifications. Another possibility is that both men had a part in trimming the map. Perhaps Weaver trimmed the pre-1935 map, or advised Transeau to trim it, to exclude his easternmost study sites, in western Iowa, from the Prairie Peninsula. Support for the suggestion that Fig.

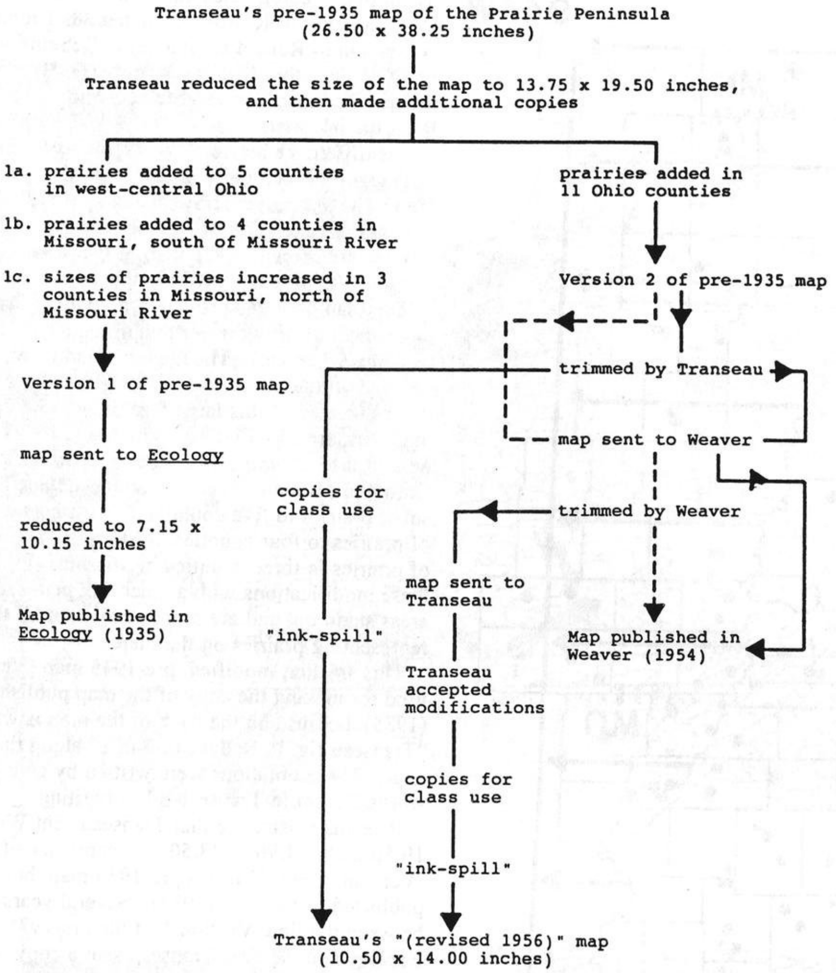

FIG. 3. Suggested origins and relationships of various versions of Transeau's map of the Prairie Peninsula.

Weaver may have had a roll in trimming the map comes from the fact that the western boundary of the Prairie Peninsula on the map in Weaver (1954) and on the Revised 1956 map of Transeau coincides very closely with the locations of Weaver's easternmost study sites in western Iowa (Fig. 2).

The only correspondence between Transeau and Weaver located is a letter (in personal possession of Ronald L. Stuckey), dated 10 September 1954, in which Weaver informed Transeau that under separate cover he was sending him a complimentary copy of *North American Prairie*. In that letter, which Transeau mounted on the inside back cover of his copy of this book, Weaver wrote, "I regret to tell you that despite the fact I marked out the new prairie on your map, that, by mistake this was not the copy sent to the engraver." What is the meaning of this statement? Does it pertain to prairies in the five counties in Ohio and the seven counties in Missouri, which are on the map in *Ecology* (1935), but not on the version in Weaver (1954)? Was Weaver supposed to have added them to the copy of the modified pre-1935 map (Version 2, Fig. 3) sent to him by Transeau?

In a letter to his student John N. Wolfe in August 1956, Transeau (1956b), probably at the urging of Wolfe, stated that he recently had been thinking about rewriting the Prairie Peninsula paper. However, Transeau concluded the task was too difficult for him and suggested to Wolfe that, "Perhaps, you might someday rewrite the whole paper..." Transeau died in January 1960, and of course, Wolfe did not rewrite the paper. Although the letter indicates that Transeau primarily was concerned about ecological factors responsible for the Prairie Peninsula, he also may have intended to publish his "(revised 1956)" map.

The Big Barrens of Kentucky and Tennessee are on all versions of the map of the Prairie Peninsula discussed above. However, Baskin and Baskin (1981) and Baskin *et al.* (1994) have presented considerable evidence against including these barrens in the Prairie Peninsula. Two strong arguments for not including the Big Barrens in the Prairie Peninsula are (1) the soils were formed under forests (Bailey and Winsor 1964), and (2) barrens of the Big Barrens Region did not originate until after the Hypsithermal Interval (Wilkins *et al.* 1991), whereas the Midwestern Tallgrass Prairies came into existence in the early stages of the Hypsithermal Interval (Wright 1968; King 1981). Thus, we suggest that any further modifications of Transeau's map of the Prairie Peninsula should include deletion of the barrens of the Big Barrens Region of Kentucky and Tennessee. Furthermore, no valid reason exists to believe that any of the other prairie areas shown on the maps in Kentucky and Tennessee, or even in Adams County in unglaciated southern Ohio, should be considered part of the Prairie Peninsula.

References

Bailey, H. H. and J. H. Winsor. 1964. Kentucky soils. University of Kentucky Agricultural Experiment Station Miscellaneous Publication Number 308. Lexington, 174 pp.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1980. Terrestrial Plant Ecology. The Benjamin/Cummings Publishing Company, Incorporated, Menlo Park, CA. xi + 604 pp.

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. Terrestrial Plant Ecology. Second edition. The Benjamin/Cummings Publishing Company, Incorporated., Menlo Park, CA. xiii + 634 pp.

Baskin, J. M. and C. C. Baskin. 1981. The Big Barrens of Kentucky not part of Transeau's Prairie Peninsula. In Stuckey, R. L. and K. J. Reese (eds.). Proceedings of the Sixth North American Prairie Conference, The Prairie Peninsula - in the "Shadow" of Transeau. The Ohio State University, Ohio Biological Survey Biological Notes Number 15, pp. 43-48.

Baskin, J. M., C. C. Baskin, and E. W. Chester. 1994. The Big Barrens of Kentucky and Tennessee: Further observations and considerations. Castanea 59: 226-254.

Crowl, G. S. 1937. A vegetation survey of Ross County [Ohio]. M.S. Thesis, The Ohio State University, Columbus. [x], 176 pp. + 33 maps.

Dale, E. E. Jr. 1986. The vegetation of Arkansas (text and map). The Arkansas Naturalist 4(5): 6-27 + 40.0 x 35.5 cm map.

Gleason, H. A. 1923. The vegetational history of the Middle West. Annals of the Association of American Geographers 12: 39-85.

Good, E. E. 1947. A history of the natural resources of Van Wert County, Ohio. M.S. Thesis, The Ohio State University, Columbus. 91 pp. (Revised under the title "The original vegetation of Van Wert County, Ohio.") Ohio Journal of Science 61: 155-160. 1961.

King, J. E. 1981. Late Quaternary vegetational history of the Prairie Peninsula. Ecological Monographs 51: 43-62.

Pound, R. and F. E. Clements. 1898. The vegetation regions of the prairie province. Botanical Gazette 25: 381-395 + plate 21.

Schroeder, W. A. 1982. Presettlement prairie of Missouri. Second edition. Missouri Department of Conservation Natural History Series Number 2. 37 pp.

Stuckey, R. L. 1981. Origin and development of the concept of the Prairie Peninsula. In Stuckey, R. L. and K. J. Reese (eds.). Proceedings of the Sixth North American Prairie Conference, The Prairie Peninsula - in the "Shadow" of Transeau. The Ohio State University, Ohio Biological Survey Biological Notes Number 15, pp. 4-23.

Transeau, E. N. 1935. The Prairie Peninsula. Ecology 16: 423-437 + foldouts of figures 1, 9, 10, and 11. (Figure 1 is the map of the Prairie Peninsula.)

Transeau, E. N. 1956a. Prairie Peninsula. Revised black and white 10.5- x 14.0-inch (26.70 x 35.60 cm) line-drawn map in the archives of The Ohio State University Herbarium. 1 p.

Transeau, E. N. 1956b. [Letter to John N. Wolfe, 21 August 1956.] 1 p. Original in the library of Joseph D. Laufersweiler, University of Dayton, Dayton, Ohio; copy in possession of Ronald L. Stuckey. The relevant portion of this letter has been quoted in Stuckey (1981).

Weaver, J. E. 1954. North American prairie. Johnsen Publishing Company, Lincoln, Nebraska. xi + 348 pp.

Weaver, J. E. 1968. Prairie plants and their environment. University of Nebraska Press, Lincoln. xi + 276 pp.

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

Wilkins, G. R., P. A. Delcourt, H. R. Delcourt, F. W. Harrison, and M. R. Turner. 1991. Paleoecology of central Kentucky since the last glacial maximum. Quaternary Research 36: 224-239.

Wright, H. E. 1968. History of the Prairie Peninsula. In R. E. Bergstrom (ed.). The Quaternary of Illinois. A Symposium in Observance of the Centennial of the University of Illinois. University of Illinois College of Agriculture Special Publication Number 14, pp. 78-88.

[illegible]

[illegible] University of Nebraska [illegible]

Weaver, [illegible] and T. [illegible]

[illegible] Mississippi [illegible]

[illegible] and [illegible] Survey, [illegible] geology [illegible]

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Ross, J. M. and [illegible]

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[illegible] survey of [illegible] County, [illegible]

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Hale [illegible] the [illegible] geology [illegible] Geological map

Gibson [illegible] A [illegible] geological history of the Middle [illegible] Association of American Geographers [illegible]

[illegible] of the [illegible] County, Ohio: M.S. Thesis, The Ohio State University, Columbus, [illegible] pp. [illegible] with the [illegible] vegetation of [illegible] County, Ohio [illegible]

King, L. L. [illegible]

[illegible] Ohio [illegible]

Powell, [illegible] L. [illegible] botanical [illegible]

June Bugs and Turkeys: Biocontrol in Oklahoma 1889-1907

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Abstract. Biological control, the nonchemical control of insect pests, has resurfaced recently as a new field in the research and development labs of agrichemical giants like Dupont, Monsanto and American Cyanimide. But "biocontrol" has a long history, beginning with USDA efforts to control cottony cushion scale, gypsy moth and boll weevil before the turn of the twentieth century. This paper discusses the history of biocontrol in Oklahoma between 1893 and 1907 and illustrates the need for environmental history's perpective in the study of entomology and ecology today.

Key words: Environmental History, Biological Control, Oklahoma, Chinch Bug, June Bug, Boll Weevil, Earth Summit

Introduction

Environmental history is defined by its practioners as the study of past ecologies. In this context, environmental historians tend to see themselves as interpretative mediators, offering to scientists and policy makers an historical perspective on present-day environmental conditions.

As in other disciplines, there is debate among environmental historians over how best to meet this objective. Some consensus does exist, however, about the major factors that account for changes in any environment that may help link my story about past prairie ecologies to present ones. Three variables are consistently at work in determining the direction environments take historically. The first variable is the physical environment itself: climate soil, wildlife, vegetation, and of course, insects. I also include human beings if they are present, although some environmental histories persistently exclude people, a legacy of the classical dualism between" man" and "nature."

The second factor at work in environments in which people are present, is the economy. This can be an exogenous factor, out of the immediate control of the human beings directly engaged in harvesting "natural resources" from the physical world around them, transforming them into abstract commodities. Markets attach positive value to some elements of the physical world and not to others, the boll weevil (*Anthonomus grandis*) for example.

The third, and least easily defined variable is culture. The sources of farming culture in early Oklahoma can be found everywhere, in popular literature, USDA guidelines and in the received wisdom of farmers passed from one generation to the next. Self identified social groups, like agriculturalists, share common values and goals that cause them to "see" problems and seek solutions in particular ways. Culture played an important role in both the rise and fall of biocontrol in Oklahoma from the time of of the first "runs" in 1889 to World War I.

Obviously the boundaries that help define terms like ecology, economy and culture are highly subjective and cannot be considered separate from one another. Identifying the various "strands" (Liebhardt, 1988) of environmental change, however, is foundational for revealing the dynamic nature of their interaction over time. It is this dynamic between the ecology of the southern plains, an emerging international market for agricultural products and farmer's and scientists' attitudes toward insects "pests" that makes the story of early twentieth century biocontrol in Oklahoma relevant for ecologist and entomologists today.

Ecologist themselves admit their studies rarely take into account socio-political or ideological factors--the stock-in-trade of historians. In fact, the science of ecology is split into so many specialized applications that ecologists attempting total systems research face grave difficulty (Worster, 1977). Significantly, the ecologist George M. Van Dyne (1974) has warned that the lack of interdisciplinary research among ecologists may retard our understanding of the Great Plains in particular, "even as these lands are called upon to provide food, water and recreation for tomorrow's growing population." As the historian Alfred Crosby has pointed out, "only the brass bottomed historian if going to be willing to spend the requisite time in the archives" (Crosby, 1990).

Biocontrol in Oklahoma

Biocontrol, which Richard Sawyer (1990) an agricultural historian has defined as the "reduction of pest populations by their enemies," has a much longer history than our post-DDT generation acknowledges. Anglo-American farmers arriving in Oklahoma between the first land run in 1889 and 1907, when Oklahoma entered the Union, faced a difficult task: converting what they perceived to be "virgin" prairie into something that approximated the farmsteads of the more settled East. Many of Oklahoma's early settlers were first time farmers, or "mechanics" and the austere landscape contained numerous surprises. Rattlesnakes, grasshoppers and blood sucking chiggers are native to Oklahoma's redbed plains and homesteaders complained loudly about the inhospitable nature of the land in terms of human comfort.

More important, farmers' dependence on the land for subsistence was precarious at best, particularly in the semi-arid counties west of present-day Oklahoma City and in the Red River valley where a corrupt system of sharecropping severely limited farmers' ability to supply their own basic needs. Even under the best of economic and regional circumstances, farmers were frequently frustrated by a highly variable climate that alternately threatened drought, hailstorm or flood. Contagious livestock diseases like blackleg, cash crop failures, prairie fires, and, of course, native and exotic insect pests all consipired to frustrate the new settlers' ambitions. As Mrs. E.J. Seig (1905) of Garfield County wrote the Oklahoma Experiment Station Director, "we experiment, in fact we try ways and ways to bring best results from an uncertain soil and climate, rain conditions and the rest. Oats were a failure. Best wheat won't make 10 bushels an acre."

Given the unremitting toil of homesteading it is not difficult to imagine farmers' despair when their hard-earned crops were devoured by insects. By far the most common and stubborn pest was the chinch bug (*Blissus leucopterus*). A stowaway insect from the East without local predators, the chinch bug fed on the underground roots and tender primary shoots of wheat, corn, millet and oats. It thrived nearly as well on the region's native bluestem, grama and buffalo grass, but it clearly preferred domestic crops. From a survey of the correspondence to the experiment station at Stillwater and the station's Bulletins, it would appear that Oklahoma farmers were at a loss to control chinch bug infestation. Unlike some insects that appeared seasonally and could be picked off the plants by hand, chinch bugs lived underground for portions of the year, escaping farmers' efforts to kill them by moving into the adjacent prairie.

It was the rapid spread of this insect in Oklahoma in the early 1890s that led to the state's first efforts in biocontrol.

Scientists working at the newly founded United State Department of Agriculture's Experiment Station in Stillwater did not invent the strategies they recommended to combat the chinch bug. Entomologists in Illinois and Kansas were already at work on the problem. They noticed that the chinch bug was fatally susceptible to a "white fungus disease" that under the right conditions spread throughout the insect population. Stillwater scientists enthusiastically directed farmers send them one or two quarts of live bugs for infection. Station staff returned the infected bugs (postpaid) to the farmer who released them back into the field to infect the rest of the chinch bug population. Farmers responded very well to the idea, and soon the stations was sending out infected specimens all over the territory.

Unfortunately, humidity was one of the necessary conditions for successful infection, rendering the entire proceedure useless in the semi-arid portions of the state where infestation was heaviest. By 1895, the station director (Morrow, 1896) had given up biocontrol of the chinch bug by infection and instead recommended control of the insect by the barrier and trap method. Farmers were not as keen on this idea as they had been on infection because it took more effort, used up valuable acreage between fields and was only effective when every farmer in an infested area participated. In spite of its dismal failure as a pest control method, written requests for more "sick bugs" continued to arrive at the experiment station as late as 1910.

Another troublesome group of insects, from the farmer's perspective, were the various borers, scales and moths partial to fruit trees. We would hardly consider Oklahoma a fruit belt today, but in 1890 many respected agricultural specialists believed in the "rain follows the plow" theory of climactic control and encouraged tree planting as a way of increasing the amount of annual rainfall. Farmers throughout Oklahoma planted large and small orchards next to their dugouts and soddies. Sold by salesmen door-to-door, most of the trees were of questionable quality and died soon after planting. Nevertheless, orchard insects were a major concern of farmers at the turn of the century. In this battle, Oklahomans looked to California for hope, where cottony cushion scale had threatened to destroy the citrus industry and was virtually eliminated by the importation of the vadalia beetle in 1888 (Perkins, 1982).

But Oklahoma's insects were more diverse, unresearched and less willing to follow suit. In terms of biocontrol, the best Station staff could do was to report on the successful use of natural predators by farmers. In an early bulletin in 1895 and in several reprints thereafter, the station's recommended remedy for eradicating the peach eater, otherwise known to us as the June bug (*Phyllophaga fusca*), was sent them by a territory farmer. Noticing that this large beetle behaved more sluggishly in the early morning hours, the farmer enterprisingly drove his flock of turkeys into the orchard to eat the insects off the ground and lower tree branches. He reported that he increased this method's effectiveness by knocking the bugs from the trees with a stick. Finally, this remarkable man claimed to have trained his hungry flock to knock the bugs from the trees themselves, which allowed him few extra minutes each morning to sleep, eat breakfast or read the paper.(Bogue, 1903)

Station staff pointed to the potential usefulness of other natural predators, such as the toad, and praying mantis. (One small toad was discovered to have 235 chinch bugs in its stomach.) By and large, however, the only effective remedy against orchard insects was the elimination of infected branches and trees, together with liberal applications of Paris Green and Bordeaux mixture. These early chemical pesticides were arsenic based, and generally did as much damage to the trees and crops on which they were applied as they did to the insects. As the Station entomologist (Bogue, 1903) warned, "the station has no mysterious means to be employed against insect ravages and it is often the case the best thing that can be done is to turn to some common means that nearly everyone has at hand."

June bugs, however, paled in economic significance to the next insect to threaten Oklahoma's agricultural industry: the Mexican Cotton Boll Weevil. The story of this insect's migration from Mexico through Texas and across the South is a familiar story among entomologists. Predicting the eventual failure of the cotton industry if left unchecked, USDA scientists and administrators committed all of their resources to finding potential natural predators to the weevil, even importing (at great expense) an ant from South America that failed to survive the Texas winter. The successful importation of the vedalia beetle (*Coccinellidae* family) raised hopes that given time, a natural enemy would be found.

In the meantime, experiment station staff and the newly organized Extension Service (created by Congress expressly to control the boll weevil) undertook a program of farmer education they hoped would keep the pest under control. Their recommendations included planting in wider rows, clean cultivation and the burning of the cotton stocks in the fall to deprive the insect of food to keep it over the winter. Here, as with the chinch bug, USDA staff ran into an unmovable wall of economic and cultural resistance. Wider rows meant less overall yield, clean cultivation required more labor and the burning of the stalks deprived farmers of the "top crop:" the small harvest of late forming bolls. Moreover, the traditional economy of cotton production was based on tenancy. Officials could not ban the production of cotton in certain areas to prevent the insect from spreading due to tenants' dependency on the crop to meet their landlord's terms. Efforts to find a natural predator to the weevil were abandoned under the time pressure of finding a solution to the problem. Social control of the insect seemed impossible given the economic and social structure of cotton farming. The most expedient solution lay in chemical control, thus beginning "ol, King Cotton's addiction" to chemical pesticides. The search for toxic substances to eradicate the weevil began in earnest after 1917 and reached its zenith with the discovery of DDT during the second world war (Perkin, 1982). Biocontrol research was relgated to the dusty back shelf of agricultural entomology.

Conclusion

The point of these examples is twofold, first, biological control was a viable component of early pest control strategies, and second, neither farmers or scientists were prepared to place it in ecological context. Contrary to popular thinking, biological control did not fail to become the dominant paradigm of pest management because it was less effective, at least before the discovery of DDT in World War II. It failed because scientists and policy makers did not take into account all the variables that shape environmental change, especially when people are an integral part of an ecological system.

Today, biological control is undergoing re-examination as numerous corporations--the same industry that produced DDT and its derivatives--are attempting, once again, to find natural predators, this time in the form of genetically altered organisms (Smart, 1992). In the years since the publication of Rachel Carson's *Silent Spring* in 1962, ecologists have had to reconsider many of the premises upon which the chemical control of insects were based. Integrated Pest Managment (IPM) is an example of post-DDT strategy that recognizes the essential interdependence of every organism in any ecological system. This was not the solution Oklahoma farmers were looking for at the turn of the century. Instead, they demanded a specific cure for an isolated problem. In other words, Oklahoma's early farmers utilized biological weapons against insect pests in precisely the same way they sprayed chemical pesticides on their trees and crops.

John Perkin, an historian of pesticide use, has called this approach "augmentive biological control." This approach to pest control is based on a mechanical view of nature wherein human beings can manipulate nature to their own ends, much like replacing the obsolete parts of a machine with new and better ones, without compromising its productivity (Botkin, 1990). The challenge facing ecologists today, is not simply to find new chemicals (synthetic or genetically engineered) to control insect damage to crops, but to develop technologies that take into account the dynamic nature of human and non-human life as they come together in complicated webs of physical, economic and cultural forces.

The recent United Nations Conference on Environment and Development, or the Earth Summit of 1991, identified biological control as one of the most promising alternatives to chemicals in underdeveloped nations. The difference, however, between the way in which agrichemical companies and environmentalists regard bio-control is a perfect example of the difference between a mechanistic view of "nature," in which economics and society are disregarded, and a more wholistic view that can accommodate human beings. As the summit report declared, "Environmentally sound technologies are not just individual technologies, but total systems which include know how, procedures, goods and services... compatible with nationally determined socio-economic, cultural and environmental priorities" (Johnson, 1993). This new emphasis on "total systems" promises to provide entomologists with a more rational context for finding long term solutions to pest control problems.

Literature Cited

Botkin, Daniel. 1990. *Discordant Harmonies*. Oxford University Press, Boston, pp 101-110.

Crosby, Alfred. 1990. An Enthusiastic Second. *Journal of American History*. Vol.74, pp 1117-1148.

Johnson, Stanley P. 1993. *The Earth Summit*. Graham and Trotman, London pp 265-286.

Leibhardt, Barbara. 1988. Interpretation and cultural analysis: Theories in environmental history. *Environmental Review*, Spring 1988. pp 23-26.

Perkins, John H. 1982. *Insects, Experts and the Insecticide Crisis*. Plenum Press, New York, pp 66-90.

Sawyer, Richard. 1990. Monopolizing the Insect Trade: Biological Control in the USDA, 1888-1951. *Agricultural History*, Spring, 1990, p 271.

Smart, Bruce. 1992. *Beyond Compliance: A New Industry View of the Environment*. World Resources Institute, 283 pp.

Van Dyne, George M. 1974. Ecosystems,Systems Ecology and Systems Ecologists. in George Cox, ed., *Readings in ConservationEcology*. Meredith Corporation, New York.

Worster, Donald. 1977. *Nature's Economy*. Cambridge University Press, New York, pp 242-250.

A Re-vision of History: Plains Cree and the Aspen Parkland of Western Canada.

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Abstract. A review of literature concerning Plains Cree historical relationships with the aspen parkland belt uncovers a series of colonial misconceptions regarding wholesale population movements from woodland to prairie, which have remained largely unchallenged. Recognizing aspen as a "fire species" provides the opportunity to employ aspen spacial density as a cultural record of a people's long-term relationship with the land. The role of fire used by the Plains Cree as an ecological management tool is investigated in terms of non-native world views conflicting with native sustainable resource-management practices.

Key words: Plains Cree, aspen, prairies--Canada, aspen parkland belt, fire, history--Canada, ecology--prairie

Introduction

David Mandelbaum, an American ethnographer, claims that the Plains Cree were displaced westward from the forests of northwestern Ontario or eastern Manitoba as a direct result of rapid expansion of the fur trade in the late 1700's (45-6). These bands apparently became so dependent on European trade goods that they quickly overharvested their homeland and, along with their Assiniboin allies, invaded the forest, parkland, and prairie of what is now western Manitoba, Saskatchewan, and eastern Alberta. Their almost exclusive use of guns forced the rival Gros Ventre, Blackfoot, Peigan, Blood, Slave, and Chipwyan from their ancestral lands, and, in turn, they displaced the Snake, Kutenai, and other groups in southern Alberta. Once Crees were established firmly on the plains, they adopted cultural forms in keeping with their new environment (Russell, 1991, 16-27).

Mandelbaum's ethnography and history of the Plains Cree is considered the definitive piece of scholarship. In semiotic terms, he has written the "classic text," a statement privileged enough to define and situate the subject so as to actually pre-exist and exceed it (Silverman, 1983, 242-5). His view rarely is questioned in the literature and still is being upheld. Milloy describes Mandelbaum as "the anthropological expert on the Plains Cree" (1991, 59) and fully adopts Mandelbaum's analysis of Cree cultural history, thereby unfortunately reproducing Mandelbaum's status as the definitive scholar in this area.

Russell (1991) points out major flaws in Mandelbaum's work and traces unsubstantiated theorizing back to writings of the explorer Sir Alexander Mackenzie. Russell states that Mandelbaum took Mackenzie's writings out of context to support his reliance on crisply defined boundaries separating woodland from prairie cultural practices. Mandelbaum's work relied on a definite break from woodland to plains environment. For the next 200 years, Mackenzie's comments have been twisted out of context and developed into historical "fact." Although ethnographic evidence, particularly from Hudson's Bay Company journals, contradicts this view, Mandelbaum's interpretation of Plains Cree history continues to persist (Russell, 1991, 84-119). Consequently, his anthropological subjects are encased firmly in a static collective identity.

Russell (1991, 22) shows that, to support his thesis, Mandelbaum denied the role of parkland transition areas in Plains Cree lives. Mandelbaum (1940, 46) believed that Cree ties to the forest were maintained until ca.1820, at which time they gradually became a "true" Plains tribe with an accompanying change in forms of cultural expression. But Russell maintained that the aspen-dominated (*Populus tremuloides*) parkland area was the Cree's home base, rather than the forest or open plains. This view is supported by the fact that all but two reservations in Saskatchewan are located in the parkland belt (Carter, 1990, xi; Russell, 1991, 218; Bird, 1961, x). The importance of bison movements between the plains and parkland, along with Cree economic reliance on bison, underscores the basis for a seasonal hunting and gathering cycle that included the parkland area to a more substantial degree (Russell, personal communication, 1993). Additionally, aspen stands provided a protective environment during harsh weather and an ecological complex that included many sources of food and important plants.

If we accept Russell's version of western Cree history, then Cree bands were established on the plains and parkland long before Europeans arrived. Margaret Hanna, curator of the Provincial Museum in Regina, reports that Cree pottery fragments in the Duck Mountain area of western Manitoba date to 800-900 years ago, and Assiniboin pottery in Saskatchewan may be 1000 years old. Hanna (personal communication, 1993) agrees with Russell that Cree movements into southern Saskatchewan observed by European explorers were from population shifts after epidemics rather than a wholesale immigration from the East (Russell, 1991, 213-17), thereby drawing points of perspective set up by Mandelbaum into question.

Cree's Use of Fire in Aspen Parkland

If we consider Russell's proposal that the aspen parkland was a major element of Plains Cree habitat, then tracing ecological relationships between the Cree and this complex habitat may be useful in future anthropological work. Use of fire by Parkland Cree (Russell (1991) suggests that "Parkland" may be a more appropriate modifier term than "Prairie") as a tool for maintaining a desirable ecological balance is a major component of their overall adaptive strategy. Descriptions of native fire technologies by Stewart (1956), Pyne (1982), Wright & Bailey (1982), and Lewis (1982) indicate that burning by natives is a determining factor in the formation and maintenance of North American grasslands.

Northern Plains First Nations systematically and routinely burned the woods and prairie for a number of reasons: as a tactical device (Pyne 1982, 72; Russell, 1991, 97-8); to stimulate soil fertility (Pyne, 1982, 74; Hughes, 1983, 66; Lewis, 1982, 15; Stewart, 1956, 120); to manipulate distribution of game (Pyne, 1982, 75; Hughes, 1983, 56; Lewis, 1982, 31-4); to clear underbrush for improved visibility and ease of travel; and to reduce large uncontrollable fires fuelled by deadfall and dead grass (Ray, 1971, 279-80). Cree economic and cultural production are integral factors in their interdependent relationship with prairie/parkland ecology, thereby physically locating them in ecological transitional zones. Mandelbaum's attempts to locate them otherwise may be ideologically intriguing, but his analysis fails to recognize the historical validity of Cree practice.

Aspen's ability to grow vigorously and reproduce by cloning makes it well suited to prairie soil. These growth dynamics enable encroachment onto the prairie, thereby expanding the parkland. Periodic fires burn off aspen stems, which stimulates vigorous resprouting. However, annual or extremely hot fires eventually weaken the clone, allowing grasses and small brush to gradually push back the parkland boundary. In the northern prairies, fire suppression by European settlers enabled aspen parklands to expand significantly (Lewis, 1982, 24; Bird, 1961, 38). If fire is acknowledged as a technology utilized by the Cree to manage the aspen parkland, then these people can be located and situated in the parkland belt for many centuries before the arrival of European explorers.

Lewis (1982) provides a strong case for the systematic use of fire by natives. A 72-year-old Cree from the Frog Lake area near the North Saskatchewan River at the Alberta-Saskatchewan border described:

> It used to be all prairie here; now it's mostly forest. My father told me that long time back there were plenty of buffalo here, all the way (north) to Cold Lake. We were Plains Cree, not like those bush people up north. Now it's all bush here too. (Lewis, 1982, 24)

Europeans' Control of Fire Practices

Ethnographic evidence apparently confirms that interruption of Plains Cree resource practices substantially increased forest encroachment on the open prairie. Historically, the question of anthropogenic uses of fire is linked with events such as development of the forestry service, settlement of the land, and loss of the commons in North America. Pyne (1982) believes that American foresters were in contact with American natives, knew of their "light-burning" techniques, and systematically prevented burnings by establishing repressive bureaucratic structures.

> In England the forester had been a hated official since medieval times, an introduction of the Norman overlords and the means by which the folk were deprived of many traditional rights of access to the woods. In the United States, too, though in a more benign form, he was again seen as the official of foreign powers and ideas and as the enemy of folk usage of forest and range. The issue of proper fire practices became more than a question of technique; it developed into a political protest against intrusion by professional forestry, a European import, and against the enclosure of common lands. (Pyne, 1982, 100)

Apparently, in the late nineteenth century, European-influenced fire control measures were linked to issues of displacement of inhabitants, both native and non-native, from common lands. Propaganda wars fought by emerging governmental administrations actively devalued folk and native skills and attitudes concerning prescribed burning (Pyne, 1982, 80-1; Schiff, 1962, 36-7). It was during this period (1870-1889) that native groups signed prairie and parkland numbered treaties in Western Canada (Dickason, 1992, 274). Numerous American forestry-inspired fire-control measures were put in place to facilitate settlement. However, these practices ultimately would generate more devastating fires in western Canada than had occurred before European occupation (Pyne, 1982; Schiff, 1962; Stewart, 1956). Suppression of native fire practices was thought to be an effective component in taming nature, yet the actual effect has been contradictory. Pyne (1982, 99) argues that the loss of grasslands to choked "forest weedlots" and "impenetrable thickets" has been the legacy of European settlements in the prairies (99). Aspen "thickets" are so difficult to control that aspen is a "weed" tree (Graham et al., 1963, 2), requiring increasing resources to control its spread.

For Parkland Cree, the question of the historical treatment of their identity and claim to the land is inextricably linked to physical evidence of their burning practices. Lewis and Ferguson (1988, 60) point out that:

> The forests, parklands, and prairies of North America had already been greatly influenced and actively managed by aboriginal peoples' widespread uses of fire. The goals of Indian uses of habitat fires were predominantly technological, with the added awareness that fire is a tool of enormous potential and that it has complex and important ecological consequences.

In classic texts of Western Canadian history, the Plains Cree, subsequent to "invading" the west, appeared to adopt positions of self-interested middlemen in the fur trade. Their primal condition of living at one with nature thereby was forsaken. Mandelbaum (1940) believed that Crees used guns to invade their neighbors and caused large-scale resettling of other native groups in the western territory. As a consequence of these actions, the Crees surrendered their forest homelands to take up residence on the open prairie. To make matters worse, the Plains Cree appeared (to the Europeans) to be abusing their new homelands by constantly setting it ablaze. A series of oppositions (conqueror/vanquished, war/peace, strife/stability, prairie/forest) were set up in classic texts that eroded European romantic illusions of the Indian as a "child of nature." The Indian, in this case the Plains Cree, was vilified by scholarly research of the day and strategically associated in the public's mind with the negative side of the oppositions. As a consequence, the Cree were regarded conveniently, through their destructive practices, to have relinquished all rightful claim to the land. Hence, the hordes of foreign settlers felt justifiably free to occupy the prairies and, in the process, to replace aboriginal technologies with their own.

Further degradation of the generalized "Indian" is demonstrated by the European view of fire. Rather than imagining parkland landscape managed by fire technology for many centuries, European invaders, ignoring the necessary relationship between land and fire, focused uniquely on fire as a destructive force, inherently terrifying and uncontrollable, an apocalyptic power to be placed under firm control for everyone's benefit (Pyne, 1982, 33). Europeans laboring under this misconception could not begin to imagine the land they had "discovered" as a sustainable resource with a long history of native management. Although they cannot have been blind to the positive evidence of native firing practices, they were unable to cast themselves as anything less than superior conquerors of primitive and virginal territory. In fact, romantic ideas of primaeval forest and unclaimed grassland wilderness were essential to the European invaders' view of themselves as rightful inheritors, entitled to the land. This self-aggrandizing myth continues to hamper the prevailing Eurocentric world view in its recognition of the long-term efficacy of native technologies. Russell's deconstruction of Mandelbaum's Plains Cree myth offers a cogent and generative critical challenge to an ecologically destructive world view.

Conclusions

The absence of reliable written records or eye-witness accounts of Plains Cree history enhances and legitimizes biological and ecological "records" as new foundations for creative methodologies. Examination of ecological patterns and practices such as fire usage potentially can provide more sensitive and thoughtful revisions of historical records and inform ecologically sound management of both prairie and parkland resources. Finally, in more immediate political and economic terms, a re-visioning of Plains Cree history holds enormous implications for upcoming land claims settlements, where use and occupancy criteria must be established so that native groups can regain control of their homelands.

Literature Cited

Bird, R. D. 1961. Ecology of the Aspen Parkland: In Relation to Land Use. Occasional Publication 1066. Research Branch, Canada Department of Agriculture, Ottawa.

Carter, S. 1990. Lost Harvests: Prairie Indian Reserve Farmers and Government Policy. McGill-Queen's University Press, Montreal & Kingston.

Dickason, O. P. 1992. Canada's First Nations: A History of Founding Peoples From Earliest Times. McClelland and Stewart, Toronto.

Graham, S. A., R. P. Harrison, Jr., and C. E. Westell, Jr. 1963. Aspens: Phoenix Trees of the Great Lakes Region. University of Michigan Press, Ann Arbor.

Hughes, D. J. 1983. American Indian Ecology. University of Texas, El Paso.

Lewis, H. T. 1982. A Time for Burning. Occasional Publication 17. Boreal Institute for Northern Studies, Edmonton.

Lewis, H. T., and T. A. Ferguson. 1988. Yards, corridors and mosaics: how to burn a boreal forest. Human Ecology 16:57-77.

Mandelbaum, D. G. 1940. The Plains Cree. American Museum of Natural History, New York. 1979. Canadian Plains Studies 9. Canadian Plains Research Centre, University of Regina, Regina.

Milloy, J. 1991. 'Our country': the significance of the buffalo resource for a Plains Cree sense of territory. In: Aboriginal Resource Use in Canada: Historical and Legal Aspects. K. Abel and J. Friesen. (eds.) Manitoba Studies in Native History 6. University of Manitoba Press, Winnipeg. pp. 51-70.

Pyne, S. J. 1982. Fire in America: A Cultural History of Wildland and Rural Fire. Princeton University Press, Princeton, NJ.

Ray, A., Jr. 1971. Indian Exploitation of the Forest-Grassland Transition Zone in Western Canada, 1650-1860: A Geographical View of Two Centuries of Change. PhD Dissertation. University of Wisconsin.

Russell, D. R. 1991. The 18th Century Western Cree and Their Neighbours. Mercury Series 143. Canadian Museum of Civilization, Hull.

Schiff, A. L. 1962. Fire and Water: Scientific Heresy in the Forest Service. Harvard University Press, Cambridge, MA.

Silverman, K. 1983. The Subject of Semiotics. Oxford University Press, Oxford, U.K.

Stewart, O. C. 1956. Fire as the first great force employed by man. In: Man's Role in Changing the Face of the Earth. W. L. Thomas, Jr. (ed.) Vol. 2. University of Chicago Press, Chicago. 2 vols. pp. 115-33.

Wright, H. A., and A. W. Bailey. 1982. Fire Ecology: United States and Southern Canada. John Wiley & Sons, New York.

Perceptions of Prairie in Corporate Settings: A Study in Adaptation

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Abstract. This study examines how employees' perceptions of prairie restorations on corporate grounds have adapted over time. The sites, two research and development corporations from suburbs in Minnesota, were selected to participate in this study. The main difference between the corporations was the length of time the prairie had been on the site. Emerging trends of this study suggest there is minimal difference between the two sites concerning employees' perception of the prairie. Additionally, employees' adaptation to the prairie occurred more quickly than originally hypothesized. Mean scores and probability of t-values suggest employees' adaptation to prairie is influenced by time, location, and employees' background. This data also indicates that employees find the appearance of prairie to be a relaxing, inspirational element in the workplace, but employees do not consider the prairie to increase work productivity.

Key words: Adaptation, Perception, Prairie restoration, Adaptation factors, Time

Introduction

Prairie ecosystems have disappeared rapidly since the western portion of the United States opened for settlement. In the past 25 years, Americans who sense the loss of presettlement ecological systems have attempted to recreate them. Prairies have been restored in diverse settings including arboretums, parks, roadsides, residences, and corporate grounds.

Hypotheses

Corporations recently have begun to include prairie restorations in their landscapes, which offer low-maintenance, ecologically acceptable design solutions for corporations and their neighbors. Employees' perceptions of prairie restorations are crucial to their success in corporate settings.

This study focuses on factors that affect employees' perceptions and adaptation to the prairie. The following three hypotheses were examined: (1) Employees frequently associate the appearance of prairie with natural ecosystems and the quality of the ecosystem. (2) Adaptation to prairie restorations are affected by employees' perception of the prairie. Factors affecting adaptation include: time, exposure, company information, and employees' background. (3) Employees perceive the prairie and its surroundings as a relaxing, inspirational element in the work environment.

Perceptions of Prairie Ecosystems

Perception is a problem that limits the success of prairie restorations. Prairies are an example of a highly structured and functional environment that is often considered weedy and unkempt in appearance (Schulhof 1989). Prairies are generally appreciated differently by people and fail to achieve high rankings with current assessment approaches (Keane 1992).

Prairie, although ecologically healthy, may not meet our social expectation of beauty in nature. "Naturalness is a concept that has no specific appearance in form; it is a cultural concept determined by social process" (Nassauer 1990). Environmental policies should address landscape appearances, not because aesthetic quality is coequal with ecological health, but because landscape appearances communicate information to the viewer (Nassauer 1990).

Factors Affecting Adaptation to the Appearance of Prairie

Care. The cared for appearance of a landscape has an effect on perception of a landscape (Nassauer 1988 b). Studies were conducted on perceptions of Grand Isle coastal landscapes (Nassauer and Benner 1984), Kane County, Illinois farm landscapes (Nassauer and Westmacott 1987), and Olmsted County, Minnesota landscapes (Nassauer 1988 a). Care in the landscape was typically demonstrated by neatness in the following forms: turf evenness or crop color, ornamental plant placement, use of fences and borders, and freedom from weeds and litter.

Care has also been shown through "messy" appearances of the landscape (Nassauer 1988 b). "Messy" forms of care include: sites planted in native or drought-tolerant grasses, undisturbed forest understories, unmown ditches and lawns, areas where wetland plants appear, agricultural minimum tillage, and conservation reserve parcels. "Messy" landscapes appear attractive when viewers know their ecological function or when the landscape indicates that the messy look is intentional. The aesthetics of care is predominantly shown through neatness but now includes the ecological function of the landscape as a form of care.

Emotion. Initial emotion is a factor that theoretically affects a viewer's reaction to a scene (Ulrich 1983). Initial emotional states are significant, because they may influence the cognitive process and, subsequently, the adaptive behavior.

Knowledge. Schahn and Holzer (1990) conducted a study on West Germans to determine the effect that concrete knowledge and abstract knowledge have on landscape assessment. Abstract knowledge asked questions like, "Ecology is best described as...". Concrete knowledge asked questions such as, "How can you save water?". This study indicated that concrete knowledge influences environmentally responsible behavior.

Familiarity. Approximately 400 Kansas State University students participated in a study that examined the role familiarity has in prairie landscape aesthetics (Keane 1992). Findings strongly supported familiarity as a positive factor in preference for prairie landscapes. Additionally, statistical analysis of the study results showed that familiarity deserves consideration in the aesthetic assessment, management, and design of prairie landscapes.

Information. Hodgson and Thayer (1980) and Anderson (1981) were able to empirically alter responses to aesthetic values assigned to landscapes simply by changing titles from a naturalistic tone to one conveying a stronger cultural influence. Lower perceived value was consistently assigned to the culturally influenced titles. This study indicated that information affects viewers' perceptions.

A fundamental challenge for prairie restorations is public perception. Current literature suggests that perceived care of the landscape, emotion, knowledge, familiarity, and information are factors that affect adaptation to a landscape. In a corporate setting, employees' perceptions of prairie restorations and how perceptions adapt to the appearance of prairie is representative of the larger public issue on perceptions.

Method

Selection of Sample Sites

To determine the factors affecting employees' perception of and adaptation to prairie restorations, two corporations with offices set in restored prairie landscapes were asked to participate in this perception study. The key difference between Corporation A and Corporation B was the age of the prairie restoration. Corporation A prairie was 2 years old, and Corporation B prairie was 10 years old at the time of this survey in 1991. Corporation A represents a prairie before maturity, and Corporation B represents a mature prairie.

Both corporations were chosen from the same metropolitan area in Minnesota and were located within suburban communities. The corporations had a comparable balance of employee types who had similar opportunities to view and interact with the prairie on corporate grounds. Prairie restorations on both corporate sites were random seedings consisting of 70-80% short and tall grasses and 20-30% forbs at Corporation B, and 70-80% short grasses and 20-30% forbs at Corporation A. Random seedings, for the purpose of this study, are nondesigned seedings. Total area for the Corporation A prairie was approximately 40 acres. The original total area for the Corporation B prairie was 10 acres, but was later reduced to 2 acres because it's appearance was considered to be weedy and unkempt.

Instrument

Personal interviews to develop survey instrument. Personal interviews were conducted with 6 to 8 employees who were representative of each work group from each corporation. Participants were asked 7 open-ended questions that addressed site context, perceptions of the prairie, and prairie information supplied by the corporation. Responses from the personal interviews were used to develop a survey questionnaire.

The questionnaire developed from the personal interviews addressed the following 11 adaptation themes:

(1) Attractiveness: Measured how attractive employees found the prairie.
(2) Wildlife and Ecological Health: Measured employees' association of prairie with wildlife and ecological health.
(3) Location: Measured employees' acceptance of prairie in relation to its location.
(4) Context: Measured if the prairie was perceived to fit in with the surrounding community.
(5) Neatness: Measured limitations of prairie acceptability because of the rustic, unkempt look of the prairie.
(6) Inspiration: Measured inspirational effect of the prairie on the employee.
(7) Information: Measured the amount of information provided to the employee about the prairie by the corporation.
(8) Maintenance: Measured response to prairie burning as a maintenance practice.
(9) Productivity: Measured the prairie's influence on work productivity.
(10) Sustainability: Measured the perception of prairie sustainability.
(11) Adaptation: Measured how time and exposure affect attractiveness of the prairie. Subheadings under adaptation include exposure, prairie establishment, and time.

Selection of survey samples. One-hundred and twenty questionnaires were completed from both corporations. Sixty-two questionnaires were returned during February 1992, with approximately 50% coming from each corporation. Corporation A respondents had worked at the corporate site for 1 to 2 years, whereas Corporation B respondents had worked at the corporate site for a minimum of 5 years. Respondents witnessed the prairie installation and maturation during their employment.

Analysis technique. The adaptation themes were rated with two different scales. Respondents answered questions 1 through 31 on a scale of 1 to 7 where:

1 = strongly agreed, 4 = neutral, and 7 = strongly disagreed.

Questions 32 and 33, related to the theme of time, ranked attractiveness of the restored prairie on a scale from 1 to 7 where: 1 = very attractive, 4 = neutral, and 7 = very unattractive. Remaining survey questions included: choosing and ranking attractive and unattractive features of the prairie, listing prairie information sources, indicating hobbies, and demographics.

Results

Mean scores and probability of t-values were calculated for the survey results from Corporation A and B. For analysis, items in the questionnaire were grouped by themes, each relating to a specific hypothesis. Under each theme, 2 to 5 questions were asked to check the validity of individual items. The 11 themes were organized under the hypothesis to which it most relates.

Hypothesis 1: Natural Ecological Systems

Hypothesis 1 states that employees associate prairies with natural ecosystems and ecosystem quality. Mean scores for the themes of wildlife and ecological health, and sustainability indicate that prairies were perceived by employees at both corporations to increase wildlife, to have a positive effect on the environment, and to be self-sustaining landscapes. Probability of t-values revealed significant differences between Corporation A and B responses for 2 of the 5 questions for the theme of wildlife and ecological health (Table 1). For both questions, Corporation B respondents, with the 10 year old prairie, were more likely to perceive the prairie to support wildlife and improve ecological health. Probability of t-values for the other e questions for the theme of wildlife and ecological health revealed no significant differences ($p < .10$) between groups (Table 1). Probability of t-values for the theme of sustainability revealed no significant differences ($p < .10$) between groups. This statistical analysis supports hypothesis 1.

Table 1. Mean scores and probability of t-values for the factor of wildlife and ecological health.

	Ques. 2		Ques. 4		Ques. 16		Ques. 28		Ques. 31	
	A	B	A	B	A	B	A	B	A	B
MEAN	1.8	1.9	5.6	4.3	1.9	1.6	2.6	2.6	1.9	1.9
PROB. OF T-VALUES	.66		.00		.07		.48		.98	

Hypothesis 2: Adaptation Over Time

Hypothesis 2 states that adaptation to prairie restorations are affected by employees' perception of the prairie. Factors affecting adaptation include: time, exposure, company information, and employees' background.

Theme: Exposure. Hypothesis 2 identifies exposure as a factor which affects adaptation to prairie restorations. Daily exposure was perceived by employees from both groups to increase prairie attractiveness in question 13 (Table 2). Probability of t-values revealed no significant differences (p < .10) between groups. This data indicated that employees perceive prairie attractiveness to increase with exposure which supports hypothesis 2.

Theme: Prairie Establishment. Mean scores for prairie establishment in question 22 (Table 2) indicated that employees perceive the prairie to become more attractive over time. Probability of t-values revealed no significant differences (p < .10) between groups. This data supports prairie establishment as a factor that affects perception and adaptation to prairie.

Table 2. Perceptions of prairie restorations in relation to exposure, prairie establishment time, and time.

	Ques. 13 Exposure		Ques. 22 Prairie Est.		Ques. 32 Time		Ques. 33 Time	
	A	B	A	B	A	B	A	B
MEAN	3.0	3.1	2.9	3.0	3.3	3.1	2.2	2.5
PROB. OF T-VALUE	.74		.60		.63		.37	

Theme: Time. Positive responses to the prairie were not expected within one year after installation. Prairie restorations generally require at least 3 years of establishment time to resemble a native prairie ecological system. A minimum period of 3 years was the expected time frame for respondents to find the prairie restoration attractive.

A comparison of Corporation A and B responses indicated that employees recall perceptions of the prairie to be attractive (Table 2, Ques.32) during the first year after installation. By the time of the survey in 1991, perceived prairie attractiveness had increased (Table 2, Ques. 33) for Corporation A and B respondents. Responses from Corporation A and B employees were very similar at the time of this survey even though Corporation B employees had viewed the prairie for 10 years while Corporation A employees had viewed the prairie for 2 years. Time appears to affect adaptation within the first 2 years after installation.

A comparison of mean scores between perception of prairie during the first year after installation and perception of prairie at the time of this survey for Corporation A and for Corporation B (Table 3) indicated that time affects adaptation to prairie for employees from both corporations. For each corporation, probability of t-values indicated significant differences (Table 3) between the respondents at the time of the prairie installation and the respondents at the time of this survey. Time appears to affect employees' perception and adaptation to prairie restorations, which supports hypothesis 2.

Table 3. Perceptions of prairie restorations over time.

	Ques. 32 Corp. A Time	Ques. 33 Corp. A Time	Ques. 32 Corp. B Time	Ques. 33 Corp. B Time
MEAN	3.3	2.2	3.1	2.5
PROB. OF T-VALUE	.00		.00	

Theme: Environmental Background. Hypothesis 2 identifies employee background as a factor which affects employees' adaptation. The analysis of employees' backgrounds examined environmental backgrounds, job relationship to the environment, and demographic information about the employee.

Outdoor hobby participation and environmental organization involvement were used to describe employees' environmental background. A high environmental background was determined by the employee having high participation in outdoor hobbies, or membership in an environmental organization. A low environmental background was determined by the employee having low participation in outdoor hobbies, and no membership in an environmental organization. Thirty-three employees had high environmental backgrounds while 29 employees had low environmental backgrounds.

Mean scores of employees with high environmental backgrounds indicated they were more likely to find the prairie:

	Theme
-attractive.	Attractiveness
-to improve wildlife and ecological health.	Wildlife and Ecological Health
-visually acceptable in a corporate setting.	Neatness
-nonhazardous and nondistracting when they are burned as part of a maintenance program.	Maintenance
-could be adapted to with time and and exposure.	Adaptation

Mean scores for the themes of context and sustainability indicated that respondents with high environmental backgrounds thought prairie fit into the surrounding community and was a sustainable landscape for 2 out of 3 questions. There were no trends indicated by the mean scores for respondents with high or low environmental backgrounds for the themes of location, inspiration, and productivity.

Probability of t-values indicated no significant differences (p < .10) between respondents with high environmental backgrounds and low environmental backgrounds for the themes of attractiveness, context, sustainability, location, inspiration, productivity, and maintenance. There were, however, significant differences (p < .10) for the themes of wildlife and ecological health, neatness, and adaptation. One of the 5 questions for wildlife and ecological health, 2 of the 3 questions for the theme of neatness, and 1 out of 2 questions for the theme of adaptation had significant differences in probability of t-values. For the theme of wildlife and ecological health, the significant difference for 1 of the 5 questions revealed that respondents with high environmental background found indigenous plants were used appropriately on the site. For the theme of neatness, significant differences in 2 of the questions found respondents with high environmental backgrounds were more likely to perceive the prairie to be in keeping with a corporate image and did not consider it to be weedy and unkempt. For the theme of adaptation, the question with significant differences revealed that respondents with high environmental backgrounds found the prairies' attractiveness to increase with age. Probability of t-values indicated that high environmental backgrounds have an effect on employees' perceptions and adaptation to the prairie for the themes wildlife and ecological health, neatness, and adaptation.

Employees' demographic backgrounds were analyzed for effects on perceptions and adaptation to prairie restorations. Mean scores indicated no significant differences between groups based on an employees' education, job position, age, gender, or childhood home. Employees' job relationship to the environment found that 17 out of 62 respondents had jobs which were related to the environment. A comparison of the 2 groups could not be made because of the small sample size.

Theme: Location. Location of prairie plantings relative to the building entrance emerged from the analysis as a factor which affects adaptation to prairie restoration. Location was not mentioned in hypothesis 2 as a potential factor. Responses from Corporation A were compared with responses from Corporation B. Mean scores and probability of t-values indicated that location affected employees' adaptation to prairie (Table. 4). Corporation A and B respondents differed significantly ($p < .10$) in acceptable prairie locations. Corporation A employees were less restrictive about prairie locations at entrances while Corporation B employees' responses indicated prairies should be located next to natural areas.

Corporation A employees indicated that prairies located at entrances were acceptable. These employees had never experienced prairies at building entrances, but had been exposed to prairies at vehicular entrances. Corporation B respondents may have been influenced by earlier experiences with prairie restorations at entrances. Several years after installation, the prairie near the building entrance at the Corporation B site was replaced with sod, trees and shrubs. According to personal interviews, prairie was removed from pedestrian entrances due to an unkempt appearance. Prior experience may have influenced Corporation B employees' perceptions of location as it relates to adaptation to prairie restorations.

Table 4. Perceptions of prairie restorations based on location.

	Question 3 Location		Question 24 Location		Question 29 Location	
	A	B	A	B	A	B
MEAN	5.3	3.7	3.8	4.6	4.5	3.4
PROB. OF T-VALUE	.00		.00		.01	

Hypothesis 3: Well-Being

Hypothesis 3 states that employees perceive the prairie as a relaxing and inspirational element in the workplace. Responses from Corporation A were compared with responses from Corporation B. Mean scores for the factor of inspiration suggest that employees from both corporations perceived the prairie to be an inspirational element in the workplace (Table 5). Probability of t-values indicated no significant differences between Corporation A and Corporation B respondents. This data supports hypothesis 3.

Table 5. Perception of inspirational effect of prairie on the work environment.

	Question 7 Inspiration		Question 30 Inspiration	
	A	B	A	B
MEAN	2.5	2.2	2.3	2.1
PROB. OF T-VALUE	.42		.42	

No trends were indicated by the mean scores for the factor of productivity. It cannot be concluded that respondents found the appearance of prairie increased their work productivity (Table 6). Probability of t-values for the factor of productivity indicated no significant differences ($p < .10$) between Corporation A and B respondents. This data suggests that productivity is not affected by the appearance of prairie.

Table 6. Perception of prairie restorations effect on productivity.

	Question 11 Productivity		Question 21 Productivity	
	A	B	A	B
MEAN	3.6	3.4	4.2	3.7
PROB. OF T-VALUE	.70		.22	

Research results suggests that Corporation A and B respondents consider the prairie to be an inspirational element in the workplace, but does not increase their work productivity.

Discussion

Results from this study supports the use of prairie restorations and prairie species in corporate settings. Prairies and prairie species require less energy inputs of water, chemicals, and maintenance than conventional forms of landscaping. Prairies are considered by the respondents to be self-sustaining landscapes that improve ecosystem health, and provide food and shelter for wildlife.

Remarkably there were few significant differences between Corporation A and Corporation B in employees' perception of the prairie. This suggests that respondents may adapt to a prairie restoration within the first 2 years after installation instead of the theorized 3 years. The respondents from the 2 year old prairie and 10 year old prairie had similar perceptions of prairie attractiveness at the time of installation and at the time of the survey. If significant differences had occurred between Corporation A and B perceptions at the time of the survey, it might suggest that adaptation continues to occur within the 2 to 10 year period. Results from this research suggest that adaptation to prairie restorations occurs within the first 2 years and further studies are recommended on factors which affect adaptation during the initial 2 year period.

This study also indicates prairie restorations should be carefully designed by landscape architects, planners, and managers to consider the factors of time, exposure, environmental background, and prairie locations before prairie installation. Viewers that are informed of the ecological intent of a "messy" landscape tend to find the unkempt appearance of the landscape acceptable (Nassauer 1988 a). Landscape architects, planners, and managers can precede prairie installations with information to help viewers adapt to prairie restorations.

Results from this research identified factors to consider when proposing a prairie restoration. Mean scores and probability of t-values for the factor of location indicated that building entrances are not perceived as an acceptable location for prairie restorations. Interviews with employees suggested that prairie areas were removed from building entrances due to their unkempt appearance. The unkempt appearance of prairie restorations can utilize forms of neatness to help viewer adaptation. According to a study of Illinois farmers (Nassauer 1988 b), care in the form of neatness is a dominant factor in determining farm landscape attractiveness. Application of care in the form of neatness may also increase acceptance of prairie restorations. Neatness can be exhibited with mow lines around prairie edges or with fences that delineate the prairie.

Factors which affect adaptation to prairie restorations can also be extended to other restored landscapes such as wetlands, and areas which are allowed to voluntarily revegetate. Landscape architects, planners, and managers can utilize these research results to address viewer concerns prior to installation of a prairie or other restored landscape.

Prairie restorations are considered to be an inspirational element in the workplace. Since many corporations have invested in wellness programs for employee health and well-being, prairie restorations could be an integral part of a corporate wellness program. Prairie restorations could provide inspirational viewing, as well as improve the ecological health of the corporate grounds.

It is evident from this study that several factors affect perceptions and adaptation to prairie restorations in corporate settings. These factors can be utilized by landscape architects, planners, and managers to affect employees' perceptions and adaptation to prairie restorations, to help employees associate prairies with ecosystem quality, and to affect employees' well-being.

Literature Cited

Anderson, L.M. 1981. Land use designations affect perceptions of scenic beauty in forest landscapes. Forest Science 27:392-400.

Hodgson, R.W., and R.L. Thayer. 1980. Implied human influence reduces landscape beauty. Landscape Planning 7:171-179.

Keane, Tim. 1992. The role of familiarity in prairie landscape aesthetics. D. D. Smith. and C. A. Jacobs (eds.) Proceedings of the Twelfth North American Prairie Conferences: Recapturing a Vanishing Heritage.University of Northern Iowa, pp 193-194.

Nassauer, Joan I. 1988 a. Landscape care: perceptions of local people in landscape ecology and sustainable development. Landscape and Land Use Planning 8:24-37.

Nassauer, Joan I. 1988 b. The aesthetics of horticulture: neatness as a form of care. Hort Science 23:973-977.

Nassauer, Joan I. 1990. The appearance of ecological systems as a matter of policy. Dissertation. University of Minnesota, Department of Landscape Architecture, Minneapolis.

Nassauer, Joan I. and M.K. Benner. 1984. Visual preferences for a coastal landscape including oil and gas development. Journal of Environmental Management 17:323-337.

Nassauer, Joan I. and R. Westmacott. 1987. Progressiveness among farmers as a factor in heterogeneity of farmed landscapes. *In* M.G. Turner (ed.) Landscape Heterogeneity and Disturbance. Springer-Verlag, New York. pp 199-209.

Schahn, Joachim and Erwin Holzer. 1990. Studies of individual environmental concern: the role of knowledge, gender, and background variables. Environment and Behavior. 22:767-786.

Schulhof, Richard. 1989. Public perceptions of native vegetation. Restoration & Management Notes 7:69-72.

Ulrich, Roger S. 1983. Aesthetic and affective response to natural environment. Human Behavior and Environment 6:85-120.

The Prairie Eye

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Abstract. A first encounter with native prairie reveals implicit habits and assumptions as to how to view it. These seem to reflect modes of seeing established by earlier writers and artists, who themselves struggled with what to make of the prairiescape. The problem they focused on was how to render imaginatively the experience of vastness within given artistic conventions and cultural constructs. The expansive possibilities of this new landscape were both inviting and strange, combining freedom and loneliness, motion with emptiness. For both writers and artists, the emphasis was on space; the prairie eye took the long view, and this perspective has dominated our view ever since. Two major exceptions point the way to a new, more complex prairie eye. Willa Cather saw the prairie not only as vast but also as filled with particulars. Her prairiescapes are dialectics of distance connected to detail. Cather's narrative perspective has parallels in the visual art of a contemporary photographer, Terry Evans, wherein micro/macro patterns merge and resonate with each other. The prairie eye of Evans (anticipated by Cather) is especially pertinent to our times, with our emphasis on biodiversity and ecosystem (and the rarity of first-hand experience of the expansive prairie).

Key words: prairies in literature, prairies in art, art and literature--U.S., landscape in literature--U.S., landscape in art--U.S., Willa Cather, Terry Evans

Introduction

Although I grew up in south-central Minnesota, it was not until a few years ago that I first saw a stand of native prairie. The landscape I knew was mainly one of corn and soybeans--occasionally oats and once or twice a field of flax--and my eye was conditioned by the nonvarying grid to see a world of orderly north/south and east/west lines containing continual abundance. It was a comforting world, no doubt, and gave a sense of security. You knew implicitly that you could never really get lost in Brown County, that all roads eventually made sense on the checkerboard layout, which is part of Thomas Jefferson's legacy to the Midwest.

And so it was a surprise when I saw a quarter section of tallgrass prairie for the first time. Surrounded by the straight rows of shoulder-high corn on all sides, Shaeffer Prairie seemed unkempt, unruly, unproductive, filled with weeds--a waste. I walked in, thinking to spend a half hour, to do my duty to Willa Cather as it were, and to be gone. It turned out that I stayed the afternoon.

Not that I had been totally unprepared for the wild prairie. As I said, I had read Cather, along with the rest of the canon of prairie novelists, and had spent time looking at the paintings of artists such as Catlin, Bodmer, and Miller. Through these images, I had felt intensely (or so I thought) the effect of the huge, level land; the long horizon; and the constant movement of the wind- driven grasses. I was expecting this scene and even saw something like it; I sought out places to stand to catch the motion of the windand angles of vision, where if I squinted, the crops nearly disappeared. I strained my imagination to multiply the immediate scene of swells and swales into peripheral and far-distant replications to simulate an endless prairie. I wanted vista, and I looked hard for it.

What I was not prepared for was the incredibly rich diversity of plants I saw with nearly every step I took. It seemed a chaotic multiplicity of color, shape, size, texture, and odor. Although I was determined to look up and out, I often was drawn to look down and in as well. Here was a different kind of abundance, one that I did not know how to read or to make sense of. Looking close was so different from looking far away, and yet both were compelling. I was at a loss as to how to relate the two experiences. As I drove home, I watched myself, with curiosity, start to see the landscape differently. I had begun, though barely, to experience the prairie with a new sort of eye.

This personal experience led me to think anew about the different ways in which we perceive landscape. Where our modes of seeing come from and how to understand them may be important clues to the larger cultural history of the prairie. How have writers and artists dealt with the primary, complex experience of seeing the prairie? Have they found ways to render imaginatively the distant view, the near view, and the interaction between the two? If they have, why was I so surprised by what I saw? I had studied them, had thought about them, and yet had found the prairiescape to be more than I was prepared for. What had my culture taught me about seeing the prairie? And why?

I cannot answer all these questions in this brief presentation but let me at least outline the direction of my thinking and give some key examples to illustrate my sense of the issue. In an earlier paper, one written for this conference 4 years ago, I argued that the prairie was a perennial--that is, recurring--symbol of many values by which the Midwest has defined itself. Its dominant meanings revolve around "the prairie as an enormous fertile and fecund space, a place of great potential for economic wealth, an area in which American democratic aspirations could truly be realized . . . ." (Scanlan 1992, p. 201). A powerful, secondary set of meanings question the optimistic assumptions of the first, seeing the prairie instead as "a sterile, barren, Godforsaken place, boring, monotonous . . ., and closed off from possiblities." (Scanlan 1992, p. 201) These constellations of meaning play off against each other in the work of writers and artists from the first explorers to the chronicler of Lake Woebegone, reappearing in complicated and various ways (Ricou 1973; Fairbanks 1986; Thaker 1989; Olson, 1994).

And I also noted that the prairie recently has become a perennial symbol in a second sense, that is, it has come to stand for "renewal, regeneration, restoration, and linking past to present. It is about ecological sanity." (Scanlan 1992, p. 203) This conference itself I take to be one part of the latest cultural redefinition of the meanings of prairie space in our lives and imaginations.

Whatever the explicit content of the cultural images of the prairie has been, implicitly the prairie has been seen--and we have been taught to look at it--from one perspective. We have celebrated (or scorned or feared) the prairiescape for its vastness, emphasizing spaciousness as its overwhelming fact. Whatever attitude they took toward encountering the prairie--and these attitudes were of a broad range--writers and artists established a relationship between their audience and their subject that typically directed attention to the meanings of the grand vista, to the empty space within which the drama of encounter and settlement took place. In some cases, this space has held the promise of ebullient growth that was both nationalistic and personal (Olson 1994). In other cases, it was where the upright human figure stood alone as a metaphor for the existential dilemma of finding meaning in an indifferent, even hostile universe (Ricou 1973). In any case, and there are many more cases, the struggle to understand the prairie and figure out what to make of it intellectually and artistically was one of coming to terms with its immensity, of grasping its distance, of filling in its emptiness (Thaker 1989). The way to understand the prairie was to eye it from the long view.

Consider one representative example. From early on, the prairie has been likened to the ocean. This image was already commonplace when William Cullen Bryant, the first significant American writer actually to see a prairiescape and then to render it in literature, travelled to Illinois in 1832. (1969) In "The Prairies" he writes:

> . . . I behold them for the first,
> And my heart swells while the dilated sight
> Takes in the encircling vastness. Lo, they stretch
> In airy undulations, far away,
> As if the Ocean, in his gentlest swell,
> Stood still, with all his rounded billows fixed
> And motionless forever. Motionless?
> No, they are all unchained again: the clouds
> Sweep over with their shadows, and, beneath,
> The surface rolls and fluctuates to the eye;
> (Bryant 1969, p. 130)

Bryant enlivens the prairie-as-ocean image through the drama of his perception: ineffable distant space is released from a static freeze-frame to become the powerful motion of rolling sky and land. The poetic line, in imitation, is ongoing, flowing past line end-stops. What Bryant sees fills him with a kind of grandeur, and he wants it to do the same to us. But the ocean metaphor directs us to one particular kind of view. Although the ocean gives us equivalences for the new experiences of scale and motion on the prairie, it does not invite us to think about detail; it is relatively featureless. Only the big picture is implied in this comparison. We see the importance of the prairie, metaphorically, from the long view. In this one way, Bryant and the ocean metaphor typify the stance of many prairie writers.

Downplaying all but the long view of the prairie caused no end of trouble for the early painters who tried to render it visually during the first half of the nineteenth century. Robert Thaker has pointed out that early artists such as George Catlin, Paul Kane, Karl Bodmer, and Alfred Jacob Miller struggled with the problem of conveying their visions of the scope and scale of this new land. "Its infinite spaces seemed to defy imaginative control, thereby rendering imported esthetic assumptions neutral, almost moot." (Thaker 1989, pp. 55-56) The painterly result, says Thaker, was a mixed one. In these early prairie paintings, the perspective is often from an actual or imagined height to give a sense of distance, but the level space itself is captured and contained between large foreground and background elevations; only occasionally does the space open up fully, Thaker notes. Eventually, a conventional solution to dealing with vast space emerged in other artists. A typical arrangement was to locate a plant in the foreground; the open space in the middle ground; and the horizon with sky, clouds, and, perhaps, some distant prominence in the background (Novak, 1980).

However, two artists have provided cultural images of the prairie that suggest a more complex view of that space. One is the greatest prairie novelist, Willa Cather, and the other is the contemporary photographer, Terry Evans. I link them for several reasons but mainly because both seem to move beyond seeing the prairie from only the long view. Although the power of the prairie vista is captured memorably in both artists' works, neither is content to exploit that perspective alone. For both, the far view is connected to the near view; indeed, one implies the other, and the two perspectives comment on each other. Each sees with both eyes open.

Cather's readers have long admired the passages in which the great expanse of the prairie is evoked for us in lyrical swells that seem to sum up 300 years of experiencing prairie spaciousness. The opening sections of *My Antonia* (1918) are justly famous in this regard. But Cather's artistry when she draws our attention to the feeling of the prairie at our feet deserves admiration as well. She not only included plants, animals, and insects of the prairie in ways that acknowledged their particularity and integrity, but she was subtle and careful in connecting these descriptions to the changing consciousness of her characters. Though her characters respond to the long view at first, as they grow familiar with the prairie, they begin to see its details; it is as if they were developing more careful and discriminating eyes.

This dual vision in Cather is expressed in the gestures and consciousness of her characters as well as in the author's narrative voice. In *O Pioneers!* (1913), for example, Alexandra's most characteristic pose is to stand apart, staring off toward the prairie horizon. What is it she sees out there? In a remarkable passage that marks Alexandra's deepest understanding of and commitment to the land, she begins by contemplating the stars and ends by thinking: "She had never known before how much the country meant to her. The chirping of the insects down in the long grass had been like the sweetest music. She had felt as if her heart were hiding down there, somewhere; with the quail and the plover and all the little wild things that crooned or buzzed in the sun. Under the long shaggy ridges, she felt the future stirring." (p. 71) Alexandra now sees the prairie as a linked experience of scales varying from the smallest creature to the largest expanse.

In Cather, the two perspectives of great and small are but one element, though an important one, in the narrative and dramatic scheme of her art. For photographer Terry Evans, exploring the complexity of these perspectives is central to her vision. In her work, Evans (1986) discovers, distills, and extends a series of prairie images that range from up close to far away as a means to refresh and renew our view of the prairie. For example, Evans uses a variety of angles along with varyious distances in her images. In the most startling ones, we look straight down (or nearly so) on a flower close up or on the Konza hills from an airplane. In either case, we have not seen the prairie in quite this way before. Moreover, the different angles and distances of individual images reinforce and comment on each other. For example, the implications of Cather's phrase "the shaggy ridges" is made apparent when Evans juxtaposes--and so fuses--views of the topography with a buffalo hide (pp. 39-41).

Thus, Evans' prairie eye directs us to an interplay between the formal patterns she finds in the prairie ground and sky, on the one hand, and the angles from which those patterns are presented, on the other hand. Although each image can be seen in its own right both as irreducible fact and as abstract design, more revealingly, Evans has us looking for replicating shapes and textures. Her favorite pattern, she tells us, is the spiral (p. 14), but circles, ovals, and complex curvilinear geometries emerge and recede as our eye is moved about. We discover consonant textures in the prairie as well as its repeating shapes. There is a dynamic motion here of developing gestalts.

Evans' images take on their richest resonance and meaning, then, when juxtaposed against each other. We experience the prairie on micro and macro scales as distinct but complementary and unified spaces. What Cather anticipated, Evans has raised to a new way of seeing. In effect, what we have is the artistry of a visual ecology of the prairie. The prairie eye of Evans is especially pertinent to our times. She reflects our emerging emphasis on biodiversity and ecosystem (and the rarity of first-hand experience of the expansive prairie). But more, the freshness and subtly of her work teaches us to see the prairie with new eyes.

Literature Cited

Bryant, W. 1969. The Poetical Works of William Cullen Bryant. AMS Press, New York.

Cather, W. 1918. My Antonia. Houghton Mifflin, Boston.

Cather, W. 1913. O Pioneers! Houghton Mifflin, Boston.

Evans, T. 1986. Prairie: Images of Ground and Sky. Unversity Press of Kansas, Lawrence.

Fairbanks, C. 1986. Prairie Women: Images in American and Canadian Fiction. Yale University Press, New Haven.

Novak, B. 1980. Nature and Culture: American Landscape Painting 1825-1875. Oxford University Press, New York.

Olson, S. 1994. The Prairie in Nineteeth-Century American Poetry. University of Oklahoma Press, Norman.

Ricou, L. 1973. Vertical Man/Horizontal World: Man and Landscape in Canadian Prairie Fiction. University of British Columbia Press, Vancouver.

Scanlan, T. 1992. The prairie as perennial symbol. *In* D. Smith and C. Jacobs (eds.) Proceedings of the Twelfth North American Prairie Conference: Recapturing a Vanishing Heritage. University of Northern Iowa, Cedar Rapids, pp. 201-203.

Thaker, R. 1989. The Great Prairie Fact and the Literary Imagination. University of New Mexico Press, Albuquerque.

Life, Literature, and Land: Perspectives on Prairie Preservation

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Abstract. Beginning in the 1970's, the Save the Prairie Society of Westchester, Illinois, applied an environmental ethic encompassing values of land stewardship, natural heritage, and attention to preservation of biodiversity in its strategy to preserve Wolf Road Prairie, 82 acres of wet prairie. Preservation of biological diversity is linked closely to a common historical heritage and an affinity with the land. A relationship of the individual to the prairie landscape is described in classical literature, nature writing, poetry, and the writings of scientists and educators in the fields of ecology and natural resources preservation. The political and economic process of acquiring land, creating public and governmental recognition, and educating the general public can lead the way in establishing ecological restoration as an actively pursued community value. As community values supporting open space and prairie wilderness develop, the argument for prairie preservation leads to a broader, more global appreciation for biodiversity within a suburban community.

Key words: Prairie, Illinois, Westchester, Wolf Road, Chicago, biodiversity

Introduction

This paper describes how citizens of Westchester, Illinois, a suburb of Chicago, worked to preserve 82 acres of land comprising Wolf Road Prairie. Together with citizens from neighboring towns, they organized a nonprofit organization called the Save the Prairie Society (STPS). The STPS then developed a mixed strategy of strong public participation in local community events, education of townspeople of all ages, fundraising, positive interaction with the local press, and legal action. One method of communication, a newsletter titled "The Prairie Pointer," was highly effective in communicating crucial political events and in expressing appreciation for natural landscapes to members of the Society. In the process of employing this strategy, the STPS defined biodiversity as it was applicable to Wolf Road Prairie preservation, linking prairie habitat to a more global argument of habitat preservation for biodiversity. This definition of biodiversity evolved out of recognizing an affinity with the land, with history, and with biology. The original group of volunteers who struggled to preserve Wolf Road Prairie felt a common bond with prairies, their unique flora and fauna, and hence their beauty.

Preserving Wolf Road Prairie expressed the need to save natural landscapes as a part of a natural historic heritage. Members and friends then communicated their appreciation for prairies as embodied in Wolf Road Prairie to other citizens and convinced them of the value of Wolf Road Prairie. They used "The Prairie Pointer" and letters to the editor that were published in local newspapers.

This paper also describes how the STPS, in its educational programs and activities, articulated a connection between human beings, land, biology, and aesthetics, which then became a powerful argument for Wolf Road Prairie preservation. Much original Illinois prairie habitat had been converted to farm land. This farm land is now being converted to subdivisions, severely altering the native landscape, creating loss of habitat, and diminishing the numbers of native species. The volunteers wished to preserve the few remaining pieces of prairie habitat left in Illinois. They faced strong opposition from developers and local politicians, but succeeded in motivating thousands of citizens from several towns to preserve Wolf Road Prairie as a natural living museum, a remnant of Illinois heritage, and a piece of prairie biological diversity.

Biological Diversity of Wolf Road Prairie

Today, humankind faces a most urgent task — to preserve and nurture the biological diversity of this planet. In a New York Times article, William K. Stevens (1995) reported that Dr. Reed Noss, one of three biologists who conducted a study for the National Biological Survey on the American landscape and its diversity, stated that "We're not just losing single species here and there, we're losing entire assemblages of species and their habitats." STPS organizers believed that each independent preservation effort is but one link in the worldwide chain to protect the world's natural resources.

What is biological diversity? A 1994 report from the Nature Conservancy (TNC) prepared in conjunction with the U.S. Environmental Protection Agency Region 5 Great Lakes Program offered a definition of biological diversity presented by botanist Peter H. Raven.

"At the simplest level, biodiversity is the sum total of all the plants, animals, fungi and microorganisms in the world, or in a particular area; all of their individual variation; and all of the interactions between them. It is the set of living organisms that make up the fabric of the planet Earth and allow it to function as it does, by capturing energy from the sun and using it to drive all of life's processes; by forming communities of organisms that have, through the several billion years of life's history on Earth, altered the nature of the atmosphere, the soil and the water of our planet; and by making possible the sustainability of our planet through their life activities now"

Wolf Road Prairie is a physical example of these communities of organisms that have formed through time. Because Wolf Road Prairie just gained state preservation status, much research conducted on species identification needs to be completed. Many of the first records of flora and fauna were conducted by biologists from the Morton Arboretum and biology teachers from the local public high schools who worked in cooperation with dedicated, trained volunteers. These volunteers consistently visited the site over a period of 10 to 20 years, recorded observations, and protected the flora in the area from theft and damage. Today, they continue to organize new volunteers to work on prairie restoration and maintenance. The state of Illinois considered the role of STPS volunteers to be important in the effort to encourage prairie restoration and designated the STPS as steward of Wolf Road Prairie. Findings recorded by volunteers provided valuable baseline information from which future research can be conducted.

From these findings, prairie experts determined that Wolf Road Prairie provides a genetic reservoir of prairie species diversity for the Chicago area and the entire state of Illinois. The STPS and prairie specialists from the Morton Arboretum maintain an inventory of species composition. According to prairie specialists, this prairie contains 347 observed plant species or about one-seventh of all the plants found in Illinois or in the Chicago region including parts of Wisconsin, Indiana, and Michigan. Volunteers also keep records on bird sightings. In an issue of the "Prairie Pointer," Kate Wapeha (1984) published a list of 90 species of birds sighted in the Wolf Road Prairie.

Believed by members of the STPS to have never been plowed, Wolf Road Prairie offers a variety of habitat such as oak savanna, wetland, and grassland. This prairie is exceptional because of its location in a highly developed suburb, its proximity to the city of Chicago, and its relationship to the Cook County Forest Preserve. For individuals living in a densely populated suburb, which is approximately 30 minutes from the center of a highly urbanized city, the possibility of walking across a street from a county forest preserve to an open prairie alters and adds a needed dimension to traditional perceptions of Illinois landscape from that of trees and forests to grasses and prairies. To be able to see a marsh hawk (*Circus cyaneus*), a state-endangered species, flying over this small area of grasses and flowers bordered by shrubs and trees, with high-rise complexes in the distance, inspires one to reconsider ideas about nature and natural places. It alters one's perception of the land as something other than a neatly clipped lawn, city park, or forest preserve. It encourages the individual to consider the possibility of being much closer to a wilder, more diverse habitat and perhaps to try to imagine what the first pioneers must have felt when they came out from the forest into an open grassy expanse.

The forest preserve provides a tree-dominated perspective that was familiar to pioneers and immigrants. The prairie exemplifies the grass-dominated, unfamiliar and perhaps frightening landscape that once covered Illinois. Trees were useful to pioneers, providing firewood and shelter. Trees signalled the presence of water. But water was harder to find on the open prairie. At Wolf Road Prairie, a nearby forest periphery provides actual examples of basic ecological phenomenon such as succession.

In 1977, Wolf Road Prairie was in danger of being developed into a residential area. The danger that development posed was the loss of habitat and the eventual destruction of species. In an issue of "Menagerie," the Lyons Township High School literary magazine, (Elkind, 1977) Jack Shouba, then a biology teacher at the school, stated, "If we wipe out the last couple of prairie areas, certain species will vanish from this earth. Here is a whole line of evolution that will be cut off just because we had to stick a house up." (Elkind, 1977) This statement served as a rallying cry to some students at the high school, and the understanding of the need for protection of biological diversity grew among a small group of people in the Chicago area.

Early Political Action to Save Wolf Road Prairie

The story of Wolf Road Prairie's preservation can be found in newspaper articles, editorials, letters to the editor, and newsletters. According to "The Prairie Pointer," the STPS organized as early as May, 1973. In the Spring 1985 issue of the newsletter, the President of the STPS, Jack Shouba, wrote a memorial to his deceased wife, Grace, co-founder, Director, and Honorary Director of the Society. She was greatly disturbed when a railroad prairie near her home town of Capron, Illinois was destroyed. The couple did not want to see another piece of prairie disappear to development. They had enjoyed their hikes together identifying flowers whose beauty they admired. They valued the differences among the varied species they studied, appreciated the knowledge they acquired, and felt an affinity with the beauty of the landscape they observed.

After taking a course offered by Dr. William Beecher at the Chicago Academy of Sciences, the Shoubas went searching for prairies. Grace Shouba found a prairie fragment on Thirty-first Street in Westchester and called the Morton Arboretum to find out more about it. She spoke to amateur naturalist, Alma Greene, who insisted on giving her a tour of the site. The Shoubas then were referred to Ruth Spevak, who had discovered the prairie on her way home from the Morton Arboretum. Shouba writes (1985, wrote), "She had vowed to save it somehow, with the help of her La Grange Park Garden Club." This sentiment to save Wolf Road Prairie seems consonant with commentary found in the epilogue of J.E. Lovelock's *Gaia*, (1979):

> "It may be that we are also programmed to recognize instinctively our optimal role in relation to other forms of life around us. When we act according to this instinct in our dealings with our partners in Gaia, we are rewarded by finding that what seems right also looks good and arouses those pleasurable feelings which comprise our sense of beauty. When this relationship with our environment is spoilt or mishandled, we suffer from a sense of emptiness and deprivation. Many of us know the shock of finding that some peaceful rural haunt of our youth where once the wild thyme blew and where the hedges were thick with eglantine and may, has become a featureless expanse of pure weed-free barley."

People who become saddened by the loss of a piece of land known in childhood, who come to appreciate the study of diverse forms of natural life, and who wish to impart this knowledge are moved to preserve the land in its natural state. After the meeting with Ruth Spevak, activity to preserve Wolf Road Prairie increased.

Shouba (1985) added that,

> "The 'prairie people' were finding each other, and in late 1972 or 1973 the first of many meetings was held to discuss ways to save the Thirty-first Street prairie. She (Grace) helped to organize the Society in May of 1974, recruiting Mrs. Carol Murray and others from the League of Women Voters. Grace Shouba published newsletters, met with political leaders, wrote letters, put together a slide show, gave talks, led walks, and generally did whatever needed doing."

In the beginning, organizing had its problems. There was no road map to follow. Shouba wrote that, "In those early years, no one knew how the prairie could be saved. The cost seemed prohibitive, the ownership pattern was too complex, the public did not know what a prairie was, and government agencies and officials simply were not interested." These barriers to prairie preservation did not stop a core group of volunteers from working to preserve Wolf Road Prairie.

The Route to Preservation

From 1974 to 1978, Jack Shouba and several others organized high school students and citizens in local garden clubs to canvass communities for petition signatures and to raise money to buy lots. They organized to convince local government officials that, because of public interest, Wolf Road Prairie should be preserved. A complex and obscure pattern of ownership continued to be largely responsible for preventing resale and rezoning of the land for development. Today, the grid of original plots is used for recording locations of endangered species or rare plants and conducting ecological studies.

In 1975, high school students, under the direction of Jack Shouba, grew plants to raise money to buy prairie lots. Because of several of these efforts, a lot, funded by the Lyons Township High School Conservation Club, was purchased for approximately $3,000 by the STPS in 1975. Another lot was purchased by the La Grange Park Garden Club for approximately the same amount. Later, as the struggle to preserve Wolf Road Prairie became greater, and landowners began to wait for market-price purchases, the STPS sought matching grants from foundations and citizens of Westchester and surrounding towns. Finally, the State of Illinois and Cook County entered into an agreement to jointly purchase the 82 acres. The land was condemned, and remaining landowners were paid a fair price for their lots. The most current battle concerning Wolf Road Prairie centers on maintaining a buffer zone of residential land bordering the prairie to protect carrying capacity for this island of prairie habitat.

During the process of preservation, members of STPS participated actively in the community, in local and state governments, and in the courts. They published brochures for distribution at libraries, churches, and supermarkets. They marched in local parades. They printed petitions for volunteers to gather signatures of citizens supporting preservation. They attended Village of Westchester and park district board meetings to advocate preservation.

In 1978, needing a strong political voice in the town where the prairie was located, STPS set up a chapter in Westchester. In 1980, the Illinois Natural Areas Inventory determined that Wolf Road Prairie was priority land for preservation. In 1984, State Representatives Judy Baar Topinka and Ted Leverenz cosponsored a special $250,000 appropriation for land purchases. This followed a $350,000 special appropriation that initiated land purchase by the Illinois Department of Conservation. With this funding, Wolf Road Prairie received statewide recognition and greater public support. The STPS continued its work with the media by writing editorials and articles in local newspapers, gathering information, organizing prairie walks, and announcing festivals and activities for children. A teacher from a nearby town, Jim Hodap, created a puppet character named Hody Coyote and performed puppet shows describing ecology and nature to small children. The STPS invited all groups of any age, from small children to middle-aged professionals and the elderly, to participate in learning about Wolf Road Prairie and its precious link to Illinois prairie heritage, the link that human beings share with other biological organisms, and ultimately to appreciate the value of biological diversity.

One of several original arguments that the STPS used to preserve Wolf Road Prairie was its intrinsic value as a natural area. A second argument was its value as a natural flood plain. A third argument was the lack of knowledge of prairies and the potential for hidden value. The overall position that the organizers, volunteers, and specialists espoused, however, was much larger. It integrated diverse philosophies of environmental writers such as Aldo Leopold, Rachel Carson, and John Madson. Major poets who also influenced the STPS were Emily Dickinson and Carl Sandburg. Elements of American literature and pioneer history and lore were also brought into the argument for Wolf Road Preservation. Themes centered on American Indian lore and use of fire.

Pioneer life on the prairie is described in newsletter submissions. These ideas and images, communicated in the "Prairie Pointer," fostered expression of a larger picture of the meaning of prairie preservation, sparking the imagination and the articulation of land values and ethics among volunteers and members. Often, they served as inspirations for volunteers during long hard hours of work. They also formed a basis for friendly, pleasant, and aesthetic communication to a public that needed to be informed.

An editorial in the *Suburban Life Citizen* "Forum" section is one example (Scanlon). Scanlon expresses clearly and strongly her sentiments toward Wolf Road Prairie preservation.

> "I grew up in Westchester. My mother lives there now. ... I attended its schools and still follow Westchester's affairs with great interest as I am contemplating a move back to Westchester. ... I have recently read of the village's intent to pave a road through the Wolf Road Prairie and am very disturbed. Are we supposed to pale and become weak when hearing that Westchester is running out of open space for development? For heaven's sake, is our mandate, in the name of progress, that we must pave and build over every last inch of ground that's left? ... I want 'access' too, access to the vestige of untouched prairie that is our natural heritage, which we can have only by leaving Wolf Road Prairie alone ... I have been proud of the fact that my home town preserved something that the whole state can be thankful for and enjoy: The Wolf Road Prairie. It is a rare jewel in a fast disappearing world of natural areas. ..."

From original volunteer accounts of working to save the prairie, there is agreement that, no matter how much individuals differed as to how to save Wolf Road Prairie, they maintained the original relationship to the land and agreed on the necessity to preserve it. For example, in an interview (La Force, 1994) Larry Godson, prairie photographer and original STPS member, stated that the work to save Wolf Road Prairie was difficult and demanded much time from its members. Members sometimes strongly disagreed over an approach, but they did not take disagreements personally, firmly believing in a democratic process of consensus building.

American literature provides many examples of the expression of an affinity with the land and more specifically with prairies. Willa Cather's *My Antonia* (1946) told a tender story of a young Bohemian girl growing up on the Nebraska prairie. Often in Cather's descriptions of the land, one finds individuals in awe of the expansiveness of the prairie to which they are connected. In a similar manner, the STPS called upon themes expressed by pioneers as they experienced the prairie, including this awe, because it is so rare in Illinois today. Cather, for example, described a young boy's first experience of traveling on the prairie.

> "Cautiously I slipped from under the buffalo hide, got up on my knees and peered over the side of the wagon. There seemed to be nothing to see; no fences, no creeks or trees, no hills or fields. If there was a road, I could not make it out in the faint starlight. There was nothing but land: not a country at all, but the material out of which countries are made. No, there was nothing but land ... I had the feeling that the world was left behind, that we had got over the edge of it, and were outside man's jurisdiction. I had never before looked up at the sky when there was not a familiar mountain ridge against it. But this was the complete dome of heaven, all there was of it. I did not believe that my dead father and mother were watching from up there; they would still be looking for me at the sheep-fold down by the creek, or along the white road that led to the mountain pastures. I had left even their spirits behind me. ... If we never arrived anywhere, it did not matter. Between that earth and that sky I felt erased, blotted out. I did not say my prayers that night: here, I felt, what would be would be."

The character is overwhelmed by the land and its raw characteristics, yet he is willing to yield to another order of things, an order that is different from the law of men, far away from the family and from familiar mountains, trees, and creeks. Yet this is a place where earth meets sky in a heavenly natural order, revealing a particular kind of fate that leaves the character feeling insignificant, nonexistent, but nonetheless belonging and at ease. Although Wolf Road Prairie differs ecologically from the Nebraska prairie, it exists to convey a historical perspective of a time long ago. Willa Cather's writings conveyed to an American nation a picture of a landscape and region of which people knew little. Wolf Road Prairie exists in an era of urban sprawl, suburban development, and advanced science and technology, and it also conveys to an American people a living picture of a landscape of which people have no memory and cannot visualize. One of the central viewpoints of the education program of the STPS is to preserve the pieces of land that enable individuals to think back to another time in history.

The relationship between human beings, the landscape, and trees is a prominent feature because there are few, if any, trees on a prairie. Cather developed this characteristic in the following passage:

> "Sometimes I went south to visit our German neighbors and to admire their catalpa grove, or to see the big elm that grew up out of a deep crack in the earth and had a hawk's nest in its branches. Trees were so rare in that country, and they had to make such a hard fight to grow, that we used to feel anxious about them, and visit them as if they were persons. It must have been the scarcity of detail in that tawny landscape that made detail so precious."

This passage describes an emotional attachment toward trees and the forests that were so familiar on the east coast of North America or from areas in the European homeland. In the STPS self-guided nature walk brochure (Murray et al. 1993), is a description of a particular bur oak (*Quercus macrocarpa*) growing in the savanna portion of the site. The brochure states that the tree is estimated to be 250 years old. "This tree was here before European settlers arrived and is recorded in *Famous and Historic Trees* by Randall and Clepper." The brochure quotes Aldo Leopold in explaining the important ecological role that the bur oak plays in prairie ecology. "Aldo Leopold writes, 'Bur oak is the only tree that can stand up to a prairie fire and live. Have you ever wondered why a thick crust of corky bark covers the whole tree ... This cork is an armor. Bur oaks were the shock troops sent by the invading forest to storm the prairie; fire is what they had to fight.'" Because of its age and unique role in prairie ecology, the tree has special value to the community. It existed before the time when immigrant farmers were converting prairies to farmland.

This approach to education combines the understanding of science with the appreciation of landscape and history. It also creates an open space that individuals can visit, and observe and where they can appreciate how earth meets sky. Although STPS organizers have not specifically quoted Willa Cather, they have quoted other writers; consulted folklore writings; and included concepts of literature, folklore, and history in their prairie education program.

STPS organizers and volunteers were influenced strongly by the works of the prairie writer, John Madson. Bonnie Bone (1985) wrote of an interview she had with Madson and his wife in their home in Godfrey, Illinois. She begins her article with an Emily Dickinson poem that Madson includes in his book.

> "To make a prairie it takes a clover
> and one bee —
> One clover, and a bee,
> And reverie.
> The reverie alone will do
> If bees are few."

Bone then describes her interview with Madson and includes the following comments:

> "I grew up with stories of sod-breaking, ... My great-grandfather moved from across the Grand Prairie of Illinois with his bride into Iowa. There he homesteaded in a grove of walnuts on a native prairie and broke the sod...."

Bone adds, 'I thought how beautifully Madson had described the overland traveler reaching the eastern edge of this once great prairie: "he might walk up out of the forested flood plain, step through a screen of sumac and wild plum, and stand blinking in a land that blazed with light and space'."

Bone adds that "Madson reflected that anything you can show people about their native landscape 'that reveals beauty to them, and drama, and something spectacular in their everyday, flat world, they're gonna greatly appreciate it. I think this is something so badly needed in the Midwest,...'" Madson continues with an aesthetic view of observing prairies.

> "You have to look at prairies with the right side of the brain. ... You have to look for the rich, naturalistic quality of these little shreds of prairie. They're very fragile, hiding here and there, cringing ... forgotten or ignored. And yet, if an Aldo Leopold or a Rachel Carson or someone points these things out to people, suddenly they start seeing them with the right sides of their brains, as Rachel and Aldo did. And suddenly they realize 'My God - we've got something here to lose! This is worth keeping! Why haven't we seen this before?'" (Bone, 1985)

The author clearly states the connection between appreciating the beauty of the prairie, finding a common bond with the biology of the prairie and then realizing the need for preservation. Valerie Spale (1992), Executive Director of the STPS stated, "Prairie articles by John Madson mentioning Wolf Road Prairie appeared in newspapers around the country. Many featured photographs ... and established Wolf Road Prairie as a nationally prominent natural area."

Madson wrote in the prologue to *Where the Sky Began, Land of the Tallgrass Prairie* (1982):

> "To those first European explorers and colonists, grassland probably meant snug meadows, deer parks, and pastures safe behind fence and wall. They had no basis for even imagining wild fields through which a horseman might ride westward for a month or more, sometimes traveling for days without sight of trees."

He continued to write on his perspective of the grassland:

> "... when the grasslands were finally met and shakily framed in some sort of geographical context, they were not really comprehended. Most arrivals ventured timidly into the edge of the grass and clung to the outriders of forest like mice hugging a wall. For this was alien land, not only in physical appearance but in its harsh rejection of familiar custom; it diminished men's works and revealed them to a vast and critical sky, and forced people into new ways of looking at the land and themselves, and changed them forever."

Madson in this section describes the harshness of the tallgrass prairie and how, through its lack of trees, water, and familiar biology, the grasslands changed the people who worked so closely with it, their perceptions of the world before them, and ultimately themselves. The prairie can be threatening, challenging, or heartbreaking to those who venture onto it.

Wolf Road Prairie, in contrast, is a remnant of that much larger expanse of land, a "survivor," a piece of the subject Madson writes about. Cather and Madson both expressed the theme that individuals, as they experience life on the prairie, undergo changes in perspective of the land and of themselves. Whether it be a shift from "mountain pastures" to "a complete dome of heaven" (Cather, 1946, pg. 8) or from "snug meadows" to a "wild fields" (Madson,1982, pg. xii) a change in viewpoint occurs in the observer. The STPS organizers worked to inspire a change in perspective on Wolf Road Prairie, from a vacant lot to a historic landscape, reminding politicians, citizens, and visitors of a long-forgotten landscape.

Major Features of Wolf Road Prairie

One of the most compelling characteristics of Wolf Road Prairie is that it allows visitors to experience what it might have been like for settlers to walk in the prairie. As individuals walk out from the oak savanna area, they see the prairie indicator plants such as rattlesnake master (*Eryngium yuccifolium*), compass plant (*Silphium laciniatium*), prairie dock (*Silphium terebinthinaceum*), and big bluestem (*Andropogon gerardii*) and little bluestem (*A. scoparius*). The prairie is wet. Mosquitos buzz nervously. A hawk circles in a cloudless blue swatch of sky, and the sun shines brightly onto a wide open space filled with multicolored flowers and gently waving grasses. In good seasons with much rainfall, the grasses grow to be 6 feet tall, and the individual who walks there feels encircled by these grasses.

These broader views of the landscape are easily apparent from a passing car or a sidewalk on the edge of the prairie. But there is also the closer view of the prairie that occurs when individuals park their cars and walk through the oak savanna area, out onto the grassland area, and among the tall grasses and colorful flowers. The STPS invites visitors to do so by providing a kiosk supplied with self-guided nature walk pamphlets. Prairie specialists provide a third, microscopic view by demonstrating flower structure with a hand lens during guided tours. On weekends throughout the year, biologists lead botany and ecology classes through the prairie, explaining, demonstrating, and observing closely the flora and fauna encountered that day. These classes encourage a closer understanding and appreciation of the biodiversity of species that can be seen in the totality of the landscape. In an interview with The Nature Conservancy (1994), Edward O. Wilson stated that there are "three large domains of benefit" of biodiversity to humanity. One benefit is the maintenance of our ecosystems in healthy condition. "Recent studies have shown that the greater the variety of animals and plants present in an ecosystem and maintained at the original levels, the more efficient in the functioning of the ecosystem and the more stable it is likely to be over the long term."

The second benefit to humanity addresses medical and pharmaceutical applications, crops, fibers, petroleum substitutes, and other products and the economic wealth to be derived. The third benefit that Wilson describes is a property he terms Biophilia, or the basic affiliation humans have for natural environments.

Wolf Road Prairie offers its own ironies and hidden features for those who wish to find them. For example, the reason that Wolf Road Prairie avoided development in the initial phases was because the developer, Samual Insull, went bankrupt during the Great Depression. Individual plot holders dispersed, and the result was a complex grid of confusing land ownership issues that the courts could not easily resolve, leading, ironically, to the preservation of this prairie.

Wolf Road Prairie has sidewalks in the southern portion of its acreage. Members of STPS do not know who built them. They are useful as pathways for visitors, preventing them from trampling plants, limiting human intrusion. Prairie specialists often remind visitors to stay on the sidewalks, to step carefully, to pay attention to what can be observed, and to be mindful that many of the plants and grasses observed from the pathway are found in few other places in the state. The seeds from the many flowers and grasses in Wolf Road Prairie are collected each fall. They then are distributed to other prairie sites in the Chicago area. Because so little native Illinois prairie remains in the "Prairie State," the last remnants have greater value.

Another hidden feature of the prairie is its wetland area, called Harrier Marsh by volunteers. Tucked deep inside the acreage, north of the sidewalks, the area offers a home to the marsh hawk and migrating water birds, which search for remnants as rest stops on their long migrations. The green heron (*Butorides striatus*) and the great blue heron (*Ardea herodias*) have been sighted in or near the marsh. The black-crowned night heron (*Nicticorax nicticorax*) and the American bittern (*Butaurus lentiginosus*), both species on the Illinois endangered species list, also have been sighted.

It is the harrier or marsh hawk that continues to amaze visitors. Larry Godson (1985) wrote of the need to protect habitat for the marsh hawk by preventing townhouse development. At that time, the STPS was working to prevent construction of a townhouse development to the north of the prairie area. It feared that the development would prevent water from the creek from flowing into the prairie area and feeding the marsh, thereby drying out the marsh.

Godson wrote:

> "At the top of the food chain in the marsh is the marsh hawk. ... Instead of soaring high in the sky when in search of food, the harrier flies low over the marsh. It systematically quarters the area with wings angling upward in a shallow "v", using its keen hearing as well as its eyes to locate its prey. ..."

The writer continued to emphasize the importance of preserving Wolf Road Prairie, so that the harrier can have a place to nest.

> "As you can see, the harriers are special birds, strongly adapted to the prairie-marsh environment that once dominated ancient Illinois. However, they too are on the state endangered species list. Their habitat is rapidly being destroyed and their egg shells are thinned by pesticides. Miraculously, the existence of harriers at Wolf Road has been confirmed recently by the numerous sightings of several expert birders. This alone is reason enough to redouble our efforts to save all of Wolf Road Prairie and with it, Harrier Marsh."

The STPS was unsuccessful in preventing the construction of a townhouse development to the north of Wolf Road Prairie. At this time, it is not certain whether Harrier Marsh will continue to exist.

A third hidden feature relates to the name of the STPS newsletter. Shooting star (*Dodecatheon meadia*) also can be found in the prairie. They were called "prairie pointers" by Illinois settlers and, hence, the name of the STPS newsletter.

A fourth irony of Wolf Road Prairie concerns fire. STPS volunteers observe that the area with the greatest variety of prairie wildflowers and grasses is where the Westchester Volunteer Fire Department used to practice fire fighting. At that time, Wolf Road Prairie was known as a "vacant lot," and considered to have no value. Today, controlled burns are conducted in small sections of the prairie as a component of the restoration and management plan.

Stewardship of the Land

The STPS has a management plan for Wolf Road Prairie. Its mission voices the values of practicing land ethics and of understanding the value of the prairie in its contribution to the Chicago area. The mission of the management plan is to increase biological diversity of species in the Chicago area, the United States, and globally. The goals of the plan are the following: use land ethics (wise ecological restoration procedures), maintain aesthetically pleasing open space, and encourage the education of citizens of all ages to learn and to appreciate the natural history of their region in order to contribute to the overall health and well-being of the Chicago area.

At this stage of its ecological restoration, Wolf Road Prairie has trees in the prairie area that must be eradicated if prairie habitat is to be restored. Several species are present: European buckthorn (*Rhamnus cathartica*), gray dogwood (*Cornus racemosa*), and box elder (*Acer negundo*). Eradication is a difficult process. The trees are either burned during prescribed burns in spring and fall, clipped throughout the year, or mowed with a sickle-bar mower. Mowing combined with clipping has proven most effective. Some of the 82 acres have more forbs than grasses. This creates less dry grassy burning material to spread a fire. Therefore, prescribed burns are difficult to conduct over large areas of prairie. For an urban prairie, this is a secret benefit. Prairie specialists can more easily isolate smaller areas for transect studies; neighbors who fear that a fire could spread out of control and damage valuable residential areas are tolerant of the smaller burns; and potential stresses on nonbotanical species such as reptiles, amphibians, small mammals, birds, and butterflies are felt less acutely.

One lead manager at Wolf Road Prairie acts as a steward and manages volunteers who work at shrub clipping and record changes in flora and fauna, including the appearance or disappearance of species. Many volunteers have stated that, in the process of participating in ecological restoration, they have come not only to learn about forests and trees, but to value the diversity of ecosystems that can be found in their town, county, and state. An issue of "The Prairie Pointer" quoted volunteers (Gitts, 1990-91). Marin Hansin, student at Riverside-Brookfield High School stated "Mr. Koch-Weser showed us a video in ecology club. He said that most of Illinois has been plowed at some point. It's almost an honor, it *is* an honor for us to work here."

One of the more well-known prairie communicators is an artist named Henrietta Tweedie. She paints Wolf Road Prairie flowers and sells prints of her works to raise funds for ecological restoration. She and a fellow artist and friend, Roberta L. Simonds illustrated a book, "Prairie Plants of Northern Illinois," by Russell Kirt. She is cited in the September 1990 issue of the newsletter for her cover design and for having been influenced by the poet, Carl Sandburg. Volunteers are aware of the historic and aesthetic value of the prairie, and they express their awareness of benefits to the community.

The entire 82 acres of Wolf Road Prairie is now owned jointly by the Cook County Forest Preserve and the Illinois Nature Preserve Commission, and Wolf Road Prairie is a candidate for National Natural Landmark status with the Department of the Interior. The STPS is the designated steward of the land. A small but steady group of volunteers attends prairie workdays and provides volunteer labor in the process of its ecological maintenance and restoration. Professionals and teachers conduct regular research-gathering studies and attempt new methods for encouraging prairie vegetation. And a visitor can still walk along a path or a sidewalk in the prairie to catch a glimpse of small piece of what must have been a breathtaking expanse of Illinois prairie.

Conclusion

The process of preserving Wolf Road Prairie has been long and complex. The awareness of the need for and the value of protecting and preserving prairies and the desire to communicate to others about the biological diversity of Wolf Road Prairie sustained volunteers in the preservation process. They share an affinity with the land and its natural heritage, value this affinity with the land, and communicate an appreciation for the prairie to citizens of the community. In the process of working to preserve the prairie, volunteers learned to organize, to plan, and to educate others so that the public may have access to the beauty of Wolf Road Prairie and share in a common bond with nature. We find this bond with the land described in the fiction of Willa Cather, the nature writing of John Madson, and the poetry of Emily Dickinson and Carl Sandburg. Two scientists and educators, Edward O. Wilson and John Lovelock, define a natural relationship with nature in terms of *Biophilia* and *Gaia*, respectively. As a cultural value actively expressed in a heavily urbanized area, a bond with nature emphasizing appreciation for history, biology, and art can be a primary force for preservation of the land and its biological diversity.

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Literature Cited

Bone, Bonnie. 1985. The Prairie Pointer. Save the Prairie Society. Spring, p 4.

Cather, Willa Sibert. 1946. *My Antonia*. Houghton Mifflin Company, Boston, MA, pp 7-8,29.

Elkind, Sam. 1977. The Prairie, Stopping Progress to Save a Natural Community, Menagerie, March. pp 18-19.

Gitts, Lana. 1990-91. Volunteer Voices, The Prairie Pointer, Save the Prairie Society. Winter, p 13.

Godson, Larry. 1985. The Prairie Pointer. Savethe Prairie Society. Spring, p 2.

La Force, Melanie. 1995. Unpublished interview with Larry Godson, Save the Prairie Society member.

Lovelock, J.E. 1979. *Gaia*. Oxford University Press, Oxford, England, p 147.

Madson, John. 1982. *Where the Sky Began, Land of the Tallgrass Prairie*. Sierra Club Books, San Francisco, pp xi-xii.

Murray, Carol, et al. 1993. Wolf Road Prairie Nature Preserve Self Guided Walking Tour, Save the Prairie Society. p 2.

The Nature Conservancy. 1994. *The Conservation of Biological Diversity in the Great Lakes Ecosystem:Issues and Opportunities*. Prepared by the Nature Conservancy with a partial grant from the United States Environmental Protection Agency, p 3.

The Nature Conservancy. 1994. A Conversation with E.O. Wilson. Nature Conservancy, 44/(4): pp 24-29.

Scanlon, Constance. 1989. Wolf Road Prairie is a Rare Jewel. Suburban Life Citizen, Wednesday, November 15, p 7.

Shouba, Jack. 1985. In Memoriam: Grace Shouba, The Prairie Pointer, Save the Prairie Society, Spring, p 8.

Spale, Valerie. 1992, The Prairie Pointer. Save the Prairie Society. Fall/Winter, p.2.

Stevens, William K. 1995. Latest Endangered Species: Natural Habitats of America. The New York Times, Tuesday, February 14, 1995, p A1.

Wapeha, Kate. 1984. List of Birds, The Prairie Pointer, Save the Prairie Society, the Prairie Lily Issue.