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Prairie:

A Multiple View

Edited by

Mohan K. Wali

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Grand Forks

PRAIRIE: A MULTIPLE VIEW

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PREFACE

A new era has dawned on the North American prairies. From the traditional role of being the bread basket of not only this continent, but indeed the world, they are now becoming the major energy suppliers for the United States and Canada. For vast deposits of coal lie under the calm and lush grasslands and must now bear the brunt on new frontiers. The decisions to be made on the fate of this landscape are staggering in scope, and the true fund of knowledge is rather low. Never before have ecological information exchanges been of such paramount importance.

This volume is based on the presentations at the biennial meetings of the IV Midwest Prairie Conference held at the University of North Dakota, August 19-22, 1974. The Midwest Prairie Conference is unique. It is a *pot pourri*. It has a most unusual, but most desirable blend of expertise: ecologists, soil scientists, wildlife managers, geographers, historians, landscape architects, conservationists, environmental activists and others. All share a common desire and goal - how best to learn more about the prairies, how best to preserve them, and how best to explain the multifaceted complexity of prairie ecosystems to the people.

From 1968 on, and travelling through the states of Illinois, Wisconsin, Kansas and North Dakota, the Conference has grown immensely. The growth, from an initial 100 or so members to over 1200 now on the mailing list, has brought on a great variety in the specialization of its members. With a heavy accent on field trips in the native prairies, the basic thought that ecology is best learned in the field has become stronger and stronger in the meetings held thus far. The Conference is still in its embryonic stage, but widespread interest and enthusiasm among its members makes one very optimistic about its continuance and future. The Conference should be nurtured and the information developed in its meetings should be transmitted to the grass root -- literally and figuratively. It would indeed be a shame, as Frank Egler would say, if there is a miscarriage of this brilliant conception.

The great variety of interests can also pose some momentary frustrations. The selection of papers and themes to satisfy the mad-after-the-numbers scientist on the one hand, and the generalist and naturalist on the other, can indeed be very difficult. We tried to strike a balance between the two and to alleviate the problem somewhat by inviting speakers with diverse backgrounds and interests. I am sincerely thankful to Francis E. Clark, Arthur Cronquist, Ralph L. Dix, Francis C. Evans, Alvin M. Josephy, Jr. and Elsie Rose for presenting these invitational papers.

This volume has been divided into four parts; the boundary lines between these parts are rather shaky, and at times the inclusion of the papers in them is arbitrary. A 7,000 reference bibliography, covering North American grasslands east of the Rocky Mountains, is being published as a Supplement to this volume.

For all the help in arranging the meetings, I am indebted to several people. The Program Committee of William T. Barker, Reid Goforth, Paul B. Kannowski, Richard H. Pemble, James F. Power, Warren C. Whitman, and William J. Wrenn spent many hours in making out a workable meeting schedule. Associate Administrator Norman A. Berg of the Soil Conservation Service, USDA, Washington, D.C., very kindly gave the banquet address on land use planning in the United States. My associates, graduate students, and staff - Elliot Shubert, Alden Kollman, Richard Bares, Mark Larson, Michael Key, Elmer Finck, Linda DeBoer, Carol Roscoe, and

Keith Killingbeck - followed an almost 18-hour-per-day schedule to make the meeting successful, and a special word of appreciation is due to them. Field trip leaders -- Paul Kannowski, Robert Seabloom, Nick Zaczkowski, Gregg Johnson, Carolyn Godfread, Fred Sandoval, William Barker, Robert Storch, John Milton, Leo Kirsch, Harold Dubbert, and Robert Stewart -- did an excellent job. Many thanks are due to all the sectional chairmen of the meetings and reviewers of the papers.

Financial assistance was made available by the University of North Dakota, North Dakota State University, and for the post-meeting field trip by Northern Prairie Wildlife Research Center, USDI. I must express my gratitude to my officers at the University of North Dakota -- Thomas J. Clifford, William E. Koenker, and Bernard O'Kelly -- for all the moral and financial support. I would be remiss in my duty if I did not pay a special word of thanks to the University's Housing and Food Services. My warmest thanks are due Judy Shubert for arranging the manuscripts for the printers.

Let us all look forward, with great anticipation, to the V Conference in 1976 at the Iowa State University and give it our vigorous support.

Grand Forks, ND — Mohan K. Wali

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Section I: PRAIRIE AND MAN

An environmental activist tries emotionally to answer an intangible: What is prairie? And two well known authorities, a modern historian and a plant ecologist, reach the same conclusion independently: Even in the '70's, modern man is colonialistic. Both share the belief that present day decisions on land use, in the Midwest for example, are being formulated and acted upon, outside of the region.

WHAT IS PRAIRIE?

Elsie Rose

When I was asked to address a few words and pictures to the subject of "The Eternal Prairie--Man's Link with Foreverness" for this assembly, I was compelled to define for myself, first of all, what is prairie?

A negative process of defining something can be a listing of what that thing is NOT. So, for instance, prairie is not desert--prairie and desert have a common denominator of low rainfall, but there most similarity ends.

Prairie also is not the deciduous woodlands of much of the eastern part of the United States.

And, while magnificent in their own right, California redwoods share little in common with prairie.

The rocky coast of Maine and the sandy shores of the Gulf of Mexico are definitely not prairie land.

High, jagged peaks of mountain country are not likely to be associated with prairie; however, geographically, mountains are responsible, in part, for the presence of prairie.

These diverse biotic communities are different, yet similar in their biological needs for oxygen, water and sunshine.

I can see what the prairie is not, but what is it?

Perhaps a specific study of the various prairie components will lead me to an answer.

I learned that life in the prairies is largely determined by climate. Extremes of temperature, rainfall amounts varying from 10" to 30", and ubiquitous winds are controlling factors of prairie climate.

Fires, caused by lightning, set by Indians, or carefully controlled by prairie people contribute to the vigor and maintenance of the prairie condition.

The deep, fertile, organic soils of rich, black humus have been formed by the decomposition of centuries of grass roots, and range from slightly acid to slightly alkaline.

And what does this particular combination of natural phenomena produce on the land?

Grasses, "the forgiveness of Nature--her constant benediction" according to a 19th century Kansas Senator, John Ingalls.

Big bluestem, better known as turkey foot to the pioneers, is one of the most widely disseminated and dominant grass species of the prairies.

June grass, a cool season perennial, is usually found in the cooler, more northerly prairie in association with little bluestem and needlegrass.

Side oats grama is a warm season, drought resistant grass that has a wide prairie range.

Buffalo grass carpets the semi-arid western prairie as its chief sod former: a handy, versatile building material for prairie settlers.

Blended in with the grasses as an integral part of prairie are the wildflowers: as profuse as they are beautiful.

Prairie violet is one of the harbingers of spring on the Great Plains.

Valuable winter forage for prairie wildlife is provided by the hips of prairie rose which usually mature by August.

Lead plant is perhaps the most conspicuous and characteristic shrub of upland prairie.

A perennial with a spreading root system, prairie coneflowers were gathered by native

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American Indians who used the dried heads for a tea-like drink

Sunlight causes the leaves of the compass plant to grow with its edges in a north-south direction, thus giving it its common name.

Goldenrod, like most prairie flora and fauna, is not exclusively indigenous to prairie ecology, but it is evocative of the mood of the prairie: tough, hardy, and attractive.

And what creatures live and reproduce in this area, among these botanical species? The fritillary butterfly that aids propagation, for one.

Grasshoppers, for another--Early white settlers of the prairies considered them to be a destructive pest. Agri-chemical products limit their devastation today.

White-footed mice turn abundant plant foods into high-protein rations for the larger predators of the prairie.

The most characteristic burrowing rodent of the plains and mixed prairies is the black-tailed prairie dog. Sociable, alert, and clever, his domain is rapidly shrinking.

A criminal by sheep growers' standards, the seemingly indestructible coyote has a distinctive call that is one of the memorable sounds of the western rangeland.

Favoring open country with the broad view characteristic of the prairie is the pronghorn antelope.

An indication of its prevalence west of the Mississippi is the meadowlarks' distinction as the state bird of five west-central states.

The prairie horned lark soars in clear prairie space while his mate is lining a scooped-out next with grass fibers.

Once considered a game bird, the upland plover (now sandpiper) is now protected in North America but not on its wintering grounds of the South American pampas.

The master pilot of wide prairie skies, the prairie falcon, has sharp eyes and rapid flight, enabling it to survive well in its chosen habitat.

The burrowing owl digs its own underground home as well as occupying abandoned prairie dog burrows. Its diet consists of mice and other rodents as well as insects and plant material, all abundant in the prairie.

Dancing and stomping his feet and shaking his tail feathers, the sharp tail grouse attempts to attract a female: Plains Indians have long copied his style.

Just knowing what grew and lived on the prairie didn't define prairie so I listened to various experts talk about prairie.

Some people spoke of how fat so many cows could get on X number of acres of native grass.

At other gatherings, people demonstrated machines that would mow prairie grasses, called meadow hay, at a fast clip.

Conferences were organized by others who were concerned about conserving wilderness prairie and black-footed ferrets.

I had attended Prairie Symposiums and learned that some people looked at prairie and saw charming wildflowers, others saw abandoned cemetery plots, some saw roots and rhizomes, others observed the effects of fire on spider distribution, while others studied the tiny creatures that lurk where the grass meets the soil.

But I had a vague feeling of still not knowing what prairie is.

So, with my family, I visited streams on the prairie where canoes floated by and eagles soared overhead. I journeyed to the watering spots of the prairie variously called potholes, lagoons, marshes, and swamps--and I saw sandhill cranes, and pintail ducks, and Canada geese, and solitary sandpipers and dickcissels.

I flew over the checkerboard pattern of the Great Plains; and I saw milo fields and corn fields and soybean fields and wheat fields and rangeland and feed lots and grain elevators.

I traveled to places where some native prairie species thrive: the mighty elk in Oklahoma, the hardy bison in South Dakota, the stately whooping crane in Texas, the quick red fox in Iowa, the swift marsh hawk in Kansas, and the prancing prairie chicken in Missouri.

I heard about coal mining and oil shale processing and missile sites and power plants.

I lived in spreading suburbia.

I walked through rows of Indian and switch grass at a native grass seed production farm, and wondered, is this prairie? After all, it was native grass on flat land with low rainfall.

No, I still didn't think I knew what prairie is.

Perhaps books and historical records would help provide an answer. Native American Indians, who were the very earliest residents of the prairies, saw the area as a land of milk and honey, designed by the Great Spirit to provide all their earthly needs.

Spanish explorers of the 16th and 17th centuries sought cities of gold and found seas of grass.

The Lewis and Clark expedition of 1804-1805, endeavoring to find the northwest passage to the Pacific, discovered the prairies to be "good land, covered with grass...void of timber."

John Fremont, the expansion-minded son-in-law of Missouri's Senator Thomas Hart Benton, emphasized the rich, arable soil, sparkling streams and lush grasses of the prairies during his expeditions of the 1840s.

And, a few years later, Francis Parkman, traveling through the landscape that Stephen Long had earlier misnamed "The Great American Desert," suggests that "the scenery, though tame, is graceful and pleasing, with...level plains, too wide for the eye to measure."

An obscure immigrant and diarist named Littleton was "delighted that the immensity of blue and green was spangled with 'wild roses, morning glories, and a large yellow flower resembling the Hollihowk'."

The characters in Willa Cather's pioneer novels alternately survive and die in their attempts to conquer, subdue, and tame the prairie.

Old Jules and *Ladder of Rivers* are true stories of the exploitation of the prairies for growing fruit trees and for fattening lean, Texas cattle.

In a modern setting, Edwin Way Teale sees the prairie as a fascinating phenomenon of natural history, worthy of our examination and study.

Sierra Club's *Floor of the Sky* dramatically links the scenery of the prairies with the people who inhabit it.

The Wilson's *Grasslands* reveals the prairie as a place of enchanting vistas and splendor.

Webster's *Dictionary* states that prairie is "an extensive tract of level or rolling land in the Mississippi valley, characterized in general by a deep, fertile soil and, except where cultivated, by a covering of tall, coarse grasses, mostly without trees."

With all this "book learning" did I finally know, what is prairie?

No, not exactly; but along with knowledge of the natural history of the prairie, the human uses and beauty of the prairie, the literature gave me some tentative answers.

It was becoming evident that one can define certain aspects of prairie but one cannot confine the whole of its meaning.

Some have described prairie but no one could circumscribe it.

It is difficult if not impossible to limit an abstraction which obviously means many different things to many different people.

If the experts cannot even agree on the geographical limitations of prairie, how can a layman begin to encompass it?

The late Dr. John Weaver of the University of Nebraska spoke of the prairie as "much more than land covered with grass. It is a slowly evolved, highly complex organic entity, centuries old. It approaches the eternal...Each grass-covered hillside is a page on which is written

the history of the past, conditions of the present, and predictions of the future. Some see without understanding; but let us look closely and understandingly, and act widely..."

Per Hansa in Rolvaag's classic, *Giants in the Earth*, referred to his Dakota homestead as "this endless Wilderness" needing only the hand of man to transform it into a "habitable land for human beings." Ironically, here we are at the 4th Prairie Conference trying desperately to preserve and restore a little patch of prairie here, an acre or two there so that our children and our children's children will see a remnant of that "Endless Wilderness," the better to understand the past and look to the future.

Maybe I haven't been able to define prairie because it is an intangible--a feeling--an emotion--a sensitivity to a special kind of quiet mood to be mostly enjoyed in solitude. My finite mind cannot comprehend the infinite prairie.

It is simple; it is complex.
It is harsh; it is tender.
It is barren; it is lush.
It is a love affair between a few special people and a special kind of land.

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THE PRAIRIE AND ITS PEOPLE: YESTERDAY'S HISTORY AND TODAY'S CHALLENGES

Alvin M. Josephy, Jr.

Throughout the world, many people today are experiencing the painful beginnings of what may be a new period for mankind -- one characterized by, among other things, continuous changes in standards and expectations. Often, the changes are so rapid and profound as to be shocking if not demoralizing to great numbers of individuals and their institutions. The principal causes for this instability are already well known. They include rapidly increasing population, accelerated growth of human needs and demands, advancing technology that responds to the ever-expanding requirements of society, and the direction of all facets of life by fewer and fewer persons presiding, often without accountability, over larger and larger interlocking political, economic, and social conglomerations of powerless employees. In many spheres of activity already, the face of the future is apparent: more and more, persons in all walks of life and of all economic levels are confronted by impersonalized forces set in motion by gears that cannot be brought to account and stopped, that bring changes that may or may not be wanted, and that fundamentally alter existence for large numbers of people.

Inherent in these changes, of course, are unending conflicts and crises, on one area of which I would like to focus this morning. I refer specifically to the frictions between those who are attempting to maintain a quality of life and environment with which man has heretofore been familiar, and those who believe -- even if they do not say so -- that man must accept and adapt to certain deteriorations, or at least change, in the quality of existence on this earth if mankind itself is to survive.

Perhaps nowhere in the world at the present moment is this particular issue drawn more vividly than in the northern prairies and plains of the United States. Here, once upon a time, was a great new land for American Manifest Destiny expansion -- for the stockman, the agriculturalist, and the settler. Listen to these words of promise: in the prairie east, Mrs. Linda W. Slaughter, a boomer of 1874, wrote of the vicinity of Bismarck: "The climate is eminently healthful...the soil is a rich black loam about eighteen inches deep...The farms which have been opened...have proven highly productive...Vegetables of all kinds are grown with but little trouble...water is abundant and of the purest quality...The country from the Missouri to the Yellowstone will be peopled with an intelligent population. Its solidary prairies will be covered with fruitful farms, its hills and valleys dotted with the happy homes of emigrants. Cities and villages will arise on every hand; railway and telegraphic lines will multiply and school houses will be built. The busy hum of industry will supplant the Sabbath stillness of the plain, and the sound of the church bell shall be heard in the land." In the same era, farther west on the plains, Theodore Roosevelt was writing: "The country is covered with a growth of short bunch grass, which cures on the stalk, into excellent hay for winter feed; it is very nutritious, and upon it range cattle become as fat as stall fed oxen...The scantiness of the water supply is no harm to the cattle men, as in summer the beasts keep within a few miles of the river, principal creeks or large water holes, and thus loose a great stretch of back country over which they have not grazed, and which afford them excellent winter feed when ice has closed up all the ponds and streams, and they are obliged to slake their thirst by eating snow." That was a hundred years ago, and much history followed the course charted essentially by writers like Mrs. Slaughter and Theodore Roosevelt. But history has not ended. Today, a large share of the burgeoning

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energy needs of the most industrialized nation on earth is apparently to be provided at the cost of a relatively rapid, continuous, and profound alteration of the life and environment that have come to mark this same prairie and plains area. In effect, a basically farming and ranching economy, adapted to the requirements of a semiarid environment, is to be changed with the speed that characterizes the new day to one whose primary demands will come from industrialization and urbanization. The change, and the rapidity of the change, are already bringing shock to people and the environment, and to the interrelations between the two.

Recently, the bewilderment of such change was reflected in human terms -- which for all of us should be the most significant terms -- by a couple in their early sixties who had just sold their ranch in southeastern Montana to an energy company, which had previously acquired the coal rights beneath their land. The man was the third generation of his family on that land, and he and his wife had known nothing else but the life and environment of that sparsely populated, undefiled part of the country. As they talked to me, they seemed, at first, resigned to what had happened to them, and not overly unhappy. They were getting on in years, they observed, and daily work on their land was growing harder for them. They were tired of the chores, tired of the harsh winters, tired of fighting the weather, tired of the occasional accidents with machinery that made things more difficult, tired of being tied down to the land and the stock, tired of not being able to relax and travel and enjoy more of the good things in life. They had not made a killing from their sale, but now they could move to a warmer and more comfortable place like Arizona and settle down to a more pleasant and easy-going existence.

As they continued talking, however, and as we started walking among their buildings and through the near pastures, the conversation took a new tone. First, there began to be nostalgic reminiscences of what they had lived through on that ranch. There was pride over what they had achieved with their lives and struggles, over what they had overcome and conquered. Then there were expressions of undisguised love -- love for the familiar, for the ranch itself, for the fragile soil, the pine-dotted hills, the huge sky and the expansiveness of the area, love for the beauty of the rolling grassland, for the cottonwoods and willows that lined their clear-running creeks, for the pure velvet air, for the privacy and stillness -- for everything, in short, that they had just sold. And then, in their conversation, came reflections of anxiety and fear. "We got more money from the coal company than we could ever have got from anybody else -- I guess," the husband said. "But, you know, truly, a person wouldn't know if it's going to be enough, or if it was worthwhile doing. It's going to be a mighty change, and we don't rightly know what it will do to us." Inflation that might eat into his new fixed income and steadily erode his standard of living wherever he settled was not alone what he meant. We talked of crowds of people, of traffic, urban life, noise, hustle, frustrations, harassments, crime, and pollution -- of the features of a material deterioration in existence itself that would make life in Tuscon or Phoenix, or wherever in the sun he and his wife resettled, a miserable change from everything they had known all their lives in southeastern Montana. But then, in the end, he put the human factor into its current -- and, inevitably, historic -- perspective. What's the difference, he shrugged. Southeastern Montana -- Tongue River, Powder River, the Birney-Decker country -- it was all going to change too. Eventually, it was going to be no better than wherever else he might go, and maybe it would be worse. Strip coal mines, power plants, gasification plants, new railroad spurs, transmission lines, construction crews, trailer camps, highways, hundreds if not thousands of newcomers, mushrooming towns, and urbanization would change the open country where he had been born and raised. "What's the difference?" he repeated. "It's a new world, and you either have to get on with it someway, or get out of it."

In a sense, that couple, like many of the inhabitants of the northern prairies and plains, have up to now been fortunate. For generations, the great forces and pressures that have urbanized and degraded the quality of life in so many other parts of the United States have by-passed

their area. In another sense, however, what they were able to enjoy was deceptive. In the background, always, was an ugly fact, no more visible than the coal beneath the soil and grasses of the land, but nevertheless ever-present. In economic and social terms, the area has, in effect, been a colonial one, whose inhabitants have rarely, if ever, been able to exert decisive control over what happened to them. It is a fact that is particularly relevant today and that has much to do with the content of the conflicts and changes that are now beginning to affect people like that southwestern Montana couple.

No one need be more than reminded, perhaps, of the forces that shaped life on the northern prairies and plains. Its semiaridity, as many observers have made clear, explains much: its soil character, vegetation, wildlife, basic wheat-and-cattle or farm-and-ranch economy, the large size of its farms and ranches, the thin and scattered population, its generally small towns, the history of out-migration of the young, high per capita costs for social services, frequent low farm income and lower than average nonagricultural income, and so forth. It has followed that the history of the relationship between the northern prairie and its inhabitants has been marked by several themes, among them being remoteness from markets and population centers, isolation, adaptation to the environment -- which is characterized by extremes of climate -- and economic dependence, particularly on outside capital.

From the beginning, dependency, like the eroding forces of wind and water, has combined the rock-like pride, courage, optimism, and energy of the people. Those latter qualities have nowhere been more admirable or staunch than among the inhabitants of the northern prairies and, in truth, have themselves been nurtured and strengthened by the many challenges of life itself in this region. Hot summers, drought, grasshoppers, cold winters, blizzards, wind, and loneliness have tested the stamina and ingenuity of the inhabitants and have helped the shaping of a sturdy, reliant, and courageous people. Isolation, remoteness, the need to cope and overcome by oneself or with the cooperative association of neighbors sharing the same tests and challenges, and the achievements of many victories over hardships and difficulties have instilled pride and a deep and pervading sense of independence. The struggles, in turn, have made man familiar and intimate with his natural environment. In most areas, he has learned to live in harmony with, and with respect and affection for, the wildlife and natural resources that compose his homeland. But, at the same time, always, there has been an ultimate lack, for, despite his own fierce sense of independence, there has been an awareness of a master elsewhere, pulling the strings that really count and giving the orders that can undo a man's work, exploit him, keep his economic level below the national norm, and in many ways truly control his family's fortunes.

Historians sometimes reach back before the coming of the first settlers to illustrate this dichotomy of independence versus dependency, and to show, perhaps, that it is an age-old manifestation of a region whose environment in the past dictated sparse and scattered population. Here were some of the continent's noblest Indians, far-ranging, expansive, proud, and self-reliant. Yet among their ranks were the most exploited tribes. The fur trade engulfed them, degraded them with alcohol, and rapidly made them dependent on the white man and his possessions. In time, the white pioneers and settlers fell victim, also, to outsiders -- to the distant owners and managers of railroads, banks, mines, and insurance companies, to the Minneapolis mills, terminals, and elevator owners, to lumber trusts and beef and packing trusts in the midwest and east. Money went out of the area in insurance, interest, storage charges, high fuel costs, equipment and supply purchases, and railroad rates heightened to secure a return on fictitiously inflated capitalization. In more recent times, the pullers of strings have changed somewhat, but by and large they are still outside the area. Some of them, agencies of the federal government, are rigid bureaucracies responding to mazes of decision-makers in Washington. Others, engaged in the oil and gas business, are based in Texas, California, New York, and elsewhere. The coal, power, and energy conglomerates of today, near-cartels almost totally

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unregulated and uncontrolled, are taking over from everywhere -- even from overseas in other nations.

In the long run, therefore, what has happened, what is happening, and what will happen in the northern plains and prairies stems in large measure from what is decided elsewhere. As a microcosm, the southeastern Montana couple mirror the impact on the people. Hardy workers and strugglers for a decent existence in a land and place they truly loved, their fate reminds one of that of the Indians of yesterday. They took pride in their independence. But when the coal company came, they had to accept and adapt to a degradation of their life and environment or get out. So it is now with a whole region and for at least several hundred thousand people. Conflict and crises are in the air, but those who believe that man must accept certain deteriorations in the quality of his existence so that mankind may survive are already here having their way and will continue to do so. These northern reaches of open land, traditional producers of food and raw materials for the urban markets, and traditional purchasers of the products of the urban areas -- always on terms set by those urban centers -- will provide the fuel and energy for others and will continue to fit the pattern of a colonial region exploited for others.

There will be those who deem this observation as too harsh or too simplistic. But, inevitably, they do not see the individual people who are involved. They deal almost entirely with "the big picture," with the facts and statistics and graphs of such concepts as economic development, progress, growth, and stability. Change, and the more rapid the better, is generally to be encouraged, and not hobbled. They are the enthusiastic supporters of such works as the Garrison Diversion project, and they use such arguments as, "If we don't use the water, someone else will get it," failing perhaps to wonder whether the water is being locked away permanently for its best use. I don't mean to disparage or deprecate such points of view. In a way, they reflect much that we cherish and admire -- the vision and go-aheadism that built this nation. But for us today, in the beginnings of this era of dislocating and demoralizing changes, they too often overlook the human bewilderment and tragedies generated by the faceless juggernauts that they set in motion. Those juggernauts, like infatuation with statistics and "the big picture," take little or no account of the opposition and helplessness of the human victims. They roll over them without responsiveness, accountability, justice, or mercy. A Bureau of Reclamation booklet put it succinctly: "No one," wrote the Bureau's Kafkaesque somebody-or-other in Washington, "No one likes to be told that he must do something, but someone's property must be acquired in the public interest or the development of our country would come to a standstill. It is unfortunate that a few persons must be inconvenienced for the welfare of all, but this happens to each of us, in one way or another, every day. This is the price of progress. It is inevitable in the advancement of society. Many landowners involved will be benefited." This refers to the Garrison Diversion project, but its attitude and point of view typify those of the public and private sources that will support, encourage, and carry out the great changes throughout the region.

Think of those words, and let me use the Garrison project as an example. There is enough of the ludicrous in that project, especially in time of great inflation and demands to cut the national budget -- thousands of productive and prosperous farms to be sliced up and destroyed at an overall cost of more than half a billion dollars of the taxpayers' funds so that an equal number of new farms can be created someplace else; shelterbelts already being knocked down by a government that once pushed farmers to plant them as a weapon against a dustbowl; wildlife habitat being eliminated and then recreated with hopes and prayers in a Happy Hooligan operation; and so on. But who among the proponents thinks enough in terms of the individual affected people, once again reminded of their helpless state of dependency, once again subjected to hardship and injustice by others who control their destiny? Along the route of the McClusky Canal, change in human terms is traumatic -- and sometimes defies decency. Dr. Strangelove cases are legion, but let me cite one. The Bureau of Reclamation took a wide

swath of fine watered hayland close to the buildings of one farm family, fenced it off, but had not yet got around to digging the canal through it. The farmer needed the pasture urgently and appealed to the Bureau for the right to use it until the canal was built. The Bureau told him to see the contractor who was going to dig that section of the canal. The farmer did so and persuaded the contractor to let him use what was once part of his own land, but only, he alleged, if he paid the contractor one-third of the hay he raised. It was public land, but the victimized state of the farmer was so acute that he begged silence on the alleged extortion to which he was subjected -- a silence still shared by the contractor as well as the juggernaut, the sometimes faceless Bureau of Reclamation.

Throughout the northern prairies and plains, coal and power development is already also exacting its toll of human tragedies as families are told to adapt or get out. It is only the beginning. But society in general -- masses of families -- faces a host of challenges and problems created for the region by the requirements of rapid change. Much study, experimentation, and discussion have already been devoted to the way land, vegetation, water, and other natural resources will be affected -- and yet much is still unknown and controversy and disagreement still shroud many vital areas of knowledge. New strip mines are proliferating, with many more promised in the near future. But ability and willingness to reclaim the stripped land of the prairie and plains are little more than vague hopes and unguaranteed promises. Despite new laws, costs and feasibility of reclamation are not well enough known; different regulations, methods, and types and lengths of efforts may be needed in individual localities; evasion of responsibility and inadequate bonding for reclamation are still a legitimate concern; and ability and commitment to enforce regulations by any agency of government must still be proved. Certainly, the record of the various agencies of the federal government and the states up to now leaves much to be desired.

The nation's energy needs inexorably will convert farm and ranching lands to coal mines, trading food for fuel. But even if successful reclamation eventually restores the land for food production and other uses, the environment and quality of life will have changed. The multi-faceted questions of what will happen to the water supplies in the semiarid region have barely been investigated, yet already in some areas aquifers, often contained in the coal seams, have been destroyed, stream beds have been diverted or interfered with, and wells have gone down or run dry. Controversy over water is further compounded by the beginning of massive new conflicts over rights to existing water supplies and proposals to divert enormous sources of water from one basin to another and from traditional users of water, the farmer and rancher, to a new user, industry. It is strange, indeed, noting the fast switch done by the Bureau of Reclamation in Montana and Wyoming, which has all but pushed its original clients, the agriculturalists and stockmen, to the back burner in favor of a new, wealthier and more politically powerful client, the energy producer. In the process of change, many widespread areas as well as specific localities will be affected, not to mention thousands of individual families, whose problems will border on survival, whose lives will become nightmarish with harassments and worries, and whose decisions, too often made for them by others far removed from the scene, will border on the tragic.

The strip mines, as is well known, are only the wellspring of the region's projected industrialization. The North Central Power Study of the Bureau of Reclamation and a variety of public utilities envisioned a massive network of up to 10,000-megawatt mine-mouth power plants dotting the northern plains and prairies and, indeed, in some places sited in lethal concentrations. Though the study was set aside, its dreams in time may well be outdone and made to seem puny by what actually occurs as a result of a planless, every-company-for-itself development boom by competitive industry. That, of course, is already beginning. The study, moreover, all but ignored additional steps of the industrialization: the erection of water-hungry coal gasification and liquefaction plants; the acquisition of corridors across the landscape for rail-

roads, highways, pipelines, acqueducts, and transmission lines; the creation of huge temporary construction camps; the incoming of large temporary labor forces and their families; the burgeoning of industrial complexes serviced by expanding urban centers and new towns; the proliferating of ghetto-like trailer settlements and surrounding honkey-tonk satellite slums; and the need for new housing, public and private services, and taxes and capital with which to meet the exploding demands.

Not touched at all by the study were the most elemental problems of environmental and social and economic impacts. Still largely unknown are questions concerning pollution damage to human health, wildlife, livestock, timber, grasses, and other vegetation caused by the emissions from the mammoth power and coal conversion plants. Certainly, there will be a marked degradation of air and water quality and therefore of the quality of life itself in a region noted for its pure and healthy atmosphere. Some of the many social and economic problems to be expected have been identified by those engaged in preparing the studies of the federal government's belated Northern Great Plains Resources program. They include control decisions made for the people of localities by corporation heads in places like Chicago, New York, and San Francisco -- certainly nothing new to this region, but, again, resulting in limited local autonomy; conflicts in attitudes, morals, standards, and ways of life between newcomers and oldtimers; fragmenting of the traditional social order; a weakening of family ties and of the traditional moral forces of the community, including the church; an impersonalization in the delivery of public services and private goods -- that is, a loss of old neighborly interrelationships; a change in the role and status of women; a vastly increased stratification of society and of income levels with increased competition, tensions, and jealousies; and changes in local leadership and power structures resulting from the arrival of newcomers from different backgrounds, with different interests, and with more and different demands than those of the outnumbered oldtimers.

The changes, it is noted, will come first to localities, perhaps widely separated through the region. And that stage, as I will describe in a moment, has already commenced. But thereafter the affected localities will increase, and the impulses of their changes will radiate outward until the whole region is affected. The impacts will be felt by individuals, families, and all groups and, again referring to the studies for the Northern Great Plains Resources program as well as to those by psychologist ElDean Kohrs of the Wyoming Counseling Center and others, will involve a dramatic deterioration in the norms and quality of daily life as it has been known in this region. There will be crowded, makeshift, slumlike living quarters set up here, there, and everywhere to overcome enormous housing shortages. There will be inflation within towns and hardships on those with fixed incomes, particularly the elderly. There will be overcrowded schools; inadequate police forces; demands for sewage systems, new roads, and other public services requiring higher taxes; hardpressed hospitals and shortages of doctors -- again falling especially hard on the elderly; and there will be increased crime, family tensions, adultery, suicides, vandalism, and mental health problems -- all documented by what is occurring where change and boom conditions have already begun.

Such is the experience already, for instance, in Rock Springs, Wyoming, where a strip mine and the construction of the Jim Bridger power plant have raised the population from 12,000 in 1970 to almost 30,000 today -- a figure higher than that projected three years ago as not occurring in Rock Springs until 1990. To the visitor who knew the Rock Springs of a few years ago, the city is a devastating shock. To the visitor who never saw it before, it is an unbelievably God-awful mess, reflecting in its rapid and planless growth all the problems previously enumerated. It is a boomtown of truck drivers, construction workers, and other newcomers, drawn by high pay; it is a mass of crowded makeshift buildings and clustered trailer camps, short of sewage and piped water facilities, schoolhouses and classrooms, public services, and capital with which to cope with the shortages. The police force is underpaid and understaffed,

and so are members of the city government. According to the Los Angeles *Times*, it has also become an alleged center of organized crime, dealing in gambling, prostitution, and narcotics. Prostitution, said the paper, was already a $3.6 million-a-year racket in the city. Jobs are plentiful, and money is abundant. But prices for everything are kited. It is the oldtimers -- and, again, the elderly and those on fixed incomes -- who suffer. No longer can they wonder where the familiar life of yesterday went. Now they are in a struggle for survival among strangers in a terrifying new environment that changes for the worse each day. In the boom environment capital will have to be found to provide services and meet social needs. But the boom will end one day, and the city will settle down. Many will move away, and then there will be more problems for those who stay. The economy will have to be maintained. New industry, new sources of capital, and new means of growth will have to be found. Urbanization will have to continue its grey processes.

There are other localities beginning to feel these changes, notably Gillette, Wyoming, and Colstrip and Forsyth, Montana. But it is only the start. Not long ago, when I hunted antelope on the sage plains west of Gillette, I could hike to the top of a pinyon-covered draw, look around at the countryside in all directions, and see not a single man-made object. No more. Gillette and its vicinity are on the way to becoming a modern-day Pittsburgh of the energy industry, a huge industrialized center of strip mines, mammoth power plants, and coal conversion complexes. At Colstrip, the director of the Westinghouse Environmental Systems Department, brought in by Montana Power to help the town adjust to a growth that may possibly rival that of Gillette, replied to a question of how the school district could find the money to finance facilities for an exploding school-age population by saying, "That's your problem, gentlemen."

Those four words were blunt, but they are significant not alone to Colstrip, but to all the northern prairies and plains. I have touched on the problems and challenges that lie ahead. They would, I think, be awesome to the inhabitants of any part of the world. But to a region that traditionally has been held in colonial or dependent status, lacking the environmental base and the capital with which to pull itself out of that status, the changes can be overwhelming. As industrialization spreads and its impacts grow more intense, human adaptation will require enormous assistance. If history is a guide, it cannot and will not come from within the affected area, for the colonial status will continue, and wealth and capital will still flow out. The best-intentioned measures of state and local governments will be undermined by command decisions made elsewhere and by low levels of public funds available to assist the people and enforce the laws. Either the exploiting corporations or the federal government must, in my opinion, meet the bills for orderly transition. It will not do to tell the inhabitants of this region, "That's your problem, gentlemen." They did not make the problem, and they alone cannot cope with it. Their land must not -- and need not -- be made into a National Sacrifice Area for the rest of the nation.

COLONIALISM IN THE GREAT PLAINS

Ralph L. Dix

INTRODUCTION

It is a remarkable coincidence that the thesis I have prepared complements the theme so forcefully presented by Josephy (1975) in the opening paper of this conference. This is fortuitous since I had no previous knowledge of his subject matter. I hope that I will be able to use this advantage to bring the persistent problems of colonialism in the Great Plains into still sharper focus.

My principal premise is that the landscape of the Great Plains is about to suffer much destruction from strip mining largely because it is a colonial area, in the sense that most of the meaningful decisions concerning its fate are made outside of and not in the interest of the area. It is obvious that Josephy and I have recognized the same apparent weakness in the present Plains culture. It is interesting that we have done so in that our backgrounds and research interests are markedly different. His interests center in the history of the American Indian while my own research has dealt primarily with the structure of vegetation. What I shall discuss in this paper are ideas which have developed during some 20 years of research on Great Plains vegetation.

I hope that my presentation will be in the same spirit as Josephy's but I propose to sketch a broader background of man's Great Plains experience. I hope to sketch briefly, with emphasis on perspective rather than detail, no less than the pre-history, history and future of man on the Great Plains.

I begin by stating several hypotheses which seem to me reasonable and useful and I will then offer evidence for their validity and usefulness.

Hypothesis 1 - With but one, and possibly two, exceptions colonialism has been and remains the usual situation on the Great Plains. By this I mean that cultural patterns on the Great Plains have traditionally been shaped and determined by peoples and forces outside the Great Plains area. The one certain and the one possible exception are:

a) The Horse Indian of the 18th and 19th Centuries
b) The Paleo-Indian who inhabited the Plains prior to 16,000 B.C.

Hypothesis 2 - That the history (i.e., the European experience) on the Great Plains has failed to develop an indigenous culture and that this failure has caused abundant human suffering by European man on the Plains, and may indeed lead to the final destruction of the Plains. This hypothesis has been abundantly documented by Josephy (1975) and I will spend little time pursuing this point.

Hypothesis 3 - That colonialism similar to that experienced on the Great Plains is not unique in world history. I will briefly attempt to place colonialism on the Great Plains into perspective by citing one current but remarkably similar example from West Africa.

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Hypothesis 4 - That it is probably still possible, even at this late date, for Plains people to develop an indigenous culture that is compatible with the Plains landscape. Perhaps the terrible threats from outside will serve as a catalyst to establish such a culture. Modern mining technology is undoubtedly capable of destroying the Great Plains. Even if that were not true today, engineering science is certainly capable of developing the machinery to fill any inadequacies in technology which may exist. Can a truly indigenous culture be established in time to save the Plains?

It seems clear that the principal questions of grassland ecology in the Plains today have to do with cultural values, ethics, aesthetics, charity and justice. The questions center on how we perceive our own best interests. The question might be asked, "Do we perceive the Great Plains as our home or simply as a piece of business?"

HYPOTHESIS 1

That colonialism is traditional in the Great Plains - the native American experience

My first hypothesis is that cultures traditionally have come onto the Great Plains from outside of the region and that these cultures have seldom been well adapted to the Great Plains environment. This is clearly illustrated by Jennings (1974; Fig. 9.2) because he presents a model displaying arrows of cultural succession through time and space. It is interesting that the arrows, regardless of the time period, always flow *onto* the Great Plains. The Great Plains are always on the margins of areas of cultural development and the cultures that exist on the Great Plains are simply pale reflections of societies which have developed in other climates and other landscapes. The important point ecologically speaking is that these cultures are not specifically adapted to the Great Plains. Looking at it chronologically the Paleo-Indian would be in the Hypsithermal interval where the Plains are virtually uninhabited, followed by the Plains Woodland area which corresponds to the Moundbuilders Burialground Period of the East, the Templemound Period of the East, and then contact with European man. These are the Periods that I will be talking about.

Two stories as to when man invaded the Northern Hemisphere are told. The conventional wisdom of the archeologists (Jennings, 1974) is that he invaded between 30-40,000 years ago. He came over with some sort of poorly developed tool kit and he developed a hunting culture based on a megafauna of very large animals, most of which are now extinct. There were three or four different species of buffalo.

We know relatively little about these people except something of their hunting techniques from a very recent study (Wheat, 1972) in eastern Colorado on a buffalo kill site. We know that these people hunted in groups. The usual procedure was to stampede the buffalo into an arroyo. They would either kill themselves by overcrowding and trampling or were easily killed by spear. Individuals had various jobs to do in the slaughter of these animals. The important parts of the buffalo were cut up and distributed by the group in assembly line fashion. Hence a higher culture based on hunting large mammals occurred on the Plains. When they had made a kill they had a very abundant supply of meat available. They usually remained at these sites until their meat supply was used up. When they had to move, they could only take what they could carry. I think the conventional wisdom of the archeologists would suggest that this culture is an indigenous Plains culture based on the large mammal megafauna and this seems to have been reasonably successful. It came to an end during the beginning of the Hypsithermal when the temperatures went up and the Plains apparently became much drier and these people vanished from the Plains.

A story that Martin (1973) tells about this Period lends much more weight to my argument about the cultures of the Great Plains being imported from someplace else. Martin's idea is that man did not come into the Great Plains until about 11,000 B.C. He came through the ice free corner of Alberta and onto the Great Plains. Within 400 years he completely occupied North America. Martin feels that man migrated down in a vast wave of high density of human population, about 20 miles wide, that desecrated the megaflora as it went along. So it left nothing behind it, but ahead of it the megafauna was very little disturbed. This supports my hypothesis that most Plains cultures really were not indigenous but many archeologists do not accept Martin's hypothesis yet. It does need more work.

Moving up the archeological time table (Fig. 1), the Burial Mounds people, the Hopewell people and the Adena people (Willey, 1966) originated the core of their civilization in the Ohio Valley but extended far out onto the grassland, even out to the Great Plains. As we look at the culture of these people, we find that their housing was not the greatest, but for that period, it was reasonably well developed. They had great artistic ability and obviously a very rich culture. The sculpture that they accomplished was truly remarkable. When we take this culture that was extremely rich and project it out onto the Plains it was continually deteriorating and much more primitive than that directly West. In the Front Range, just north of Fort Collins, Colorado, an archeological dig turned up very faint remnants of this woodland culture, this so called Plains Woodland culture. But by the time it penetrated into the Plains there was very little left of it. These people apparently followed the wooded areas and were really woodlands people. The only evidence that we find of it now are spear points and fireplaces of this time. We also find enough pottery to clearly identify it with the Woodlands culture of the east.

On the archeological scale once more we come to the so-called Templemound Builders. This is centered in the Mississippi Valley and it radiated out again and penetrated parts of the grasslands. Probably the best understood site of this is the Cahokia site near St. Louis. At Spiro, Oklahoma, one can see the influence of Meso America with the temples on top of mounds, indeed a very advanced culture. Sculpture and pottery were very well advanced and showed strong influence of Meso America. As this culture again migrated from the St. Louis area out, along the Mississippi and the Missouri Rivers and along their tributaries, it was just a pale reflection of the eastern material. This, we call then, the Plains Village culture. It was well developed along the Middle Missouri, with large complex earth structures. These were farmers now, and they were Woodland types. They grew corn, squash and beans. Populations were very large. While they were out in the grassland areas their activities were restricted almost entirely to the riverbottoms where they farmed. It is true that they did carry on some hunting activity but couldn't move very far on the Plains without some sort of convenience, some sort of power, like a horse. These Plains Villages were in operation when white man came onto the scene. Archeologists have recently dug a number of these sites along the Middle Missouri and we know a great deal about them. There were very large numbers of people living in the grasslands but they were agriculturalists, they were Woodlands peoples living in the bottomlands. Their pottery was of quite good quality but certainly nowhere near the quality of the people at Cahokia and along the Mississippi itself. As we get into the Middle Missouri country there is a deterioration of the culture of these people. If we go further down to the Plains from the Republican River that flows along the Kansas-Nebraska line, the so-called upper Republican phase of the Plains Village culture, we notice that the culture deteriorates even further. The pottery is no longer as good. The sculpture is certainly not of a high quality and if we conrast it with that of Spiro in eastern Oklahoma, we see it is deteriorating as it comes out of the Plains. Here, then, we see up until European man came into North America, all of the cultures Indians had on the Plains, with the possible exception of the Paleo-Indian, were infused from outside and even at that time the Plains were a colonial area.

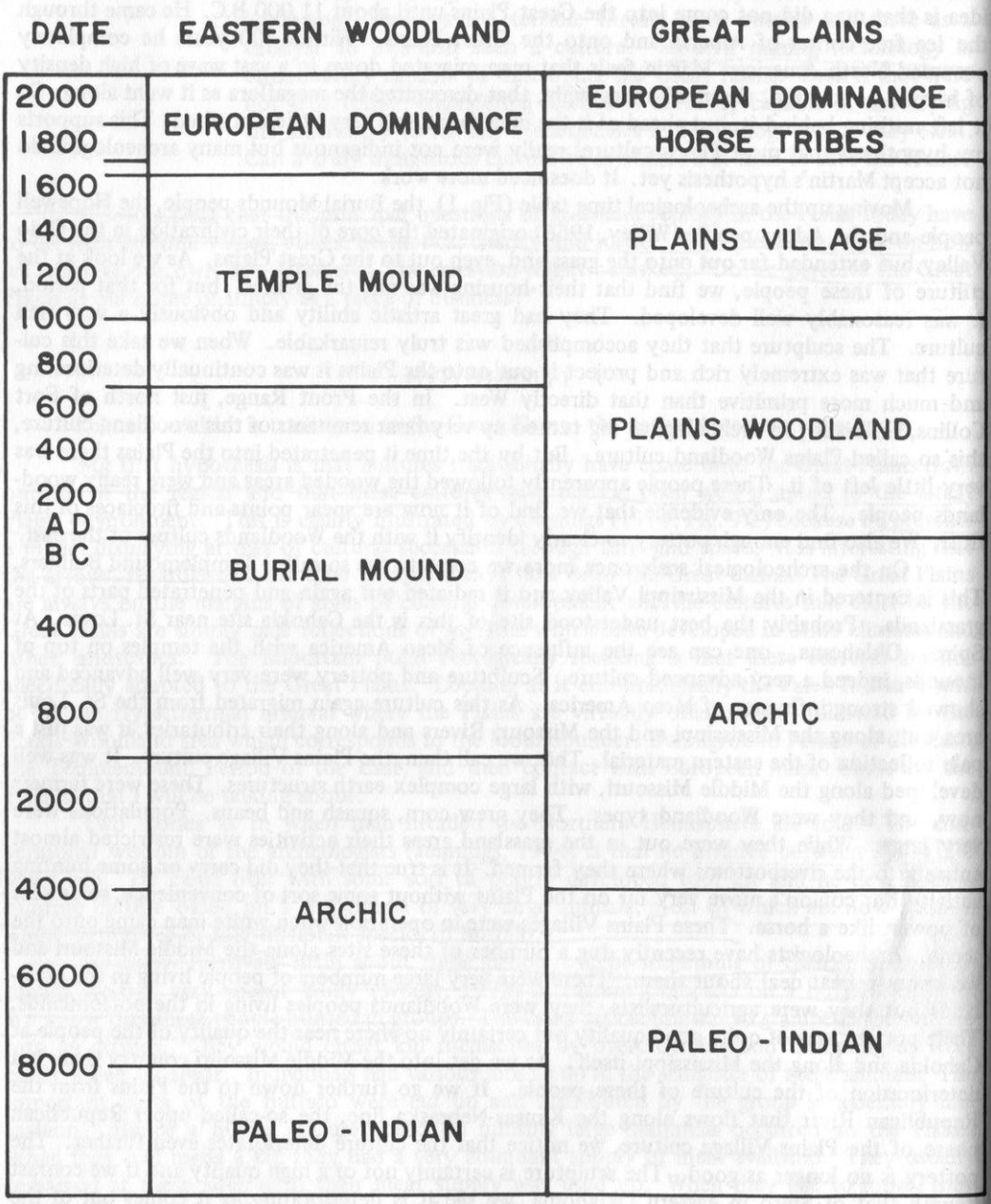

Fig. 1. Comparative chronologies of man in the Eastern Woodland and Great Plains. Note that the flow of cultures is always from east to west.

The introduction of the horse is just an estimate of how and when the horse migrated into the Plains; around Santa Fe, New Mexico, about 1600, by 1720-1725 into the central Plains, by 1750 in the Northern Plains, by 1770 into the Minnesota area, 1770 also in southern Saskatchewan, and of course, a little earlier, 1690, down in the Texas area (Roe, 1955). The horse really revolutionized the Plains and did, I suggest, give rise to the only undisputed case we have that an indigenous culture did arise on the Plains. The horse was captured. We usually visualize the horse as increasing the Indian's ability to utilize buffalo. I suspect that was not the case. The buffalo were not that difficult to hunt and it was not buffalo or the supply of buffalo meat that was a limiting factor for the Plains. The real limiting factor was transportation. As long as they were limited to the dog and the sled situation, they were probably not going to transport very much material. Hunters were not limited by what they could kill, but they were limited by what they could bring back to the camp. So with the introduction of the horse, transport on the Plains became very important. The early European riders on the Plains, in many documented cases, had high priority use of the horse, not for the warrior but for the transport of families; comparable to our station wagon at the present time. Once the horse was available, then, they had indeed a Grassland culture on the Plains. They could move villages, materials, supplies, and were not limited to carrying things over from one camp to the other. This then gave rise to a real revolution of the Plains that developed very quickly into a Plains culture indigenous to the area.

The Plains grasslands were probably not inhabited very much before the arrival of the horse (Wedel, 1961). It is interesting that most of the Indian tribes that we think of as Plains Indians or Horse Indians migrated onto the Plains very soon after the horse came. We think of the Commanches, for example, as being the terrors of the Southwestern Plains, but it turns out that Commanches only came onto the Plains in the 1700's. Before the 1700's they were inhabitants of western Colorado and western Wyoming and when they got the horse moved out onto the Plains and very quickly culturated to the Plains. This, then, is an indigenous culture.

Another example, of which there are many, are the Cheyenne Indians, which we think of as native Indians of the center of the West Central Plains but are actually the Cheyenne Indians from Minnesota. As late as 1750 they are known to have been in Minnesota. They acquired the horse and moved out to the Mandan area where they came into contact with Adatsun and Mandan Indians and got some of their culturation. Remember that the Cheyenne at this time were corn growers, they were agricultural Indians. They then moved out onto the Plains further down into the Black Hills and very quickly split off into the north where the Cheyenne occupied the Tongue River area of Wyoming, and the southern Cheyenne migrated as far south as the Arkansas River. At Bent's Fort on the Arkansas River by 1830, the Cheyenne were clearly there and clearly a Plains Indian. They very quickly acculturalated into a Plains Indian from a Woodland agricultural Indian. Once the horse was available, the Indian could live on the Plains. If you live on the Plains, you have a different attitude toward them than if you simply go out there to hunt, or if you simply go out there for a brief period during the year.

With the arrival of the horse, the development of the Plains Indians had a very unique situation in the long history of man. These nomadic people were also affluent. This, I think, is a very important point. Although nomadic and because of the great abundance of buffalo meat, they had the leisure to develop an extremely high art and culture. They had the leisure to develop ceremonies and laws. The amazing legal system of the Cheyenne is something to behold. It is much more complex than ours. I am sure the Supreme Court would probably uphold most of their law decisions. The Sun Dance ceremony which has been pretty well documented, in fact all of their ceremonies, were centered around the horse and buffalo. Very ritualistic, each tribe and each little group had its own way of painting the traditional buffalo skull and this had to be done in a prescribed way. All of which, of course, took time and effort

and it was only the buffalo economy which permitted them to do that. They had the opportunity to develop the dance and hide painting. Hide painting was characteristic and best developed by the Plains Indians; hides were something that were mobile, and when the time came to move on, they could fold them up and transport them some distances. Hide painting became a rich and a luxurious type of art form on the Plains. The art prehistorians, people that are interested in primitive art, regard these as highly sophisticated, stylized and symbolized art forms. They spent a great deal of time painting teepees and these they could carry with them. Their histories and stories were told on these paintings. They were not simply, I have to confess I often thought that, just primitive kinds of paintings. The buffalo hide obviously is painted in a highly abstract way. This is meant to be. It is an interpretation of the entrails of a buffalo and is a kind of a painting that was done only by women in the community, in fact by specialized women. It was a specialized type of labor and a highly developed art. So we have to credit the Plains Indian with having extremely rich culture. A parflash, a little container which was used to fold up meat, was very highly decorated, and of course, so were the warriors' types and their shields.

Just for a moment, let me contrast the art of the Plains Indian with the art forms of the Northwest Indian which have received better press coverage than the Plains Indian. The Northwest Indians were woodcarvers while the Plains Indians were painters of hides. But the art historians tell us that the Plains Indians were every bit as competent and their art forms as advanced as the Northwest forms. Both were similar in that neither of these rich cultures were dependent upon agriculture. They were both hunting tribes and in the case of the Northwest Indians, they were fishing societies. The Northwest Indians were stable, while the Plains Indians were nomadic people. Their life forms were naturally quite different. My hypothesis then is that the Horse Indian on the Plains was probably a well developed indigenous culture, ideally suited for the Plains, and would probably have survived indefinitely because the Plains Indian was in balance with the environment. However, he was not left alone for very long. White settlers came to the Plains, immediately after the civil war, and warfare developed. With their decimation, the Plains Indians came to a halt at Wounded Knee in 1890 with the death of Chief Bigfoot.

HYPOTHESIS 2

European Man

I would like to go next to European man as the historical part of the history of the Great Plains. Man's arrival in the Plains has been very well described by Webb (1931). With the windmill he cultivated his crops but I think the important thing is that he essentially brought a European culture with him and he has not modified that culture sufficiently for life on the Plains. Therefore, the people that live on the Plains at the present time, the Europeans, still look back to the east for their roots. I think that there has been partial, but not entire, acculturation. One example from a little town of Hardmore, South Dakota, may be illustrative. One, that the European man was not content to live on the Plains. Even though this is in western South Dakota, one of the first things that these people did was to institute a deciduous forest environment by planting trees, thus making a little island of deciduous forest on the Great Plains. This, I think, prevented them from becoming acculturated to the Plains. Familiar to us also is the abandonment of homes and of schools in many Plains towns. The few old people that are around these towns are really not too well acculturated to the Plains and probably are looking back East for cultural enrichment and so forth. They are still basically in a deciduous forest habitat.

HYPOTHESIS 3

Africa

I would like now to go over the hypothesis. What has happened to the Great Plains is not a unique feature as shown by a current example from West Africa (Wade, 1974). It is a drought area in the sub Sahara and has traditionally been occupied by the Sahelian tribe. These people were nomadic herdsmen and they had developed over the centuries, much as the Plains Indians and the Horse Indians had, a culture that was very finely in tune with the environment. They migrated with the seasonal rains, they had herds and the limiting factor in the number of cattle was the availability of water. The availability of water was controlled by wells which the tribal chiefs controlled, doled out, and with a little bit of paternalism, perhaps, controlled the size of the herd. What's happened now in this area is that the French and American engineers and others have gone in. In order to increase the balance of payments of some of these new nations that were established, they wanted to export cattle. They have increased the numbers of cattle because they have drilled deep wells and tapped the aquifers, some of these wells being as much as 1000 feet deep. So, no longer is water the limiting factor. But now grass has become the limiting factor. Nothing in the culture of the Sahelian people tells them that this is going to be a problem because they never had to limit the number of cattle. Since water is available, the herds multiply out of bounds, and it is the overgrazing that has decimated the area in the present time. Ecologists working there tell us that drought at the present time is not unusual. But at the present time because of the destruction of the grasses by overgrazing, the landscape is no longer able to maintain that balance and therefore the grasses have been destroyed, winds have blown the sands and they now face a very hard situation. This is familiar to those who were around in the 1930's in the Great Plains. The ranching couple in Montana that had to give up their ranch to acculturation (Josephy, 1975) had the option of moving to Arizona. But the woman with her child in West Africa (Wade, 1974) had no options and had to pay an even greater price for the lack of cultural considerations and the balance between the culture and landscape. I think as ecologists we have to worry about these things and make our point heard in some of these problems.

The question you might ask now is, can I come up with any examples from modern man, apart from isolated primitive tribes; that is, modern man in relationship to an acculturation which is in keeping with the landscape. I think there are some good examples. Certainly the British Isles, at least up to 1960 when I was there last, may serve as an example. A British landscape shows families living on lands, generation after generation, living and dying and probably one could find in the area the tombstones of people 5 and 6 generations gone. I am not saying that each one of them possesses an undisturbed landscape. I don't think as ecologists we can any longer, with human populations being what they are, talk about natural undisturbed pristine vegetation. Vegetation is often modified. But nonetheless erosion does not occur here and it is a stable landscape. I think the European man, at least up until World War II, had developed a culture which was in keeping with the landscape. The church, the peasants, and the peasant-church relationship was a very close one and it is not surprising that this European culturation of this type worked reasonably well. It was superimposed on the deciduous forest in eastern North America. But it was a disaster in the Great Plains in the 1930's.

HYPOTHESIS 4

Future of the Plains

I would like to talk now about the events in the future of the Great Plains. I would like to review a few ideas, on something I've called Industrial Revolution, which occurred back in

the 17th and 18th centuries. As far as the landscape is concerned, it certainly did damage. In an old mining area in Cripple Creek, Colorado, there was a great deal of local disturbance but man's ability to disturb the landscape was not all that great. Localized disturbances recurred but a total destruction was not there, and there was enough natural area to absorb that additional shock, because man's ability to move earth was somewhat limited. Perhaps some of you remember Fresno dredges. I remember as a kid watching them build a bridge using this kind of equipment. These dredges would handle 300 lbs of soil at one time and if you move soil at the rate of 300 lbs at a time, the landscape probably can withstand that kind of a shock. Well, if you are moving dirt in that fashion, you can't really move enough that the successional, or the recuperative properties of the landscape, are not able to handle. But along came industrial revolution. I think a reasonable date for that is the end of World War II and things changed drastically, not so much in time but in the ability to move large quantity. I am talking about very large industrial plants, and the ability of the machinery to move land. This, I think, is one of the frightening things that has happened. Present day technology removes over 45 sq. yards of overburden in one scoop. Trucks used in the development of the coal striping in the Great Plains carry 200 tons of material, that is equivalent to two boxcars full of material, and are capable of moving on the flat at 60 miles per hour. On an upgrade it will move at about 25 miles per hour. So when you are moving earth at this rate, your ability to destroy a landscape is really phenomenal. If your neighbors or friends read in the paper that you have been given a grant of $150,000 to do some research on reclamation of strip mining out there, they would probably be very impressed. Perhaps you would be impressed too, because how many of us really manage to obtain that much money to do reclamation work. Let us consider the money involved, let us consider some other yardstick of financing of reclamation work appropriate to mining costs. It turns out that a set of tires for a hauling truck costs $75,000, so if someone hands you $150,000 for research on reclamation, what he is really giving you is two sets of tires to do work on reclamation. When we talk to mining people we really have to be aware of that. Miners seem to be willing to spend hundreds of thousands of dollars on equipment but when you come down to buying a few bags of fertilizer, that's a different problem. Somehow I guess it is just not in their cultural heritage to appreciate that plants need nitrogen while it is in their heritage to understand that trucks need tires.

If you feel that the Great Plains are not capable of being stripped or that the strip mines are going to be very isolated, very small, because there is a bit overburden concern, let me frighten you a bit more by telling you how a mountain near Aspen, Colorado, is literally being removed. It is primarily iron ore with a little limestone in it which is just going to be tossed aside for essentially it is a mountain of iron ore. A very simple process; they simply drill a hole, put dynamite in it, explode it, loosen the material and dump it into trucks. Just a small truck holds 25 tons of material. The material is carried down the mountain, put on a railroad and moved to Pueblo, Colorado. Literally a mountain is being taken down at Aspen and put on the train for 200 miles to Pueblo. Over there, we are apt to create a mountain of giant slag heap or at least cover a certain amount of prairie grassland with the waste from that mine. No comfort is to be taken in the idea that there is a bit of overburden on the coal seams on the Great Plains. It if becomes economically feasible they can certainly take those seams.

I think the real question that we have to ask is not concerned with technology or how we are going to grow plants. Given enough money we can grow plants on concrete or even on blacktop. I think the important thing is how do we view the world. There are several ways in which we view the world. One is that there is a real world out there somewhere which we are not capable of understanding or appreciating. It is a real world that exists. But the real differences come in where whatever we see, whatever comes into our senses, comes into an area already occupied. This is an area of mental artifacts, our own mind. It is the mental image that we have of a landscape. This I think is where it is really at. What are we going to do about

it? How are we going to visualize the world? I might illustrate this with the common wheel. Our vision of the wheel is an industrial tool that does work for us. But other cultures have not visualized the wheel as that. The Americans invented the wheel long ago. They considered the wheel a little thing that you put on kids' toys. They did not consider it as something we had to rush in and use in an industrial way. So how we perceive the wheel, how we pass the perception of that wheel unto our children, is very important. And the same is true with how we perceive the landscape, how we pass on that information to our children, and how they perceive the landscape. Working with drastically disturbed areas one finds out several things in a hurry. One is that companies are willing to put almost any amount of money into a project depending upon how much public relations they can get out of it. And they are very anxious to hire any kind of consulting firm that is willing to give them the answers they want. I am afraid that like most people that have operated in this area, I have become extremely cynical about consulting firms. They are so dependent upon financing that they are almost bound to provide answers the company wants. We have cases where groups of companies set up environmental institutes that do their bidding for them and keep newspapers off their back to some extent.

This is obviously an emotional approach to landscape problems. I think there is also a way by which ecologists can get at the problem. A paper by Odum and Odum (1972) from Georgia presents another approach to evaluate a landscape. Using a model worked out in Georgia, they found that about 40% natural landscape and about 60% developed area gave a maximum yield. They found, for example, that one acre of undisturbed deciduous forest in that area was equal in cost to the total cost of absorbing pollutants, wastes, and other materials of modern civilization. They also found that an ordinary deciduous forest was worth about $25,000 per acre per year. That is an appreciable sum when we tend to take the natural landscape for granted. We assign very few values to the natural landscape, what economists would call external costs. Costs are externalized by putting them someplace else. We are not accustomed to doing this with natural landscapes. I suspect in North Dakota we probably would not be able to develop as much land and would be apt to leave more as natural areas. Certainly in western Colorado we probably could not get away with more than about 20-30% development and about 70-80% natural areas to get generated cost.

CONCLUSION

The most important concept in grassland ecology is to bring about the development of visualizing the Great Plains landscape. If we visualize the Great Plains as simply a place of business, we will probably be satisfied with the present situation. And, let me assure you, that mining interests are perfectly willing to let it go at this. As one mining engineer told me, miners don't have problems, ecologists do. But I think if we consider the Great Plains as our home, we might consider ordered landscape development.

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Section II: ECOLOGY - ANIMALS, PLANTS AND SOILS

This section has an assortment of papers by experts treating their own fields of specialization. These studies have been conducted in diverse prairie regions, involve a multitude of organisms, and data have been gathered from over a few to 25 years as is reflected in the story of the old field in Michigan.

THE NATURAL HISTORY OF A MICHIGAN FIELD

Francis C. Evans

INTRODUCTION

This is essentially a progress report on a continuing study of the assemblage of plants and animals associated with an abandoned field in southeastern Michigan. The study was begun in 1948, under the sponsorship of the Laboratory of Vertebrate Biology of The University of Michigan, and so this account represents a quarter-century of observation and investigation – a fairly long period for a progress report, but only a brief moment in the time scale by which we evaluate the successional development of a bare-land surface to the mature, climax community that under stable climatic conditions may be able to persist for centuries. Although I have served as principal investigator for the study, many of its aspects have been developed by my colleagues in the University, by both graduate and undergraduate students, and by visiting scientists from other institutions; the complete list of names of collaborators, including those of the taxonomic specialists who have provided identifications, is too long to give here, but their assistance is nonetheless gratefully acknowledged. Included in this report is a full list of scientific publications that have resulted to date from this study, but the intent of this account is not so much to summarize its observations as to provide a general survey or overview.

When this project was begun, the concept of a community of plants and animals interacting with one another and with their physical-chemical environment as an integrated, coordinated *ecosystem* was just beginning to take shape. Much initial impetus for the study of such systems came from the now-classic essays of Lindeman (1942) and Watt (1947), which emphasized the dynamic nature of community structure and function. The choice of a site suitable for a long-term investigation of "pattern and process" under natural conditions fell upon an abandoned field on the University's Edwin S. George Reserve, which promised freedom from disturbance for the foreseeable future and easy access at all times of year. It was hoped that its small size – estimated at approximately 5-6 ha (12-15 acres) of open field in 1948 – and its rather simple vegetational structure – essentially two-layered, with a ground stratum and a field stratum – would permit a reasonably thorough acquaintance with its flora and fauna. Furthermore, there was a very considerable acreage of abandoned land in this part of southeastern Michigan, indeed in much of the eastern half of the United States, and a consequent need for a better understanding of old-field growth and development. Over the years since, this need has been responded to by a growing literature of research on old fields, among which are included the papers of Bard (1952), Beckwith (1954), Golley (1960, 1965), Hurd et al. (1971), Odum (1960), and Odum et al. (1962, 1963), as well as those emanating from the present study. As a result, the old field ecosystem has received a considerable share of attention from ecologists and land managers and has contributed substantially to the modern view of community organization. The strategy of the particular study described in the present paper has been to concentrate on a single community which seemed typical of old fields in this region and which might serve as a "case history" for comparison and contrast with other old field communities elsewhere.

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Location and Prehistory

The old field in question is located in the southwest quarter of the northeast quarter of Section 19 of Putnam Township, in Livingston County. This part of Michigan owes most of its present natural landscape features to the deposits and activity of meltwater as the ice sheet receded during the Cary substage of the Wisconsinan glacial period, which has been dated from about 16,000 to 13,500 years before the present (Dorr and Eschman, 1970). The field itself lies on a large, flat glacial outwash plain, at an elevation of 300 m and is approached from the east by a steep esker-like ridge about 0.8 km in length (Cantrall, 1943).

There is evidence to suggest that the land now occupied by the old field was, after the retreat of the ice, gradually covered by boreal forest. A short distance southeast of the field is a small lake, whose bottom sediments, from a depth of about 15 m, have been radiocarbon-dated at 11,450 years (Crane, 1956) and found to contain pollen grains of spruce (mostly *Picea glauca*), soapberry (*Shepherdia canadensis*), twinflower (*Linnea borealis*), silverberry (*Eleagnus commutata*) and other elements of typical northern woodland vegetation (Andersen, 1954).

The boreal forest was eventually replaced by predominantly deciduous woodland. Original Government Land Office records (checked some years ago by F. N. Hamerstrom, Jr., and F. Hamerstrom) indicate that the land on which the field is situated was surveyed in 1825; the notes of Joseph Wampler, Deputy Surveyor, describe it as "land level, timber white and black oaks, etc., undergrowth the same." It is unlikely that much beech (*Fagus grandifolia*) or sugar maple (*Acer saccharum*) were present, as the porous, well-drained upland does not provide sufficiently mesic conditions to support these species. Indeed, "the presence of mature oaks and hickories along many of the old fence lines and the rapidity with which oak is reproducing itself in the grassy upland bordering the oak-hickory forests indicate that, at one time, most if not all of the upland was covered with an oak-hickory forest of much the same nature as is now present on restricted parts" of the Reserve (Cantrall, 1942).

Climate

The climatic regime of the region has been characterized (Cantrall, 1943; Evans and Dahl, 1955) as a humid, mesothermal type, with low thermal efficiency and generally adequate precipitation at all times of year. Weather records maintained at the Reserve indicate the average annual precipitation for the period 1949-1974 to be 80.5 cm (31.7 inches), of which approximately 60 percent has fallen during the growing season from April through September; exceptionally wet growing seasons, with more than 7.5 cm in excess of the average, occurred in 1956, 1961, 1968, and 1970, and exceptionally dry ones, with 7.5 cm or more below average, in 1958, 1963, 1971, and 1974. Not infrequently the vegetation of the old field has shown signs of moisture stress, when drought conditions have combined with high temperatures. During this same 25-year period, the length of the frost-free season (defined as the period between the last killing frost – or the last freezing temperature in the few years when no killing frost occurred – in spring and the first killing frost in the autumn) has averaged approximately 167 days. The only killing frost occurring as late as June was recorded in 1972, and in 15 of the 25 years, the date of the last killing frost in the spring has fallen between April 25 and May 10, while in 17 of these years the date of the first autumnal killing frost has occurred between October 3 and 26. Snow cover is rarely sufficiently deep or long-lasting to prevent some photosynthesis and animal activity for more than a few days at a time, and the old-field community is therefore in a more or less quickened state for at least half of the annual cycle.

Cultural History

The first entries of land ownership in Putnam Township were recorded in 1828 (Ellis, 1880). The 40 acres which included what is now the old field were purchased from the United

States Government in 1836, by Bennet(t) Sewall of Ann Arbor; the price of $1.25 per acre suggests that property was at that time still in an unimproved state. When it was sold again, twelve years later, it went for $6.00 per acre, and it appears likely that by then it had been cleared of woods and was being cultivated. The township had undergone extensive clearing by 1850 (Ellis, op. cit.) and well-drained, level sites like that of the old field would probably have been among the first to be cut.

Ownership of the field changed hands a number of times in the next half-century, but it seems to have continued under cultivation over the years. Corn, wheat and oats were among the principal agricultural products of Putnam Township in 1875 (Ellis, op. cit.), and Mrs. Margaret Hanes Swartout, who was born in 1903 on the farm that included the old field and who lived there until 1920, recalled that her father, Frank Hanes, had also planted these, with Navy beans as a cash crop. Without modern fertilizers, however, these upland sandy soils did not long sustain a high level of productivity, and Mrs. Swartout indicated that farming had been difficult even in her childhood. Mr. Hanes ceased farming the land four or five years before it was sold to Colonel George in 1930. Thus the time of abandonment of the old field can be fairly accurately dated to 1925 or 1926. It was not being used as a pasture at the time, and although the Colonel quartered two or three horses there up to 1948 it was never subjected to extensive grazing by domestic stock.

There have also been no fires on the field since the time of the Colonel's purchase. In fact the only known major disturbance to which the vegetation has been subject has come from a herd of white-tailed deer (*Odocoileus virginianus*). These are the descendants of four does and two bucks placed on the Reserve by Colonel George in 1928. Free from hunting and predation, the herd increased to more than 200 animals by 1934 (Jenkins, 1964) and began to have severe effects on the vegetation of the Reserve, this being especially visible on open areas like the old field, where the stunted growth of young junipers (*Juniperus virginianus*) and hawthorns (especially *Crataegus crus-galli*) and the topped specimens of *Solidago, Liatris, Hieracium* and other forbs bore eloquent testimony to their foraging pressure. Annual cropping of the deer herd was instituted in the 1940s and has continued ever since, although the size at which it has been held has varied, from a high of 132 in 1963 to a low of 57 in 1973 (D. R. McCullough, pers. comm.). The generally smaller herd that has existed in recent years seems to have provided some degree of release for the vegetation, and the old field junipers and hawthorns have increased markedly in height and have assumed their normal shape. In retrospect, it seems clear that the browsing of the deer, along with the general sterility of the soil, has been an important factor impeding the progress of a return to forest conditions.

Dimensions and Physiography

The field is roughly rectangular in shape and is oriented with the long axis running almost exactly on a north-south line. Efforts (made in 1953) to trace the location of the old fence lines resulted in an estimate that the field originally covered an area of nearly 7.7 ha (19 acres). By 1951, however, the growth of young trees at the boundaries of the field had somewhat reduced the amount of open area; in that year, the field was measured at approximately 200 m wide by 330 m long, and because a piece in the southeast corner had been left in woodland, the actual field area was estimated at 6.1 ha (15 acres).

The surface of the old field might well be described as gently rolling, with little in the way of relief (cf. Fig. 1 in Evans and Dahl, 1955, for a contour map of the field). The difference between the highest and lowest levels is approximately 3.05 m, and the steepest slope does not exceed 15 percent. Nevertheless, this has offered opportunity for differential erosion and deposition and there is evidence of gully formation, prior to the start of this study, at several points on the periphery of the field. Perhaps the most important physiographic feature of the field is the presence of 13 shallow, round-to-oval shaped depressions or "swales", from 5 to

20 m long and from 3 to 10 m wide. Similar depressions exist in the adjoining woodland areas, and they were certainly present at the time of clearance; indeed, repeated ploughing seems to have resulted in a graduation of their contours as they filled in with silt and clay particles from the higher elevations. At present they form miniature frost pockets, and their surficial soil has distinctly greater water-holding capacity than that of the upland areas.

Soils

The soil of the old field has been variously classified as sandy loam of the Bellefontaine or Fox series, or as Oshtemo loamy sand. It is a gray-brown podzolic soil, the surface horizon of which characteristically consists of a light brown sandy material to plow depth, i.e. 15-20 cm, with a humus zone of 2.5-3.5 cm. Below the surface horizon is a layer of lighter colored friable sandy loam 15-35 cm thick; this is underlain by gravelly sand mixed with clay and colored reddish-brown or orange by iron compounds. At a depth of approximately one meter the sand gradually gives way to a gray gravel. There is little or no carbonate at the surface, but the gravel substratum effervesces readily with the addition of hydrochloric acid. A number of soil samples taken at widely scattered sites on the field have yielded small pieces of charcoal at depths of 20-25 cm, documenting the depth of the plow line and suggesting recourse to fire in the process of clearing.

In the swales, the surface material contains up to 75 percent of silts and clays (cf. Table 7, Evans and Dahl, 1955) and classifies texturally as silt loam. This has accumulated to a depth of 1 m or more in some of the depressions. Beneath it, the soil profile is developed in much the same manner as that of the field uplands. Because of its topographic position, its texture, and its dense covering of vegetation, the silt loam not only retains considerably more moisture, but also has a higher organic content, than the sandy soil of the uplands.

Special Characteristics

A feature of special significance on this old field has been the vehicle tracks or roadways which angle over the field to enter the adjoining woods and which have been present there since at least 1933. Occasionally, these roadways have been mowed, but in general they were maintained simply by occasional use. The soil in these tracks is somewhat compacted, and here and there a clay lens is created which will sustain a puddle of water for a short time after a heavy rain. Although the 725 m of roadway, averaging about 3 m in width, constitute less than 5 percent of the total field area, they provide a distinctive habitat for both plants (e.g. *Eragrostis spectabilis, Juncus tenuis, Plantago aristata*) and animals (e.g. *Cicindela punctulata, Dissosteira carolina, Acanthomyops latipes*) and seem to have served as an important avenue for the invasion of new species. About 12 percent of the herbaceous flora of the field is largely if not entirely restricted to the roadway, and since 1948 the following species not previously observed on the field have been found in or by the side of these tracks: *Mollugo verticillata, Veronica arvensis, Eragrostis spectabilis, Polygonum aviculare, Trifolium repens, Dianthus armeria, Berteroa incana, Cerastium arvense, Verbena stricta.*

Another feature of particular interest on the field is the presence of three large hickory (*Carya ovalis*) trees, which were either left or planted by the early settlers, perhaps to provide shade or a crop of nuts. Since the time of abandonment, the comparatively mesic conditions beneath these trees have provided little oases of forest environment which are the sole sites of occurrence on the field for a number of plants (e.g. *Galium circaezens, Parthenocissus quinquefolia*). The assemblage of soil organisms beneath the hickories was found to be quite different from those of the open uplands and swales (Hairston and Byers, 1954). Observations during the period 1949-57 of Vesper, Field and Chipping Sparrows (*Pooecetes gramineus, Spizella pusilla,* and *S. passerina*, respectively) nesting on the field indicated that they used these tall trees as their major songposts, which were therefore important factors in the establishment of

territorial boundaries. From the outset of the study, then, these three individual trees have had a considerable influence on the organization of the field community.

Floristic Composition

To date, 153 species of flowering plants have been recorded from the old field (Table 1), 90 of which were present in 1948. At that time, the vegetation was clearly dominated by grasses, *Poa compressa* and the later-flowering *Aristida purpurascens* in the upland area, *Poa pratensis* in the swales. These upland dominants showed high frequencies of occurrence in samples (e.g. *P. compressa* 99%, and *A. purpurascens* 84%, in eighty 0.25 m^2 quadrats), and their air-dry biomasses (averaging 68.2 g/m^2 for *P. compressa* and 45.3 g/m^2 for *A. purpurascens*) constituted 46 percent and 31 percent, respectively, of the total standing crop of herbaceous vegetation (Evans and Cain, 1952). Scattered among this graminoid matrix, however, was a considerable diversity (61 spp. in 1948) of forbs, the most conspicuous of which included species of *Antennaria, Solidago, Liatris* and *Lespedeza*; many of these occurred as more or less isolated individuals or as small clumps showing various degrees of coalescence. (The distributions of *Solidago rigida, Lespedeza capitata* and *Liatris aspera* were mapped and analyzed statistically, in a series of papers [Cain and Evans, 1952; Clark and Evans, 1954; Dice, 1952; Evans, 1952; Thompson, 1952. Cf. also, Morisita, 1959] to develop a method of measuring population dispersion.) Apart from the swales, with their distinctive vegetation marked by the prominence of *Poa pratensis, Setaria glauca,* and such forbs as *Asclepias syriaca* and *Cirsium vulgare*, the superficial appearance of the field was remarkably uniform and homogeneous.

A closer look at the vegetation, however, indicated the existence of an underlying patchwork or mosaic structure. Such patchiness is not unusual; indeed, it seemed similar to that observed in many montane regions, where numerous small communities co-exist in limited areas and where the vegetational differences cannot be recognized by exclusive species. In the old field, there was sufficient evidence of stratification to warrant recognition of (1) a ground layer including the mosses (notably *Polytrichum piliferum, P. juniperinum* and *Ceratodon purpureus*), lichens (*Cladonia cristatella, C. clavulifera* and others), and the basal rosettes of *Antennaria, Hierachium*, and other forbs, and (2) a field layer of low, medium and tall herbage to a height of about 1 m. Phytosociological differences in these layers led us (Evans and Dahl, 1955) to describe some 11 more or less distinct vegetation types which seemed to owe their characteristics to gradients in light intensity, in soil moisture and silt content, and in the general stability of the soil. (For a complete description of these types, see the paper by Evans and Dahl, 1955). In August, 1974 the field's vegetation was re-examined, to see if these types could still be recognized; although several, e.g. the *Leptoloma cognatum* and *Setaria glauca* types, had evidently disappeared, the majority were still recognizable despite some changes in densities of the component species. In fact, the species complex for the field as a whole has altered surprisingly little over the past quarter of a century: 85 percent of the species of grasses and forbs recorded in 1948 were still present in 1974. The principal change has been in the relative abundance of various forb species. From 1949 to 1953, grasses made up 85-93 percent of the peak standing crops of vegetation, but by 1960 they had decreased to 47 percent (Wiegert and Evans, 1964). Forbs have continued to increase their dominance, the most notable of these being *Liatris aspera, Lepedeza virginica* and *L. capitata, Solidago juncea,* and *Rubus flagellaris* (Table 2). At the present time, the field vegetation seems to be in what Beckwith (1954) described as "the mixed herbaceous perennial stage of succession."

Dynamic Features of Vegetation

Within the longer term successional framework, however, there are other dynamic vegetational processes taking place on the field. One such process is the cyclic change that is associated with the growth and development of populations of perennial species. A good

Table 1. Higher plants (Spermatophyta) recorded since 1948 from Evans Old Field, E. S. George Reserve, Michigan, with year of first observation. - , still present in 1974.

Pinaceae
- Juniperus communis L. 1948-
- Juniperus virginiana L. 1948-

Gramineae
- Agrostis gigantea Roth. 1948-
- Agrostis scabra Willd. 1948-
- Andropogon gerardi Vitman 1948-
- Andropogon scoparius L. 1948-
- Aristida purpurascens Poir. 1948-
- Bromus tectorum L. 1970-
- Cenchrus longispinus (Hack.) Fern. 1948-
- Danthonia spicata (L.) Beauv. 1948-
- Eragrostis spectabilis (Pursh) Steud. 1953-
- Leptoloma cognatum (Schultes) Chase 1948- (*)
- Panicum depauperatum Muhl. 1948-
- Panicum lanuginosum Ell. 1948-
- Panicum oligosanthes var. Scribnerianum (Nash) Fern 1948-
- Panicum sphaerocarpon Ell. 1948-
- Phleum pratense L. 1948-
- Poa compressa L. 1948-
- Poa pratensis L. 1948-
- Setaria glauca (L.) Beauv.
- Setaria viridis (L.) Beauv. 1948-
- Sporobolus vaginiflorus (Torr.) Wood. 1948-
- Vulpia octoflora var. tenella (Willd.) Fern. 1951-

Cyperaceae
- Carex bicknellii Britt. 1948-
- Carex cephalophora 1963-
- Carex muhlenbergii var. enervis Boott. 1948-
- Carex pensylvanica Lam. 1948-
- Cyperus filiculmis Vahl. 1948-

Juncaceae
- Juncus tenuis Willd. 1948-

Commelinaceae
- Tradescantia ohioensis Raf. 1970-

Liliaceae
- Asparagus officinalis L. 1948-

Iridaceae
- Sisyrinchium albidum Raf. 1951-2

Salicaeae
- Populus tremuloides Michx. 1968-

Juglandaceae
- Carya ovalis (Wang.) Sarg. 1948-

(*) referred to Panicum capillare L. by Evans & Cain (1952)

Table 1 (Continued)

Boraginaceae
Lithospermum canescens (Michx.) Lehm. 1951-
Lithospermum croceum Fern. 1948-
Verbenaceae
Verbena stricta Vent. 1974-
Labiatae
Hedoma hispida Pursh. 1948-
Monarda fistulosa L. 1948-
Pycnanthemum virginianum (L.) Durand & Jackson 1970-
Solanaceae
Physalis heterophylla Nees. 1948-
Scrophulariaceae
Penstemon hirsutus (L.) Willd. 1951-1970
Verbascum thapsus L. 1948-
Veronica arvensis L. 1951-
Plantaginaceae
Plantago aristata Michx. 1948-
Plantago lanceolata L. 1953-
Plantago rugelii Dcne. 1952-
Rubiceae
Galium circaezens Michx. 1953-
Galium pilosum Ait. 1948-
Houstonia longifolia Gaertn. 1948-
Campanulaceae
Lobelia spicata Lam. 1951-53
Compositae
Achillea millefolium L. 1948-
Ambrosia artemisiifolia L. 1948-
Antennaria fallax Greene 1948-
Antennaria neglecta Greene 1948-
Aster azureus Lindl. 1948-
Aster pilosus Willd. 1963-
Carduus nutans L. 1966-
Centaurea maculosa Lam. 1969-
Chrysanthemum leucanthemum var. pinnatifidum Locoq & Lamotte 1953-
Cirsium arvense (L.) Scop. 1972-
Cirsium discolor (Muhl.) Spreng 1972-
Cirsium vulgare (Savi) Tenore 1948-
Erigeron canadensis L. 1948-
Erigeron strigosus Muhl. 1948-
Gnaphalium obtusifolium L. 1948-
Helianthus divaricatus L. 1973-
Hieracium aurantiacum L. 1951-
Hieracium florentinum All. 1963-
Hieracium gronovii L. 1948-
Hieracium longipilum Torr. 1948-

Table 1 (Continued)

Fagaceae
Quercus velutina Lam. 1948-
Urticaeae
Urtica dioica L. var. procera Muhl. 1963-
Polygonaceae
Polygonum aviculare L. 1963-
Polygonum convolvulus L. 1953-
Polygonum tenue Michx. 1948-
Rumex acetosella L. 1948-
Rumex crispus L. 1974-
Chenopodiaceae
Chenopodium album L. 1963-70
Aizoaceae
Mollugo verticillata L. 1950-
Caryophyllaceae
Cerastium arvense L. 1973-
Dianthus armeria L. 1970-
Ranunculaceae
Anemone cylindrica Gray 1948-
Anemonella thalictroides (L.) Spach. 1969-
Cruciferae
Arabis hirsuta (L.) Scop. var. pycnocarpa (Hopkins) 1948-52
Berteroa incana (L.) DC 1970-
Lepidium virginicum L. 1951-
Saxifragaceae
Ribes cynosbati L. 1954-
Rosaceae
Crataegus crus-galli L. 1948-
Crataegus sp. 1948-
Fragaria virginiana Duchesne 1948-
Potentilla argentea L. 1948-
Potentilla arguta Pursh. 1948-
Potentilla intermedia L. 1953-
Potentilla norvegica L. 1963-
Potentilla recta L. 1948-
Potentilla simplex Michx. 1948-
Prunus serotina Ehrh. 1948-
Prunus americana Marsh 1970-
Pyrus malus L. 1970-
Rosa carolina L. 1953-
Rubus flagellaris Willd. 1948-
Rubus occidentalis L. 1953-
Spiraea alba Du Roi. 1952-
Leguminosae
Desmodium canadense (L.) DC 1963-
Desmodium illinoense Gray 1948-

Table 1 (Continued)

Leguminosae (con't.)
Desmodium marilandicum (L.) DC 1948-
Desmodium paniculatum (L.) DC 1973-
Desmodium sessilifolium (Torr.) T. & G. 1948-
Lespedeza capitata Michx. 1948-
Lespedeza hirta (L.) Hornem. 1948-
Lespedeza intermedia (S. Wats.) Britt. 1963-
Lespedeza virginica (L.) Britt. 1948-
Medicago sativa L. 1948-
Trifolium pratense L. 1952-
Trifolium repens L. 1963-
Vicia villosa Roth. 1948-
Oxalidaceae
Oxalis stricta L. 1948-
Polygalaceae
Polygala polygama Walt. 1951-
Euphorbiaceae
Euphorbia corollata L. 1948-
Rhamnaceae
Ceanothus americanus L. 1953-
Vitaceae
Parthenocissus quinquefolia (L.) Planch. 1953-
Vitis sp. 1951-
Guttiferae
Hypericum perforatum L. 1948-
Hypericum punctatum Lam. 1951-
Cistaceae
Helianthemum bicknellii Fern. 1953-
Lechea villosa Ell. 1948-
Violaceae
Viola sagittata Ait. 1948-
Onagraceae
Oenothera biennis L. 1948-
Oenothera rhombipetala Nutt. 1948-
Oenothera tetragona Roth. 1951-
Umbelliferae
Daucus carota L. 1952-
Cornaceae
Cornus stolonifera Michx. 1953-
Apocynaceae
Apocynum androsaemifolium L. 1948-
Apocynum cannabinum L. 1948-
Asclepiadaceae
Asclepias syriaca L. 1948-
Asclepias tuberosa L. 1948-
Asclepias verticillata L. 1963-
Asclepias viridiflora Raf. 1953-

Table 1 (Continued)

Compositae (con't.)
Hieracium pratense Tausch. 1973-
Krigia virginica (L.) Willd. 1948-
Lactuca canadensis L. 1948-
Lactuca pulchella (Pursh) DC 1948-
Liatris aspera Michx. 1948-
Rudbeckia hirta L. 1948-
Solidago ?canadensis L. 1953-
Solidago graminifolia (L.) Salis. 1948-
Solidago juncea Ait. 1948-
Solidago nemoralis L. 1948-
Solidago rigida L. 1948-
Taraxacum officinale Weber 1951-
Tragopogon pratensis L. 1948-
Vernonia altissima Nutt. 1948-55

Table 2. Changes in the frequency of occurrence of plant species on Evans Old Field from 1953 to 1974. (Species whose frequency has never exceeded 5 percent have been omitted.)

Species	F %		
	1953[1]	1964[2]	1974[3]
Grasses:			
Poa compressa	94	84	96
Aristida purpurascens	89	89	65
Poa pratensis	28	14	14
Panicum oligosanthes	28	20	18
Cyperus filiculmis	20	9	0
Leptoloma cognatum	16	29	10
Panicum depauperatum	13	17	28
Danthonia spicata	6	15	32
Forbs:			
Rumex acetosella	93	81	78
Solidago nemoralis	83	76	60
Hieracium gronovii	46	41	3
Antennaria neglecta	43	74	57
Lespedeza capitata	41	74	63
Hieracium longipilum	39	48	26
Solidago rigida	37	42	44
Ambrosia artemisiifolia	30	2	1
Antennaria fallax	27	35	27
Liatris aspera	26	61	76
Oxalis stricta	25	16	12

[1] Based on 200 random sq.-yd. quadrats taken June 25-July 2.

[2] Based on 200 random sq.-yd. quadrats taken July 20-21.

[3] Based on 100 random sq.-yd. quadrats taken July 10-12.

Table 2.

Species	F %		
	1953[1]	1964[2]	1974[3]
Erigeron strigosus	21	6	15
Solidago juncea	19	41	36
Gnaphalium obtusifolium	16	2	0
Tragopogon pratensis	13	10	13
Hedeoma hispida	12	0	1
Lactuca canadensis	10	8	5
Physalis heterophylla	10	7	4
Lechea villosa	9	6	3
Asclepias syriaca	8	5	2
Hypericum perforatum	6	3	8
Euphorbia corollata	6	9	13
Rubus flagellaris	5	10	17
Lespedeza virginica	4	32	64
Potentilla intermedia	3	3	8
Monarda fistulosa	2	5	6
Fragaria virginiana	1	6	16
Galium pilosum	1	9	16
Houstonia longifolia	1	6	21
Desmodium sessilifolium	0	10	29
Hieracium aurantiacum	0	2	16
Hieracium florentinum	0	1	17

Table 3. Seasonal shift in vegetational stratification on Evans Old Field, as indicated by the numbers of herbaceous species in various stages of growth and maturation encountered in each stratum. Names and limits of the strata follow those of Elton & Miller (1954).

	April	May	June	July	Aug.	Sept.
Ground Zone[1]						
Seedling & growth stages	37	26	4	1	0	0
Flowering stage	2	7	2	0	0	0
Fruiting stage	0	1	8	7	1	0
Low Field Layer[2]						
Growth stage	0	33	24	10	0	0
Flowering stage	0	4	18	16	8	0
Fruiting stage	0	2	13	16	37	13
High Field Layer[3]						
Growth stage	0	0	0	4	0	0
Flowering stage	0	0	0	3	5	0
Fruiting stage	0	0	0	0	4	6

[1] up to 15 cm. (6 in.)

[2] 15 - 90 cm. (6 in. - 3 ft.)

[3] 90 cm. (3 ft.) and up. The tallest herbaceous growth is about 135 cm. (4.5 ft.).

illustration from the old field is found in the "microcycle" centered about the life history of *Panicum depauperatum* (Evans and Cain, 1952). Seeds of this grass seem to germinate best in small erosion pavements where bare soil is exposed through animal activities such as the nest-building of ants and the burrowing of ground squirrels, or through the decay and removal of previous plant materials. A sequence of developmental phases can be discerned in the subsequent life of the panic grass (Fig. 1), related to the formation of a mature clump and to its ultimate death and disappearance, a course which on this field seems to last from 15 to 20 years. The end of the degenerate phase is usually a bare area, suitable once more for the development of a new clump. The cycle of these changes bears much similarity to the "regeneration complex" described by Watt (1947) for tussock formation in fescue (*Festuca ovina*) grassland and to the "erosion complex" of heath communities (Burges, 1951). I interpret the process as a means by which such populations, and the vegetation types of which they are a part, tend to perpetuate themselves, thereby holding off for some time the ultimate effects of successional change.

Another dynamic feature of the old field vegetation is its characteristic *phenology* or seasonal development stemming from the differences in time of vegetative growth and maturation of its component species. As the season progresses, there is a shift in plant species diversity relating to changes in vegetational stratification (Table 3), with increasing emphasis upon the upper layers. There is also the familiar progression of floral change, as the bloom of one species gives way to that of another (Table 4). The old field's flowering season, in recent years, has begun typically in late April or early May, with the blooming of pussytoes (*Antennaria neglecta* and *A. fallax*) and wild strawberry (*Fragaria virginiana*), which is followed by hawthorn (*Crataegus crus-galli*) and Houstonia (*Houstonia longifolia*). June brings a colorful sequence of hawkweed (*Hieracium florentinum* and *H. aurantiacum*), cinquefoil (*Potentilla intermedia* and *P. recta*), daisy (*Chrysanthemum leucanthemum, Rudbeckia hirta*) and St. Johnswort (*Hypericum perforatum*). These give way in July to milkweed (*Asclepias syriaca* and *A. tuberosa*), bergamot (*Monarda fistulosa*), and various thistles (*Carduus nutans, Centaurea maculosa,* and *Cirsium vulgare*). August and September are characterized by the bloom of blazing star (*Liatris aspera*) and goldenrod (*Solidago juncea, S. rigida,* and *S. nemoralis*). As shown in Table 4, the overlapping flowering periods of those species judged to have contributed significantly to pollen and nectar resources reveal a marked rise in the diversity of bloom available at any one time to insect visitors, from 2-3 species in the very early part of the season to a level of 9-12 species throughout much of the summer, which then gradually diminishes as autumn approaches. Changes in the standing crop biomass of plant growth during the season showed a similar trend and correlated quite well with changes in the diversity of insect species observed on the field (Fig. 2). The activities of larger animals, too, were often geared to these trends in plant phenology, e.g. the Field Sparrow, which frequently nested on the ground in May, tended to place its nests at higher levels as the small hawthorns and oaks expanded their foliage later in the season, and it is clear that the seasonal changes in vegetation had a significant impact on the whole old-field community.

The Animal Community

The old field flora supports a quite diverse assemblage of animal species; an inventory of the numbers of species of vertebrates and invertebrates collected or observed there during the period 1949-74 is presented in Table 5. Given the mobility of most animals, and the diversity of their activities and behavior, necessitating a wide variety of collecting techniques (see, for example, Evans and Owen, 1965), such an enumeration of a fauna of this magnitude is not likely to be complete. On the other hand, the number of species present on the field in any one year or season was probably less than the total number (1997 spp.) reported in Table 5, as some of them were undoubtedly transients, strays from the adjacent woods, or accidentals set down

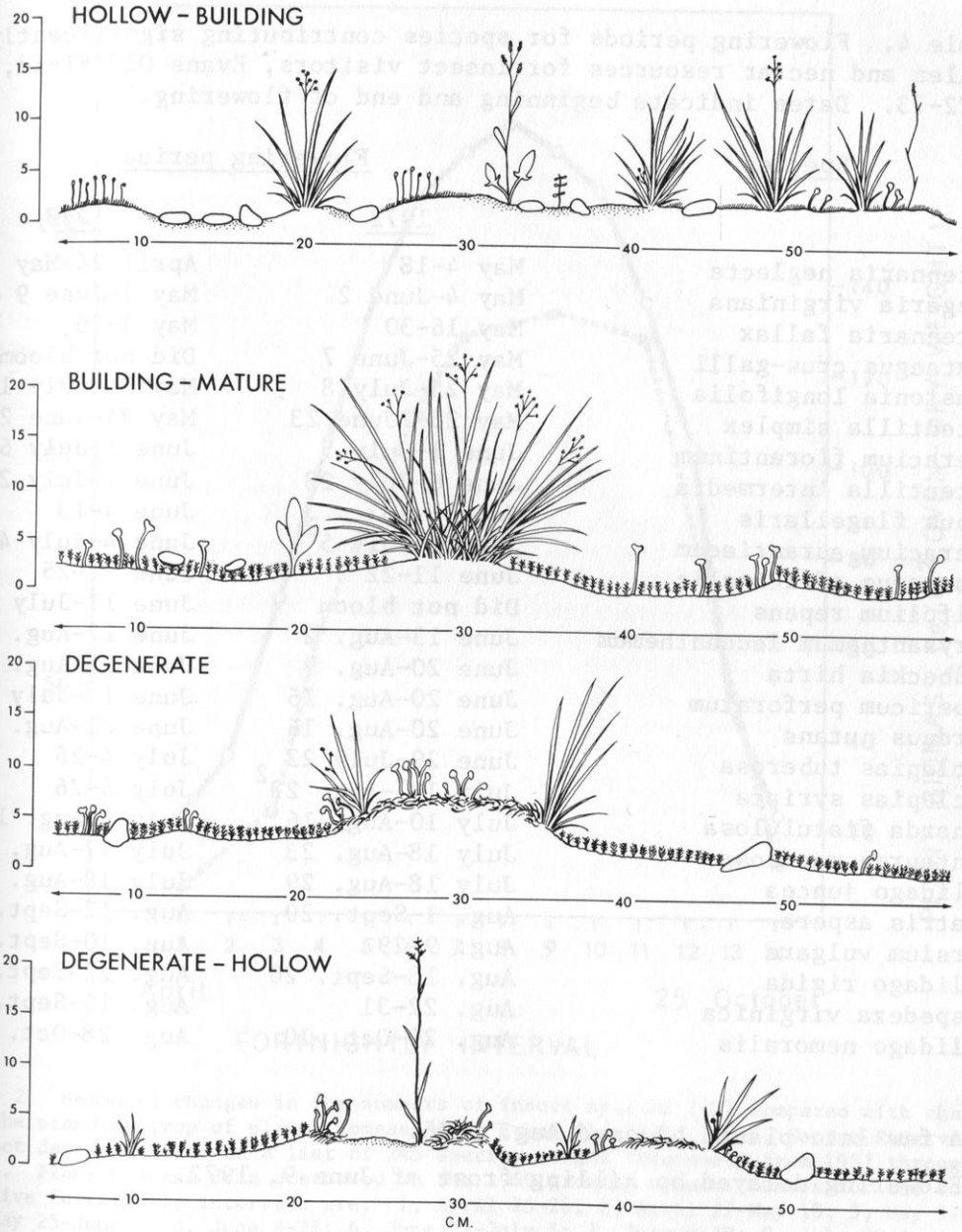


Fig. 1. Developmental phases in the Panicum depauperatum microcycle on Evans Old Field, E. S. George Reserve. Phase terminology is that of Watt (1947). Local erosion pavements provide a suitable germination bed for P. depauperatum seeds (hollow phase). Successful establishment (building phase) leads to development of an elevated mound or tussock with considerable dead material at its base (mature phase). With senescence, the central portion of the clump dies back and is covered by a mat of Cladonia spp., leaving a ring of lateral shoots at the periphery (degenerate phase). Final dissolution of the clump results in new erosion pavements. Completion of this cycle requires 15-20 years. (Re-drawn by Mark Orsen from original by F. C. Evans.)

Table 4. Flowering periods for species contributing significantly to pollen and nectar resources for insect visitors, Evans Old Field, 1972-73. Dates indicate beginning and end of flowering.

Species	Flowering period	
	1972	1973
Antennaria neglecta	May 4-18	April 24-May 26
Fragaria virginiana	May 4-June 2	May 1-June 9
Antennaria fallax	May 16-30	May 1-26
Crataegus crus-galli	May 25-June 7	Did not bloom
Houstonia longifolia	May 25-July 8	May 24-July 19
Potentilla simplex	May 25-?June 23	May 24-June 27
Hieracium florentinum	June 1-July 5	June 1-July 6
Potentilla intermedia	June 6-July 28	June 1-July 21
Rubus flagellaris	June 6-16	June 4-13
Hieracium aurantiacum	June 6-July 5[1]	June 4-July 4
Asparagus officinalis	June 11-22	June 11-25
Trifolium repens	Did not bloom	June 11-July 20
Chrysanthemum leucanthemum	June 13-Aug. 2	June 12-Aug. 9
Rudbeckia hirta	June 20-Aug. 9	June 25-Aug. 17
Hypericum perforatum	June 20-Aug. 16	June 19-July 21
Carduus nutans	June 20-Aug. 16	June 21-Aug. 11
Asclepias tuberosa	June 29-July 22[2]	July 4-26
Asclepias syriaca	July 18[2]-Aug. 23[2]	July 4-26
Monarda fistulosa	July 10-Aug. 16	July 6-Aug. 10
Centaurea maculosa	July 18-Aug. 23	July 17-Aug. 22
Solidago juncea	July 18-Aug. 29	July 18-Aug. 29
Liatris aspera	Aug. 1-Sept. 20	Aug. 12-Sept. 18
Cirsium vulgare	Aug. 9-29	Aug. 10-Sept. 2
Solidago rigida	Aug. 18-Sept. 20	Aug. 22-Sept. 25
Lespedeza virginica	Aug. 22-31	Aug. 15-Sept. 2
Solidago nemoralis	Aug. 29-Oct. 10	Aug. 28-Oct. 12

[1] A few late plants bloomed Aug. 9-16.

[2] Flowering delayed by killing frost of June 9, 1972.

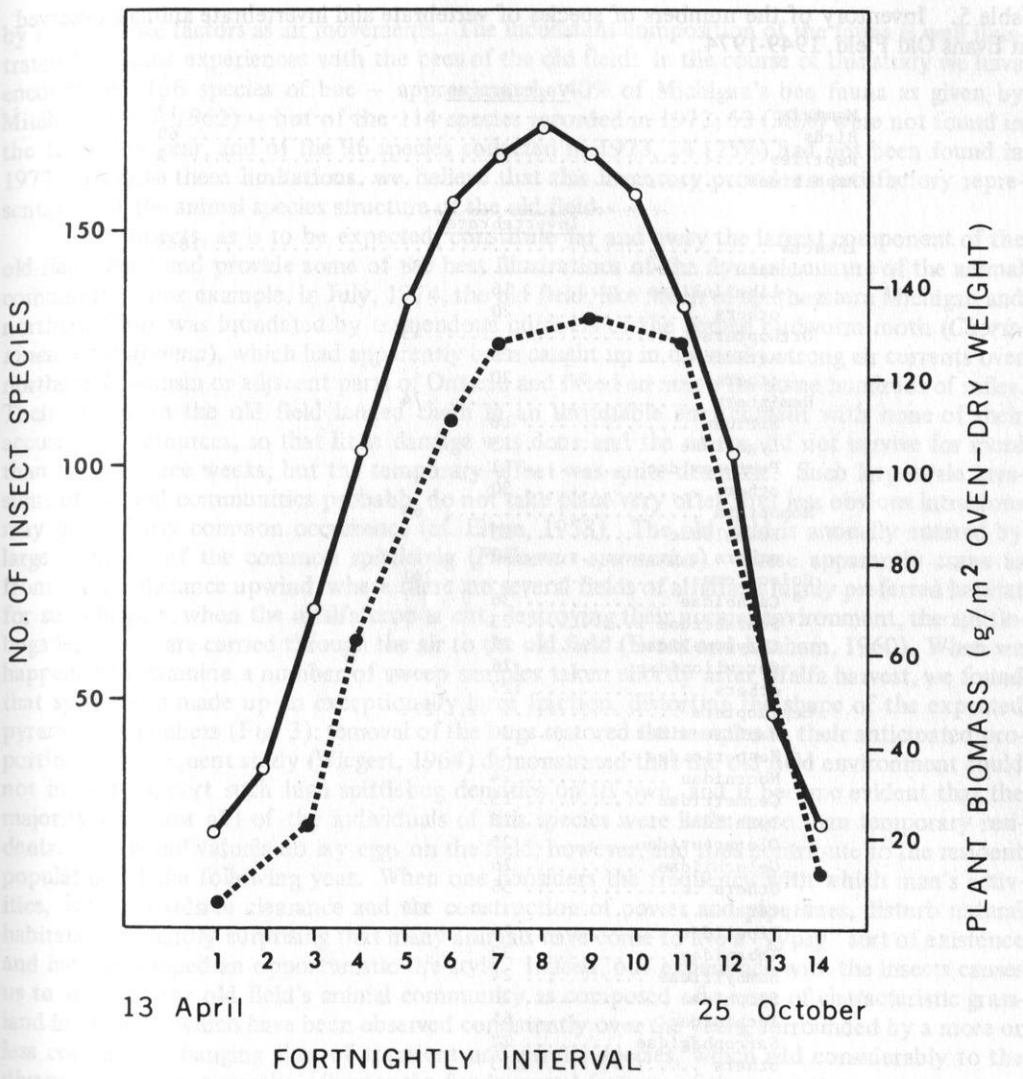


Fig. 2. Seasonal changes in the numbers of insect species (O) compared with changes in the standing crop of plant biomass (●), Evans Old Field, E. S. George Reserve. Insect data are based on a list of 245 species caught frequently from 1957 through 1966. Plant biomass data are based on the 1960 growing season. Dates for the successive fortnightly intervals are: 1, April 13-26; 2, April 27-May 10; 3, May 11-24; 4, May 25-June 7; 5, June 8-21; 6, June 22-July 5; 7, July 6-19; 8, July 20-August 2; 9, August 3-16; 10, August 17-30; 11, August 31-September 13; 12, September 14-27; 13, September 28-October 11; 14, October 12-25. (Re-drawn, with permission, from Evans and Murdoch, 1968, by Mark Orsen.)

Table 5. Inventory of the numbers of species of vertebrate and invertebrate animals observed on Evans Old Field, 1949-1974.

Vertebrates	
Mammals	17
Birds	60
Reptiles	3
Amphibians	6
Invertebrates	
Insects	1845
Odonata	36
Libellulidae	16
others	20
Orthoptera	43
Acrididae	23
others	20
Hemiptera	74
Miridae	18
Lygaeidae	15
Pentatomidae	11
others	30
Homoptera	63
Euscelidae	23
others	40
Coleoptera	241
Carabidae	36
Scarabeidae	23
Chrysomelidae	29
Curculionidae	26
others	127
Lepidoptera	271
Papilionoidea	30
Hesperioidea	17
Noctuidae	74
Geometridae	15
Pyralidae	28
Olethreutidae	25
Gelechiidae	26
others	56
Diptera	396
Tipulidae	24
Tabanidae	22
Bombyliidae	24
Syrphidae	26
Tachinidae	65
Sarcophagidae	22
others	213
Hymenoptera	702
Ichneumonidae	178
Braconidae	67
Chalcidoidea (est.)	100
Formicidae	31
Pompilidae	26
Sphecidae	49
Andrenidae	30
Halictidae	34
Megachilidae	29
others	158
Other Orders	19
Spiders	57
Harvestmen	2
Diplopods	1
Isopods	1
Pulmonate land snails	5

by such chance factors as air movements. The inconstant composition of the fauna is well illustrated by recent experiences with the bees of the old field: in the course of this study we have encountered 156 species of bee – approximately 40% of Michigan's bee fauna as given by Mitchell (1960, 1962) – but of the 114 species recorded in 1972, 53 (38%) were not found in the following year, and of the 96 species collected in 1973, 24 (25%) had not been found in 1972. Despite these limitations, we believe that this inventory provides a satisfactory representation of the animal species structure of the old field.

The insects, as is to be expected, constitute far and away the largest component of the old-field fauna and provide some of the best illustrations of the dynamic nature of the animal community. For example, in July, 1974, the old field, like much of southeastern Michigan and northern Ohio, was inundated by tremendous numbers of the spruce budworm moth (*Choristoneura fumiferana*), which had apparently been caught up in unusually strong air currents over northern Wisconsin or adjacent parts of Ontario and lifted en masse for some hundreds of miles. Their arrival on the old field landed them in an unsuitable environment with none of their accustomed resources, so that little damage was done and the moths did not survive for more than two or three weeks, but the temporary effect was quite dramatic. Such large-scale invasions of natural communities probably do not take place very often, but less obvious intrusions may be of fairly common occurrence (cf. Elton, 1958). The old field is annually entered by large numbers of the common spittlebug (*Philaenus spumarius*). These apparently come in from a short distance upwind, where there are several fields of alfalfa, a highly preferred habitat for such insects; when the alfalfa crop is cut, destroying their normal environment, the spittlebugs leave and are carried through the air to the old field (Evans and Lanham, 1960). When we happened to examine a number of sweep samples taken shortly after alfalfa harvest, we found that spittlebugs made up an exceptionally large fraction, distorting the shape of the expected pyramid of numbers (Fig. 3); removal of the bugs restored the samples to their anticipated proportions. Subsequent study (Wiegert, 1964) demonstrated that the old field environment could not in fact support such high spittlebug densities on its own, and it became evident that the majority (but not all) of the individuals of this species were little more than temporary residents. A few individuals do lay eggs on the field, however, and thus contribute to the resident population of the following year. When one considers the frequency with which man's activities, such as roadside clearance and the construction of power and pipe lines, disturb natural habitats, it is hardly surprising that many animals have come to live a "gypsy" sort of existence and have developed an opportunistic life-style. Indeed, our experience with the insects causes us to visualize the old field's animal community as composed of a core of characteristic grassland inhabitants which have been observed consistently over the years, surrounded by a more or less constantly changing flux of transient and erratic species, which add considerably to the diversity but do not greatly influence the fundamental features of the ecosystem.

Although far less numerous and diverse than insects, the vertebrate animals of the old field are on the whole more readily seen and conspicuous. Characteristic mammals include the thirteen-lined ground squirrel (*Citellus tridecemlineatus*) and the prairie deermouse (*Peromyscus maniculatus*), both open ground species, and the bog lemming (*Synaptomys cooperi*) and meadow vole (*Microtus pennsylvanicus*), which were usually restricted to the swales. Densities were never observed to be very high, although the ground squirrel population in 1950 was estimated as 30-50 individuals, representing at least three families and their parents (Evans, 1951). The woodmouse (*Peromyscus leucopus noveboracensis*) and the chipmunk (*Tamias striatus*) were abundant "edge species" and sometimes even came out into the center of the field. The most important birds were the four species which for many years were the only ones nesting on the field: the Vesper, Field, Chipping, and Grasshopper (*Ammodramus savannarum*) Sparrows, the first three of which maintained densities of about 7-9 breeding pairs each. More recently, the Goldfinch (*Spinus tristis*), Indigo Bunting (*Passerina cyanea*), Towhee (*Pipilo erythroph-*

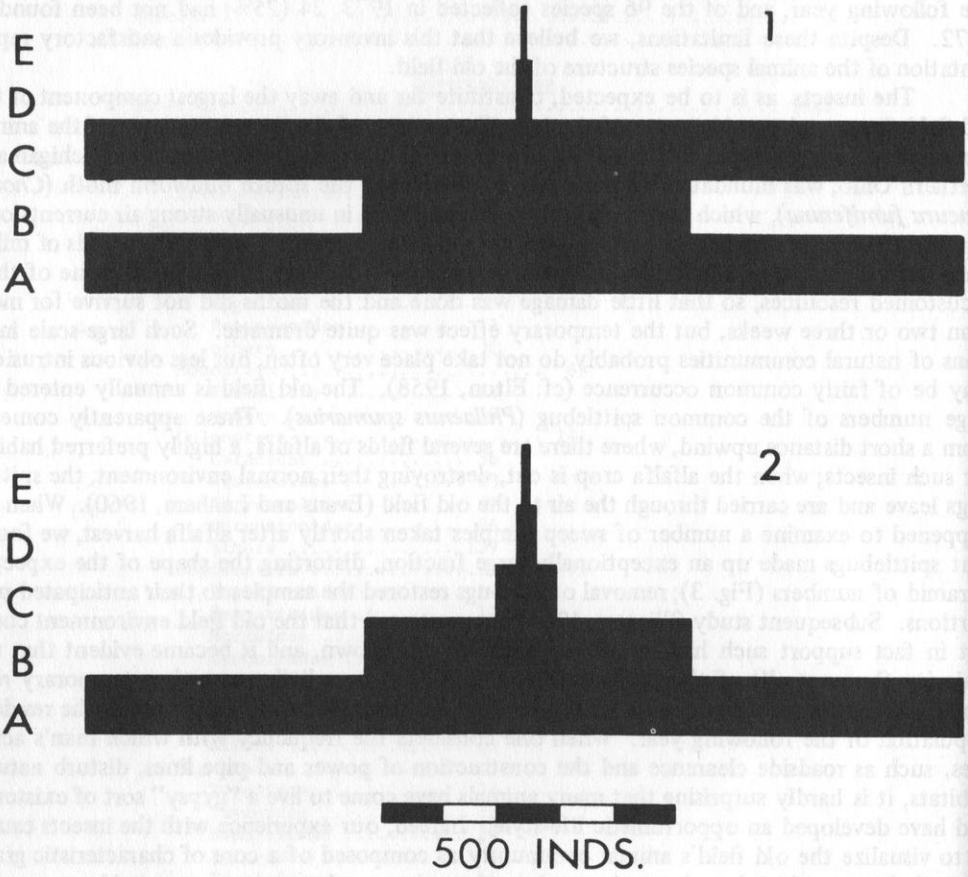


Fig. 3. Ecological pyramids of numbers for the insects of the herbaceous stratum in an old-field upland grassland community, E. S. George Reserve, based on a series of sweep samples collected July 21, 1958. (1) Pyramid for total sample. (2) Pyramid after removal of all specimens of the spittlebug Philaenus spumarius. Size classes of specimens (in mm): A, 0.6-2.5; B, 2.6-4.5; C, 4.6-6.5; D, 6.6-8.5; E, 8.6-10.5. (Re-drawn, with permission, from Evans and Lanham, 1960, by Mark Orsen.)

thalmus) and Blue Jay (*Cyanocitta cristata*) have begun to nest on the field, as the growth of young trees has provided them with suitable sites. Some of these birds and mammals have fallen prey to the Blue Racer (*Coluber constrictor flaviventris*), which at times was frequently seen in the juniper bushes and hawthorns out in mid-field, whereas the garter snake (*Thamnophis sauritus*) appeared to be more of an edge species. In general the field was too dry for amphibians, but an occasional Common Toad (*Bufo americanus*) or Tree-toad (*Hyla versicolor*) was encountered after a period of rain.

Ecosystem Productivity and Energetics

As yet we have no complete analysis of the energy dynamics of this old field ecosystem and can only make some rough estimates of production and energy flow. Two independent series of vegetation samples, one in 1959 and another in 1960, indicated the annual net primary production above ground (i.e. the production of shoots) to be 1328 kcal/m^2 and 1392 kcal/m^2 respectively for the upland portions of the field, and 4102 kcal/m^2 and 4629 kcal/m^2 for the swales (Wiegert and Evans, 1964). Estimates of root production were considerably less satisfactory; our 1960 figures, almost certainly minimal values, were 631 kcal/m^2 for the upland and 1573 kcal/m^2 for the swales.

Only a beginning has been made on the study of energy flow in consumer organisms on the old field. Wiegert (1964) carried out a thorough investigation of the spittlebug population's energetics (Fig. 4), providing an estimate of annual energy flow (intake of metabolizable energy) of 0.6 kcal/m^2 for 1959 and 1.2 kcal/m^2 for 1960; it is evident that a species' energy flow can vary greatly from year to year. Engelmann (1961) studied the role played by soil arthropods in the field's energetics and constructed a balance sheet for the annual energy flow for oribatid mites (Fig. 5), among the field's most important decomposer organisms. Using such data, Wiegert and Evans (1967) made a minimal estimate of the annual energy utilization by primary consumers (i.e. herbivores) on the field (Table 6). Unfortunately this estimate does not include the contribution by ants, a very significant component in primary consumption; indeed, their total ingestion of plant material may have been 1.4–4.0 times as much as that of all other herbivores combined. The figures given above, however, permit an estimate that only 1% of the field's annual net primary production is utilized by herbivores, admittedly an unrealistically low value, but even if the consumption by ants and other neglected components had been included, it is unlikely that total herbivore utilization would have been as much as 5%. Indeed, the total annual energy flow (equivalent to "Assimilation" in Table 6) on the field was estimated at not more than 22 times the average standing crop of energy, a very low ratio compared with those observed on old fields elsewhere, e.g. in South Carolina (Odum, Connell and Davenport, 1962). Perhaps these low productivity and energy values attest to the extent to which Evans Old Field was depleted of its accumulated nutrient resources prior to abandonment.

Successional Changes, 1949-1974

With the passage of time, the vegetational appearance of the old field has slowly but surely changed from its purely grassland physiognomy in the direction of a woodland or forest aspect. As already indicated, this physiognomic change is characterized not so much by replacements in floristic composition as it is by changing dominance and by maturation of relatively long-lived arboreal species present from the start as seeds and seedlings but inhibited from rapid development by a combination of physical and biotic forces. Some species replacements have been observed in the animal community, attributable to additions or losses of food-plant species (for example, the Regal Fritillary [*Speyeria idalia*], once fairly common, has disappeared with the dwindling population of violets [*Viola sagittata*], whereas Milbert's Tortoise Shell [*Nymphalis milberti*] did not make its appearance on the field until the establishment of

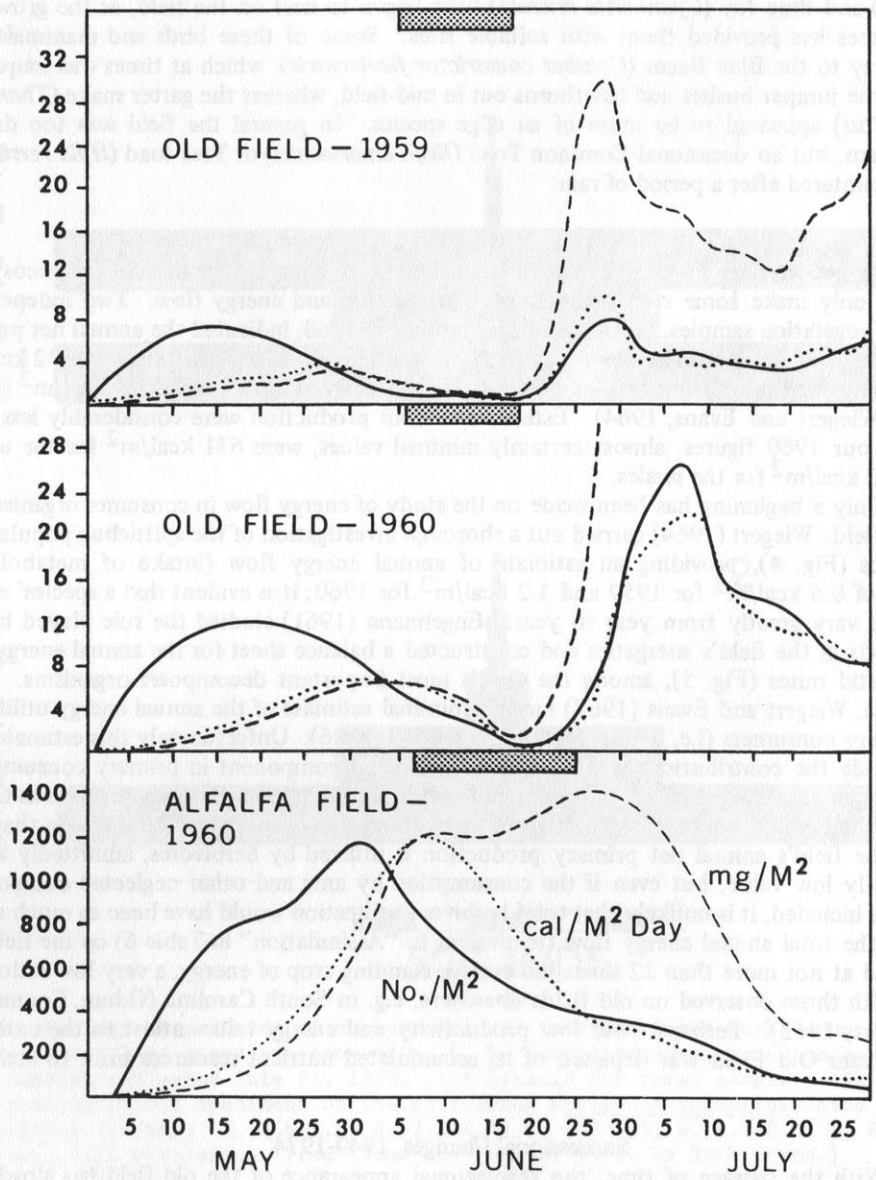
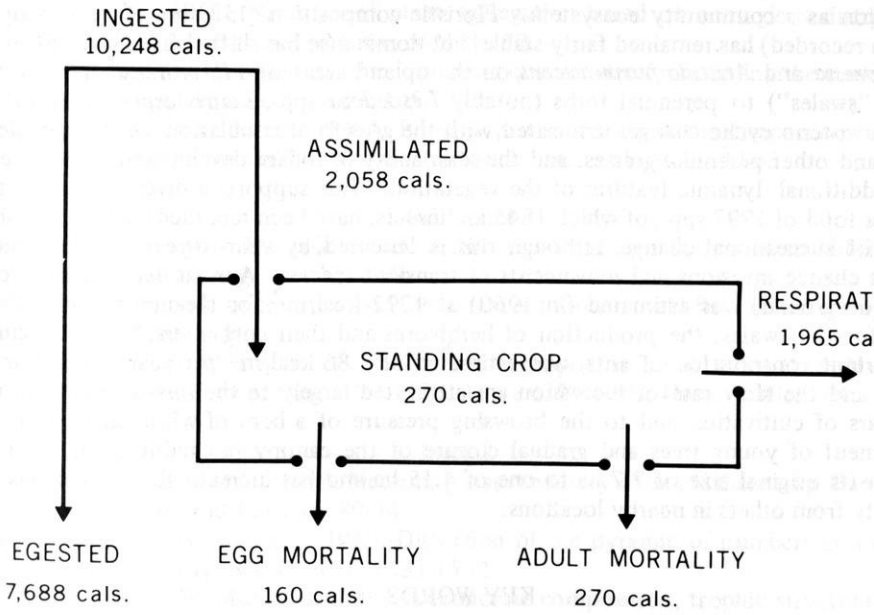


Fig. 4. Fluctuations in energy flow, numbers and biomass of populations of the spittlebug Philaenus spumarius on Evans Old Field, E. S. George Reserve, in 1959 and 1960 and on a nearby alfalfa field in 1960. The stippled bars indicate periods when both nymphs and adults were present. Diel energy flow in cal/m^2 is shown by the dotted line, number of individuals per m^2 by the solid line, and biomass in mg/m^2 by the dashed line. (Re-drawn, with permission, from Wiegert, 1964, by Mark Orsen.)

Table 6. Summary of annual energy utilization by primary consumers on a 30 year old field in Southern Michigan (U.S.A.). Data from Wiegert (1964, 1965), Evans (1951, 1964) and Evans unpublished. Values are expressed as kcal/m^2. Standing crop values are averages for period when organisms active in the ecosystem. (From Wiegert & Evans, 1967).

Category	Standing crop	Respiration	Secondary production	Assimilation	Ingestion
Spittlebugs	0.14	0.80	0.08	0.88	1.51
Grasshoppers	0.16	0.86	0.51	1.37	3.71
Other herbivorous insects*	0.03	0.16	0.10	0.26	0.71
Deer mice	0.003	0.62	0.01	0.63	1.05
Sparrows	0.05	2.29	0.05	2.34	2.55
Ground squirrels	0.05	3.69	0.11	3.80	5.60
Totals	0.43	8.42	0.86	9.28	15.13

* Ants not included. Energy values assumed in same proportion to mean standing crop as grasshopper values.



7,688 + 2,058 = 9,744 (504 cals. UNACCOUNTED FOR)

1,965 + 270 + 160 = 2,395 (337 cals. OVERESTIMATED)

Fig. 5. Annual energy balance sheet for the oribatid mites found on a square meter of Evans Old Field, E. S. George Reserve, in 1958. The arrows indicate the direction of energy flow. The rectangle represents the protoplasm of the oribatid population. (Re-drawn, with permission, from Engelmann, 1961, by Mark Orsen.)

a colony of Nettle [*Urtica dioica*]) but by and large the "core" species have remained fairly constant over the years. Perhaps the most noticeable feature of change has been the gradual closing in of the open field area by the steady encroachment of the adjoining oak-hickory woods; as of August 1974, the estimated extent of open field had been reduced to about 4.15 ha (10.25 acres), a decrease of 46% from the original cleared area. This reduction of the space occupied by the old field community has been accompanied by a steady widening of the woods-field ecotonal margin, which, together with the development of young trees at the bases of the large hickories on the field, has had the effect of blurring the community boundaries, so that there is now a distinct gradient, rather than an abrupt change, from woods to field. Slowly but surely the field community is being squeezed into a smaller and smaller space. Indeed, the closing of the canopy that will develop as the young trees mature can be expected to occur at an accelerating pace. Also, as the ecotones expand, the degree of isolation of the old field from other nearby open areas will increase, lowering the likelihood of receiving further "field-tolerant" species. It will be of interest to see if the next twenty-five years will witness the complete replacement of the field community by the forest.

ABSTRACT

From 1949 to 1974, an old field (originally cleared of oak-hickory woodland prior to 1850 and finally abandoned in the mid-1920s) in southeastern Michigan has been under investigation as a community ecosystem. Floristic composition (153 spp. of Spermatophyta have been recorded) has remained fairly stable, but dominance has shifted from grasses (notably *Poa compressa* and *Aristida purpurascens* on the upland areas, and *P. pratensis* in the depressions or "swales") to perennial forbs (notably *Lespedeza* spp., *Liatris aspera,* and *Solidago* spp.). Short-term cyclic changes associated with the growth of populations of *Panicum depauperatum* and other perennial grasses, and the seasonality of foliage development and flowering, provide additional dynamic features of the vegetation. This supports a diverse community of animals (a total of 1997 spp., of which 1845 are insects, have been recorded), which also shows evidence of successional change, although this is obscured by year-to-year variation and by numerous chance invasions and movements of transient species. Annual net primary productivity (aboveground) was estimated (in 1960) at 1392 kcal/m^2 for the uplands and at 4629 kcal/m^2 for the swales; the production of herbivores and their consumers, but not including the important contribution of ants, was estimated at 0.86 kcal/m^2 per year. Such low productivity and the slow rate of succession are attributed largely to the loss of humus through many years of cultivation and to the browsing pressure of a herd of white-tailed deer. The encroachment of young trees and gradual closure of the canopy has reduced the open field area from its original size of 7.7 ha to one of 4.15 ha and has increasingly isolated this field community from others in nearby locations.

KEY WORDS

Succession, floristic composition, stratification, microcycle, phenology, invasions, pyramid of numbers, edge species, net primary production, energy flow.

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GRASSLANDS OF NORTH DAKOTA

W. C. Whitman and M. K. Wali

North Dakota has about 5.67 million ha (14 million acres) of grassland, one-third of the total land area of the state. The North Dakota Conservation Needs Inventory (1970) indicates that there are 5,067,785 ha of grassland in more or less permanent grazing use as pasture and range. In addition, there are 636,789 ha of federal land, most of which is also grassland. The bulk of the existing native grassland is in the western two-thirds of the state although significant areas of native grassland occur elsewhere, especially in areas where unfavorable soil conditions have prevented plowing of the original cover.

The grasslands of the western two-thirds of the state are largely of the mixed grass prairie type, dominated by midgrasses, shortgrasses, and upland sedges (Weaver and Clements, 1938). In the east, a tall grass type in which big bluestem (*Andropogon gerardi*) was one of the original dominants, still exists in remnant stands. A rather broad transition grassland type, in which the taller grasses gradually decrease in abundance and stature toward the west while the mid- and shortgrasses increase, originally joined the two major types (Küchler, 1964). Both the mixed and tall grass types are intermingled throughout the entire state, with the mixed grass extending almost to the eastern border on dry sites, while the tall grass type dominated by big bluestem is found in fragmentary stands under situations of favorable topography, soil depth, and moisture conditions to the extreme western edge of the state.

Several other grassland types have been recognized in the state. A small area of the bluebunch wheatgrass (*Agropyron spicatum*) type occurs in association with ponderosa pine (*Pinus ponderosa*) in the southwestern part of the state (Potter and Green, 1964; Dodd, 1970). The occurrence of the rough fescue type (*Festuca scabrella*) in scattered stands along the northern border of the state has been documented by Cosby (1965). A sagebrush-grass type is found in the extreme southwestern part of the state, however the dominants are primarily the species of the mixed grass prairie (Nelson, 1961). Slough and low prairie grassland types are of considerable importance in the eastern two-thirds of the state and have been described in some detail by Dix and Smeins (1967), Smeins (1967) and Stewart and Kantrud (1972). Deciduous forests with a very small areal distribution occur in stream valleys and on the floodplains of major rivers and have been investigated in detail by Nelson (1964), Wanek (1967), Burgess et al. (1973), Wikum and Wali (1974), and Killingbeck and Wali (1974). A generalized map of original vegetation of the state is presented in Fig. 1.

GENERAL PHYSICAL CONDITIONS

The topography of North Dakota has been likened to a series of steps becoming progressively higher from east to west (Laird, 1962) (Fig. 2). The Red River Valley, the former basin of glacial Lake Agassiz, occupies the eastern edge of the state, ranging in altitude from 228.6 m (750 feet) to 304.8 m above sea level. Immediately west of the Valley is the Drift Prairie, lying at an altitude of 426.7 to 487.7 m and extending in a broad curve from about one-third of the way across the state at the southern border and two-thirds of the way across at the northern border. South and west of this lies the Missouri Plateau rising from about 550 m on

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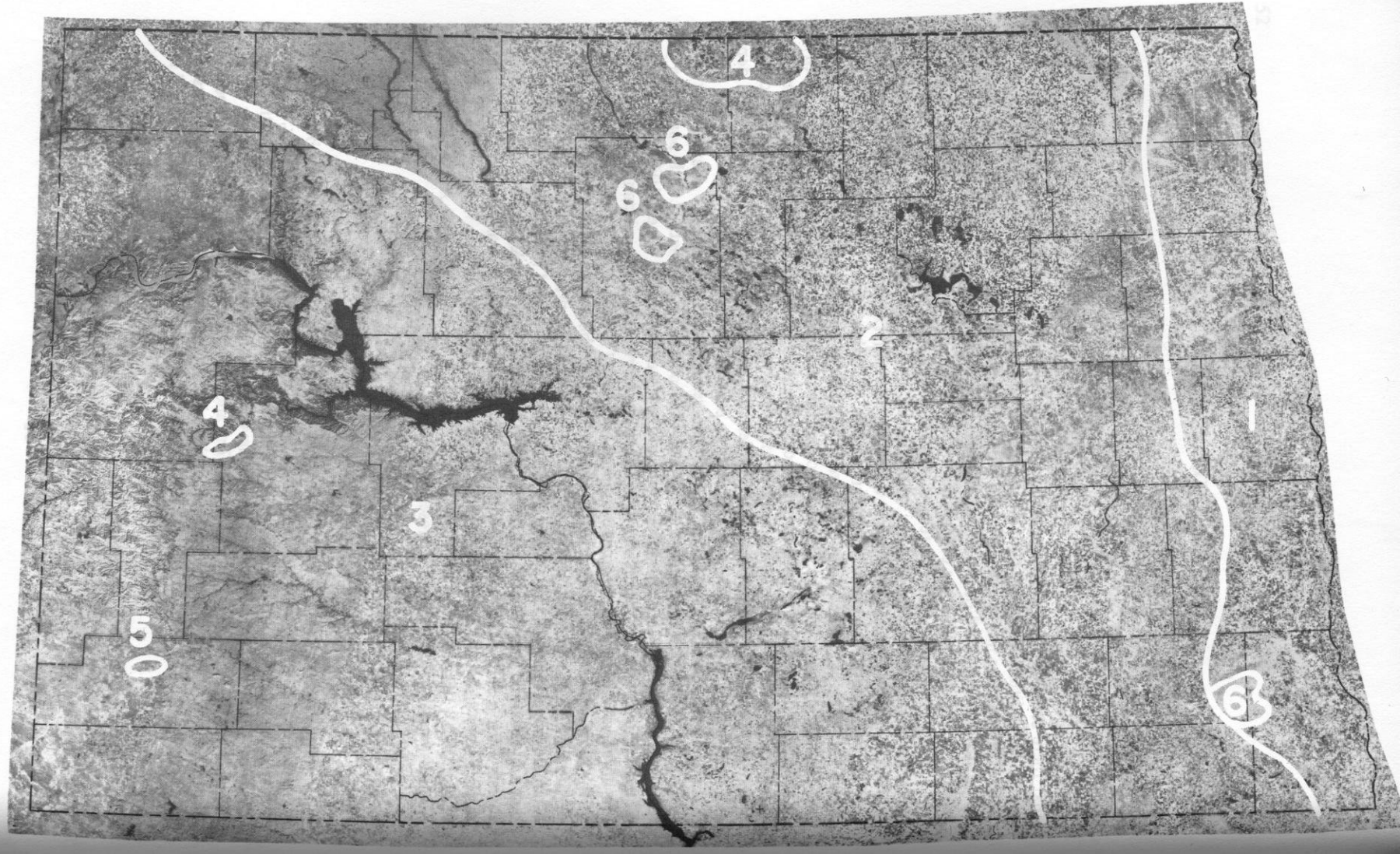
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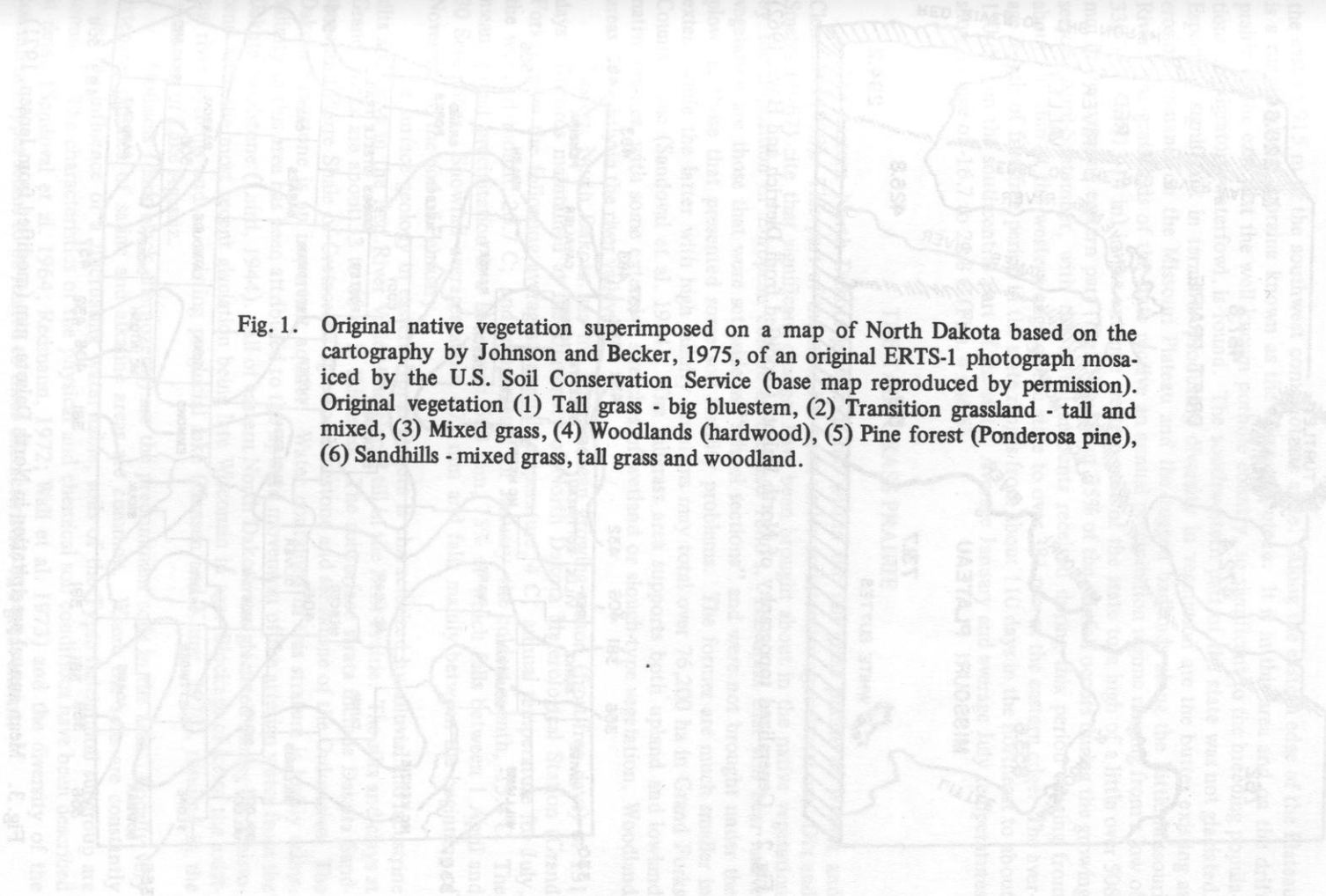

Fig. 1. Original native vegetation superimposed on a map of North Dakota based on the cartography by Johnson and Becker, 1975, of an original ERTS-1 photograph mosaiced by the U.S. Soil Conservation Service (base map reproduced by permission). Original vegetation (1) Tall grass - big bluestem, (2) Transition grassland - tall and mixed, (3) Mixed grass, (4) Woodlands (hardwood), (5) Pine forest (Ponderosa pine), (6) Sandhills - mixed grass, tall grass and woodland.

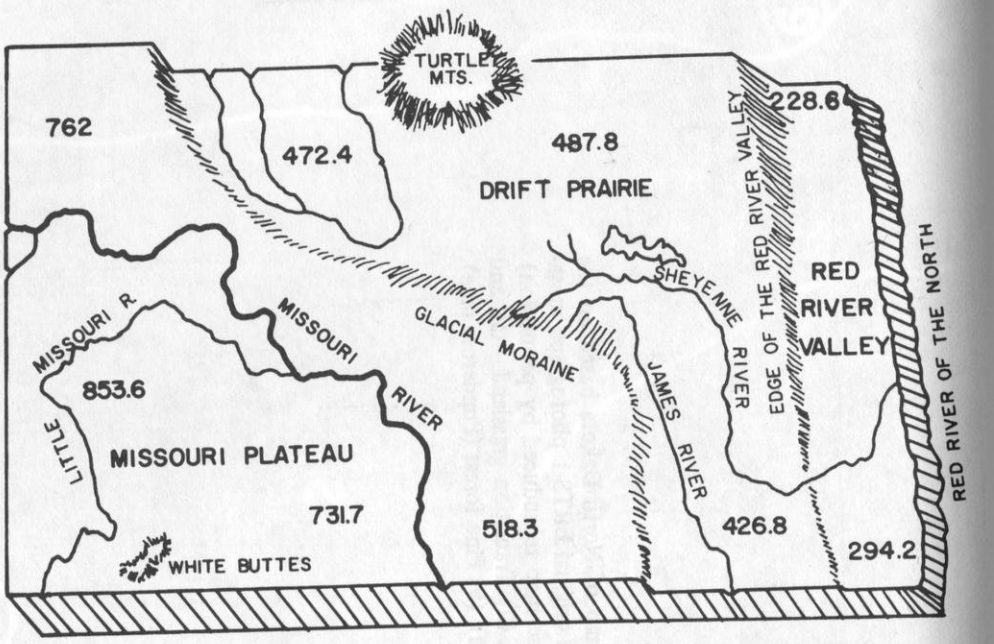

Fig. 2. Generalized topography of North Dakota (modified from Dietrich and Hove, 1962).

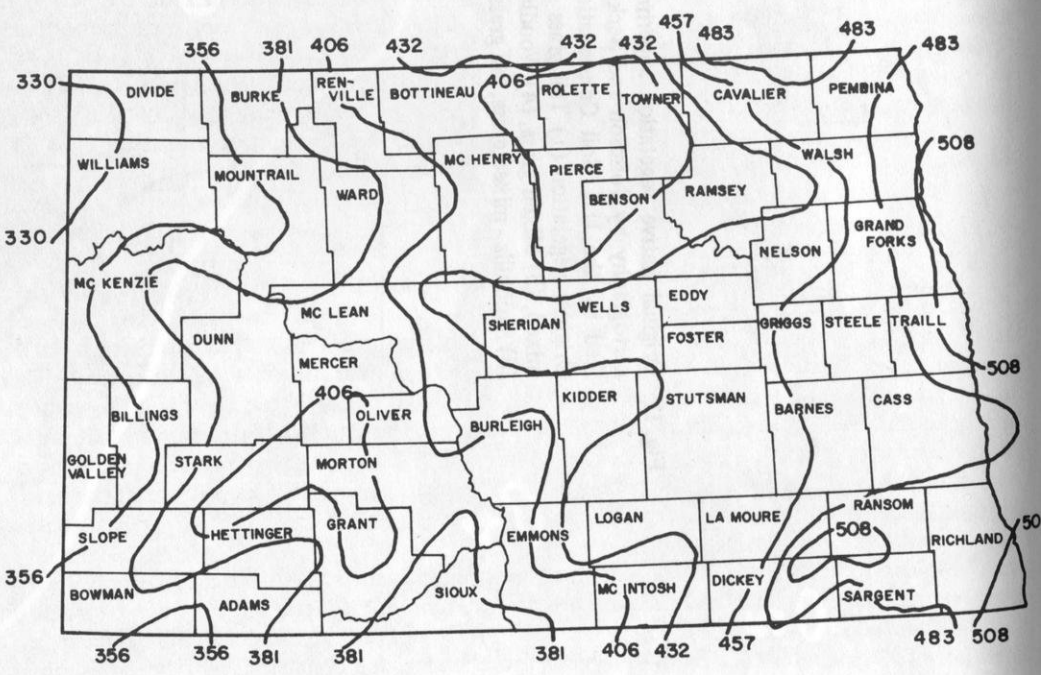

Fig. 3. Mean annual precipitation in North Dakota, mm (modified from Jensen, 1971).

the east to 915 m in the southwest corner of the state. Along the eastern edge of the Plateau is a rugged glacial moraine known as the Missouri Coteau. It is in this area and on the drift prairie to the east that the well known pothole country, so significant to the breeding populations of migratory waterfowl, is found. The southwestern part of the state was not glaciated. Especially significant in terms of producing diversity in vegetation are the buttes existing as erosion remnants on the Missouri Plateau and the rugged badlands along the Little Missouri River. The grasslands of the state receive an annual precipitation regime ranging from a low of 330-356 mm (13-14 in) in the extreme western part of the state to a high of a little over 508 mm in the extreme eastern part (Fig. 3). About 75% of the rainfall occurs during the growing season, April-September, with the actual amounts received during this period ranging from about 254 mm at the western edge of the state to over 381 mm at the eastern edge. The average length of frostfree period in the state ranges from about 110 days in the northeast to about 130 days in the southcentral part of the state. Average January and average July temperatures show a range of -16.7 to 22.8 C (Figs. 4 and 5).

THE TALL GRASS PRAIRIE

The eastern North Dakota grasslands fall within the tall grass prairie of Weaver and Clements (1938). This part of the state has been under an intensive agricultural use. Dix and Smeins (1967) cite that significant changes have been brought about in the native vegetation by the imposition of European culture in the mid 1880's. The areas that still bear native vegetation are those that were set aside as "school sections" and were not brought under the plow, or those that presented some soil fertility problems. The former are much smaller in extent while the latter with high salinity problems may total over 76,200 ha in Grand Forks County alone (Sandoval et al. 1964). The tallgrass area supports both upland and lowland native prairies, with some extensive stretches of wetland or slough-type vegetation. Woodland areas are mainly in the river valleys.

Eastern North Dakota has the longest mean growing season (frost-free days) of 131 days. Records maintained at the University of North Dakota Meterological Station (Grand Forks) show the following averages: annual temperature, 4 C; annual temperature for July, the warmest month, 20.7 C; and temperature for January, the coldest month, -15.4 C. The mean annual precipitation is a little over 500 mm, 75% of which falls between 1 April and 30 September. Snowfall averages about 875 mm and falls mainly between the beginning of November to the end of February.

The surface geology in eastern North Dakota is characterized by alluvial and lacustrine silts and clays in the Red River Valley and glacial till in the Drift Prairie. The silts and clays at Grand Forks are about 33 to 66 m in thickness. The subsurface strata include Dakota Sandstone and Pierre Shale of Cretaceous age, and limestone and sandstone of the Ordovician. The Dakota Sandstone is an important aquifer. Water contained in this stratum is highly saline. Salinity in this area has been attributed to the upward movement of the artesian water from the Dakota Sandstone (Laird, 1944). All of eastern North Dakota was glaciated during the Pleistocene, with the most recent glaciation being late Wisconsin in age. Blockage of ice of the existing river systems and an existing preglacial lake (Hansen and Kume, 1970), resulted in the formation of Lake Agassiz.

Mollisols (dark black chernozems) are the predominant soils in the area. Locally very extensive patches of saline and alkaline areas are common. Where the soils are constantly under the influence of a fluctuating water table, soils of the Typic Calciaquoil subgroup are common. The characteristics of the physical and chemical soil conditions have been described in detail (Sandoval et al. 1964; Redmann, 1972; Wali et al. 1973) and the diversity of the community types seems to be related to these characteristics to a great extent.

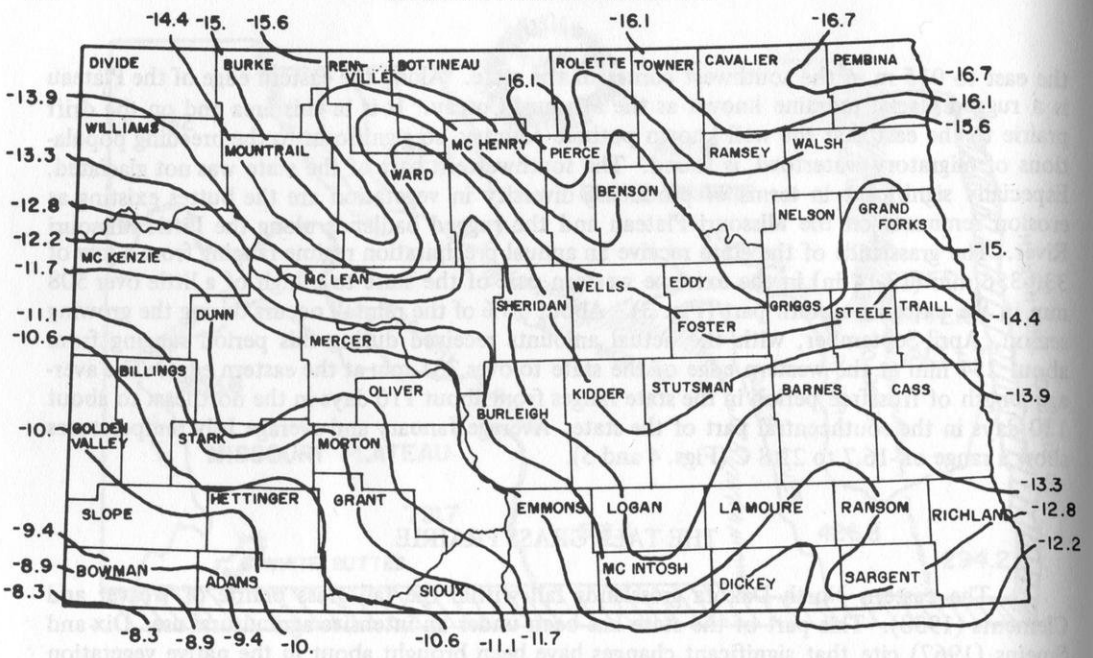

Fig. 4. Mean January temperature (°C) isohyets for North Dakota (modified from Jensen, 1971).

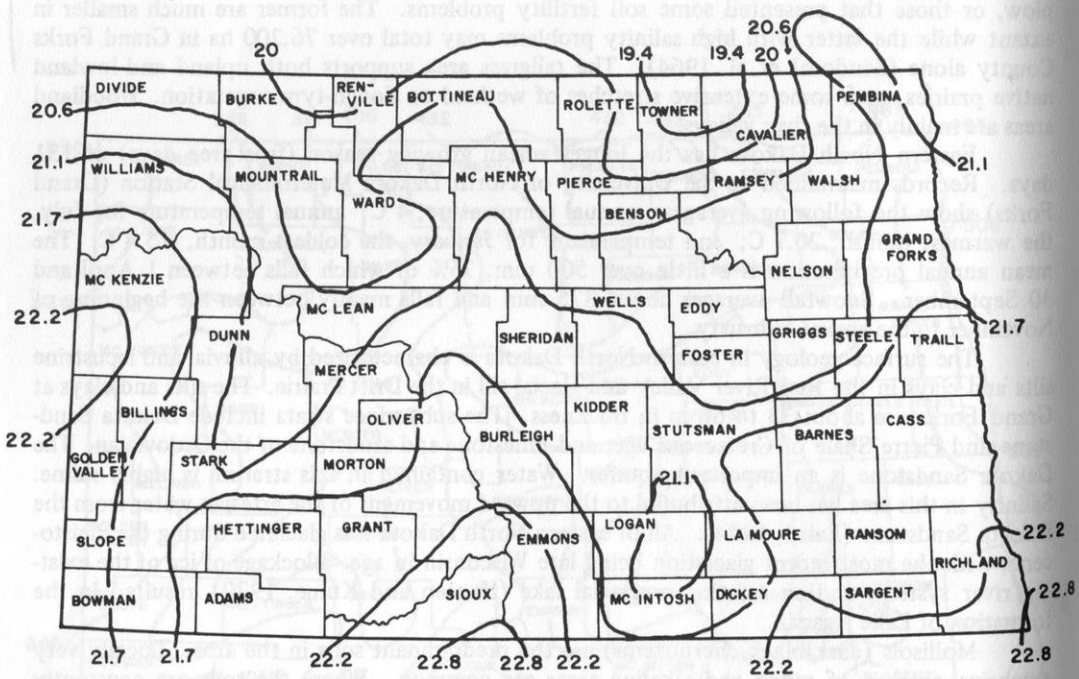

Fig. 5. Mean July temperature (°C) isohyets for North Dakota (modified from Jensen, 1971).

The grasslands of eastern North Dakota are mainly located in the Red River Valley. Following an earlier drainage gradient set up by Dix and Smeins (1967), Ralston (1968) recognizes four divisions. The excessively drained *high prairie* is dominated by needle-and-thread (*Stipa comata*), big sandgrass (*Calamovilfa longifolia*), prairie Junegrass (*Koeleria cristata*) and sideoats grama (*Bouteloua curtipendula*). The *mid prairie*, where water received approximately equals that of the precipitation, is dominated by big bluestem (*Andropogon gerardi*), little bluestem (*Andropogon scoparius*), prairie dropseed (*Sporobolus heterolepis*), western wheatgrass (*Agropyron smithii*), mat muhly (*Muhlenbergia richardsonis*) and green needlegrass (*Stipa viridula*). Since porcupine grass (*Stipa spartea*), little bluestem and green needlegrass reach dominance in both high and mid prairie, Ralston considers them as transitional species in the two divisions. In *low prairie*, moisture is always in excess of incoming precipitation because of poor drainage and is dominated by big bluestem, northern reedgrass (*Calamagrostis inexpansa*) and prairie cordgrass (*Spartina pectinata*) with lesser dominance of little bluestem, mat muhly, Indian grass and prairie dropseed. Northern reedgrass and prairie cordgrass dominated the *high meadow* where inundation by water occurs for a few weeks in spring.

Several distinctive communities along a gradient of surface and subsurface salinity have been recognized by Redmann (1972). The prairie cordgrass community occurs with foxtail (*Hordeum jubatum*), slender wheatgrass (*Agropyron trachycaulum*), scratchgrass (*Muhlenbergia asperifolia*), mat muhly and northern reedgrass on moderately saline surface and strongly saline subsurface soils. The foxtail type occurs with minor representation of plains bluegrass (*Poa arida*), scratchgrass and prairie wedgegrass (*Sphenopholis obtusata*) on strongly saline surface and subsurface soils. On very strongly saline surface and strongly saline subsoils, saltgrass (*Distichlis stricta*) communities were found, while on the most saline zone, glasswort (*Salicornia rubra*) is the only dominant. Species that are found along the edges of glasswort communities include sea blite (*Suaeda depressa*), salt meadowgrass (*Puccinellia nuttalliana*), and, in some cases, *Distichlis* and *Hordeum*.

Table 1: Relationship between species diversity, net production and salinity in three poorly drained, lowland community types in eastern North Dakota (Hadley and Buccos, 1967).

Community type	Number of Species	Salinity Mmhos/cm	Net Production gm/m^2/day
Distichlis-Hordeum-Poa	29	11-12	0.97
Distichlis-Hordeum	16	17-23	0.59
Salicornia-Suaeda	4	27-28	0.30

A decrease of net production along an increasing salinity gradient was found by Hadley and Buccos (1967) (Table 1). For pure stands of many halophytic species, however, the net production rate appears to be higher than reported by these authors (Wali and Moseley, unpublished). Hadley (1970) had reported a peak community production for an upland *Stipa-Andropogon* community in eastern North Dakota of 430 gm/m^2 after burning. This appears very close to the community production reported for a northwestern Minnesota community of similar composition and under relatively similar conditions, by Smeins and Olsen (1970) and Wali et al. (1973). Hadley believes that fire in eastern North Dakota may stimulate production by upland communities while it may depress both production and species diversity in lowland communities. For the wheatgrasses (*Agropyron trachycaulum* and *A. repens*), maximum variance in primary production has been attributed to soil moisture, sodium and nitrogen (Johnson, 1975).

The distribution of low prairie and wetland vegetation of the Red River Valley and Drift Prairie regions of North Dakota has been studied by Smeins (1967). He has recognized six physiognomic vegetation-types along a gradient of duration and depth of inundation (Fig. 6). Within each type, several dominants may occur and their importance in any one type is influenced primarily by a combination of moisture regime, salinity, and kinds and degree of inundation. According to Smeins, these factors account for a large amount of observed variation in the vegetation, but segregation of species groups (shown in Fig. 6) may occur under the influence of other factors. Wali and his coworkers (Wali, 1972; Wali, Blinn and Kollman, unpublished; Kollman and Wali, 1975) have recently studied the influence of environmental factors, particularly major and trace elements, on the primary production of these wetland systems.

SANDHILLS TALLGRASS

The Sandhills tallgrass area in eastern North Dakota has received considerable study in recent years. This tallgrass type is developed in the sandhill area of southeastern North Dakota on the old delta of the Sheyenne River where it emptied into glacial Lake Agassiz (Fig. 2). Even though the area is not large, about 28,340 ha of unplowed grassland vegetation still exist with most of the grassland being either grazed, or in the case of the lower meadows, cut for hay. Other areas of this type of vegetation exist on deep sands elsewhere in the state, but the total area occupied by this type probably does not exceed 61,000 ha.

The floristic composition of the sandhill tallgrass has been discussed in considerable detail by Wanek and Burgess (1965). They found a total of 156 species of vascular plants on the sand prairies of this region. Sandhill bluestem (*Andropogon hallii*), sand dropseed (*Sporobolus cryptandrus*) and prairie sandreed (*Calamovilfa longifolia*) were the characteristic arenicolous species. Big bluestem, switchgrass (*Panicum virgatum*), little bluestem, Canada wildrye (*Elymus canadensis*), prairie Junegrass, Kentucky bluegrass (*Poa pratensis*) and needle-and-thread were especially important in most stands. Penn sedge (*Carex pennsylvanica*) was found in all stands examined. Characteristic tall grass species which were present in lesser amounts included Indiangrass, porcupine grass, sideoats grama, prairie dropseed, and several rosette panic grasses, including especially *Panicum leibergii* and *P. scribnerianum*.

A large number of forbs and shrubs are found in the type with perennial ragweed (*Ambrosia psilostachya*), white sage (*Artemisia ludoviciana*), several goldenrods (*Solidago* spp.) narrow-leaved puccoon (*Lithospermum incisum*), stiff sunflower (*Helianthus rigidus*), blazing star (*Liatris punctata*), white prairie aster (*Aster ericoides*), golden aster (*Chrysopsis villosa*), prairie rose (*Rosa arkansana*) and leadplant (*Amorpha canescens*) being especially prominent. Burgess (1965) regards sandhill bluestem as a pioneer dominant, little bluestem an "intermediate accessory" and big bluestem as an important constituent of the climax com-

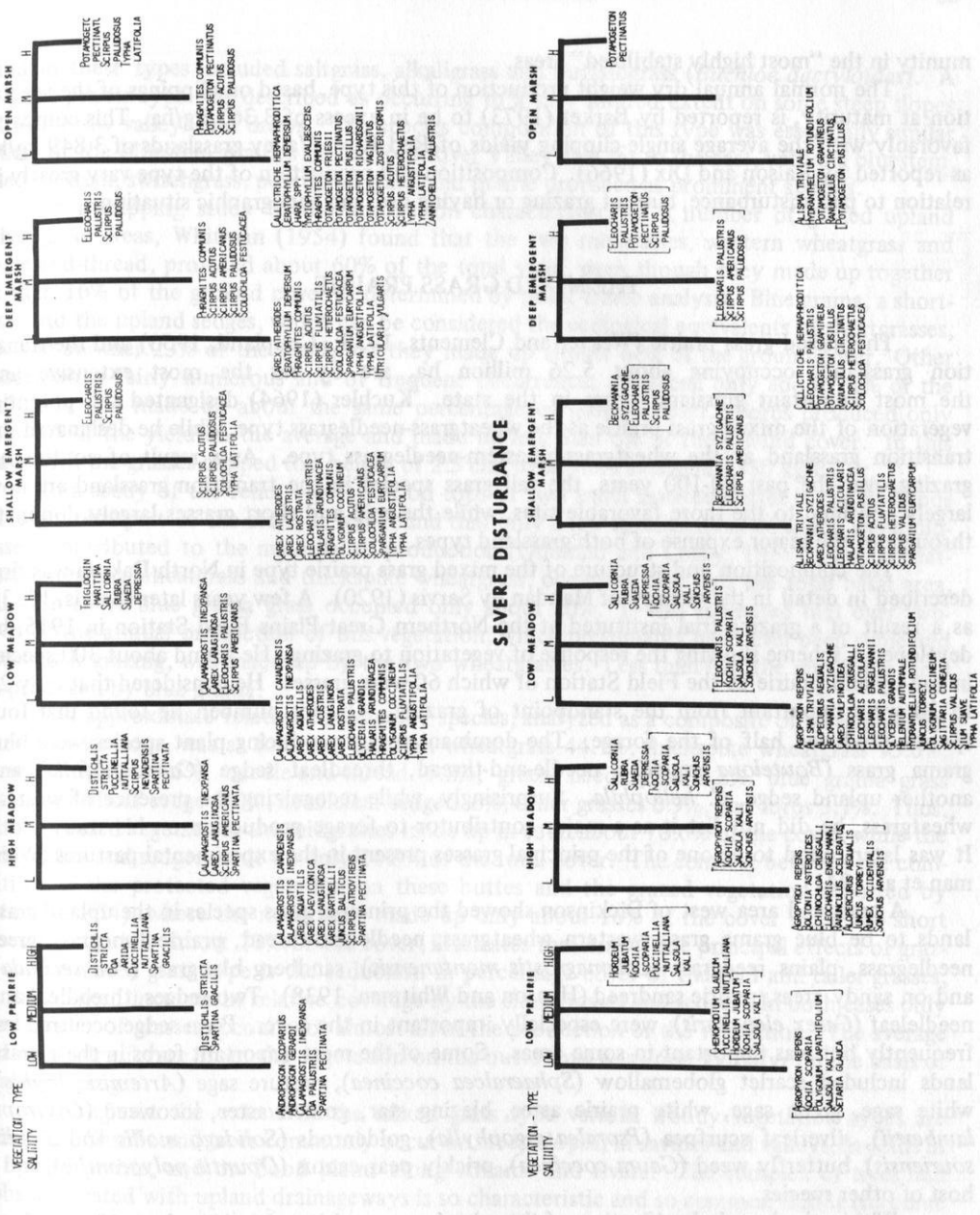

Fig. 6. Distribution of wetland vegetation in relation to disturbance and moisture gradients in the Red River Valley and Drift Prairie regions of North Dakota (modified after, and by, Smeins, 1967).

munity in the "most highly stabilized" areas.

The normal annual dry weight production of this type, based on clippings of the vegetation at maturity, is reported by Barker (1973) to be in excess of 3,363 kg/ha. This compares favorably with the average single-clipping yields of Red River Valley grasslands of 3,849 kg/ha as reported by Ralson and Dix (1966). Composition and production of the type vary greatly in relation to past disturbance, current grazing or haying use, and topographic situation.

THE MIXED GRASS PRAIRIE

The mixed grass prairie (Weaver and Clements, 1938; Coupland, 1950) and the transition grassland, occupying about 5.26 million ha, are by far the most extensive and the most important grassland types in the state. Kuchler (1964) designated the potential vegetation of the mixed grass prairie as the wheatgrass-needlegrass type, while he designated the transition grassland as the wheatgrass-bluestem-needlegrass type. As a result of continuous grazing over the past 80-100 years, the tall grass species in the transition grassland are now largely confined to the more favorable sites, while the mid and short grasses largely dominate throughout the major expanse of both grassland types.

The composition and structure of the mixed grass prairie type in North Dakota was first described in detail in the vicinity of Mandan by Sarvis (1920). A few years later (Sarvis, 1923), as a result of a grazing trial instituted at the Northern Great Plains Field Station in 1915, he developed a scheme showing the response of vegetation to grazing. He found about 300 species in the upland prairie at the Field Station of which 60 were grasses. He considered that only 25 to 30 were important from the standpoint of grazing. Of this number, he found that four species produced half of the forage. The dominant forage-producing plant species were blue grama grass (*Bouteloua gracilis*), needle-and-thread, threadleaf sedge (*Carex filifolia*) and another upland sedge, *C. heliophila*. Surprisingly, while recognizing the presence of western wheatgrass, he did not list it as a major contributor to forage production on his study plots. It was later found to be one of the principal grasses present in the experimental pastures (Whitman et al. 1941).

A grassland area west of Dickinson showed the principal grass species in the upland grasslands to be blue grama grass, western wheatgrass, needle-and-thread, prairie Junegrass, green needlegrass, plains reedgrass (*Calamagrostis montanensis*), sandberg bluegrass (*Poa secunda*), and on sandy areas, prairie sandreed (Hanson and Whitman, 1938). Two sedges, threadleaf and needleleaf (*Carex eleocharis*), were especially important in the cover. Penn sedge occurred less frequently but was important in some areas. Some of the most important forbs in these grasslands included scarlet globemallow (*Sphaeralcea coccinea*), pasture sage (*Artemisia frigida*), white sage, green sage, white prairie aster, blazing star, golden aster, locoweed (*Osytropis lambertii*), silverleaf scurfpea (*Psoralea argophylla*), goldenrods (*Solidago mollis* and *S. missouriensis*), butterfly weed (*Gaura coccinea*), prickly pear cactus (*Opuntia polyacantha*), and a host of other species.

Within the broad classification of the mixed grass prairie, a number of specific grassland types occur. Hanson and Whitman (1938) distinguished 10 types in their study area in southwestern North Dakota. These included: (i) little bluestem type on slopes and low hills which is actually a common and widely distributed type in both the glaciated and unglaciated sections of the state; (ii) a type dominated by prairie sandreed, which was designated the sandgrass type; (iii) a sagebrush type in which the principal aspect dominant was valley sagebrush (*Artemisia cana*) while grass species in the type were primarily from the mixed grass prairie. Thickspike wheatgrass (*Agropyron dasystachyum*) and slender wheatgrass were fairly common in this type. In addition, several types occurring on salty and alkaline soils were recognized. Species

found in these types included saltgrass, alkaligrass and buffalograss (*Buchloe dactyloides*). A tall grass prairie type was described as occurring to a very limited extent on some steep slopes and in narrow valleys and draws. The species composition of this type was essentially similar to that of the bluestem prairies of the Red River Valley area far to the east, with big bluestem, little bluestem, switchgrass, porcupine grass, and prairie dropseed as prominent species.

In a clipping study of the production characteristics of a number of grazed upland native grass areas, Whitman (1954) found that the two midgrasses, western wheatgrass and needle-and-thread, provided about 60% of the total yield, even though they made up together less than 16% of the ground cover as determined by point-frame analysis. Blue grama, a short-grass, and the upland sedges, which can be considered the ecological equivalents of shortgrasses, provided another 23% of the yield, but they made up almost 68% of the ground cover. Other grasses, while fairly numerous and of frequent occurrence, produced only about 11% of the total yield and made up about the same percentage of ground cover. Forbs produced only about 7% of the yield on the average and made up less than 6% of the ground cover. In this study, with the grasses clipped to a height of 2.5 cm, total yield averaged 1350 kg/ha/yr.

In a study of the relict vegetation on tops of two small isolated buttes in the Badlands of the western part of the state, it was found that only a few species, most of which were mid-grasses, contributed to the majority of production (Quinnild and Cosby, 1956). Two wheat-grasses, western wheatgrass and thickspike wheatgrass, occupied over half the total basal area, while the short blue grama grass occupied only about 20%. It was estimated that over two-thirds of the annual production of this vegetation, which presumably had never been subjected to livestock grazing, was made up by the two wheatgrasses. Less than half the remaining yield was produced by blue grama.

The approximate relative coverage by species, analyzed as a composite of all samples on the two butte tops, was as follows: western wheatgrass 44.1%, thickspike wheatgrass 13.6%, prairie Junegrass 5.5%, needle-and-thread 5.2%, green needlegrass 2.2%, blue grama grass 20.9%, threadleaf sedge 2.3%, needleleaf sedge 1.6%, other grasses 0.9%, and forbs 3.7%. Thus, in this ungrazed vegetation, the midgrasses made up in total about 70.6% of the cover, while the short grasses and sedges made up only 24.8% of the total cover. The contrast between the composition of the protected vegetation on these buttes and the grazed vegetation reported by Whitman (1954), where the midgrasses made up only about 16% of the cover while the short grasses constituted almost 70% of the cover, illustrates that one of the principal effects of grazing on the mixed grass type is the reduction in percentage cover of the mid and taller grasses, and the marked increase in relative coverage by the shortgrasses and sedges. In both cases only a few species of grasses account for almost all of the production of the vegetation. The average yield of air-dry forage from the vegetation on the butte tops was 2665 kg/ha/yr on the basis of a single clipping.

Throughout the extent of the mixed grass type various woody vegetation types are developed. Shrubs and trees commonly occur on steep slopes, in ravines and valleys, in folds in the upland prairie, and on flood plains along streams and rivers. The complex of trees and shrubs associated with upland drainageways is so characteristic and so common that it has come to be referred to as the "hardwood draw ecosystem" (Crowston et al. 1974).

Woodlands in North Dakota are considered to occupy less than a total of 202,450 ha, with much of this area concentrated along streams and on some of the higher eminences (Warner and Chase, 1956). No accurate estimate is available for the combined extent of natural woodlands and shrubby vegetation types in the mixed grass prairie region, but probably the total area does not exceed 283,400 ha. This woody vegetation is important, however, far beyond its actual extent because it provides travel routes, cover, and winter food for much of the big game population of the prairie region. Without this woody vegetation so widely interspersed through the grassland the area could not support any sizable big game population.

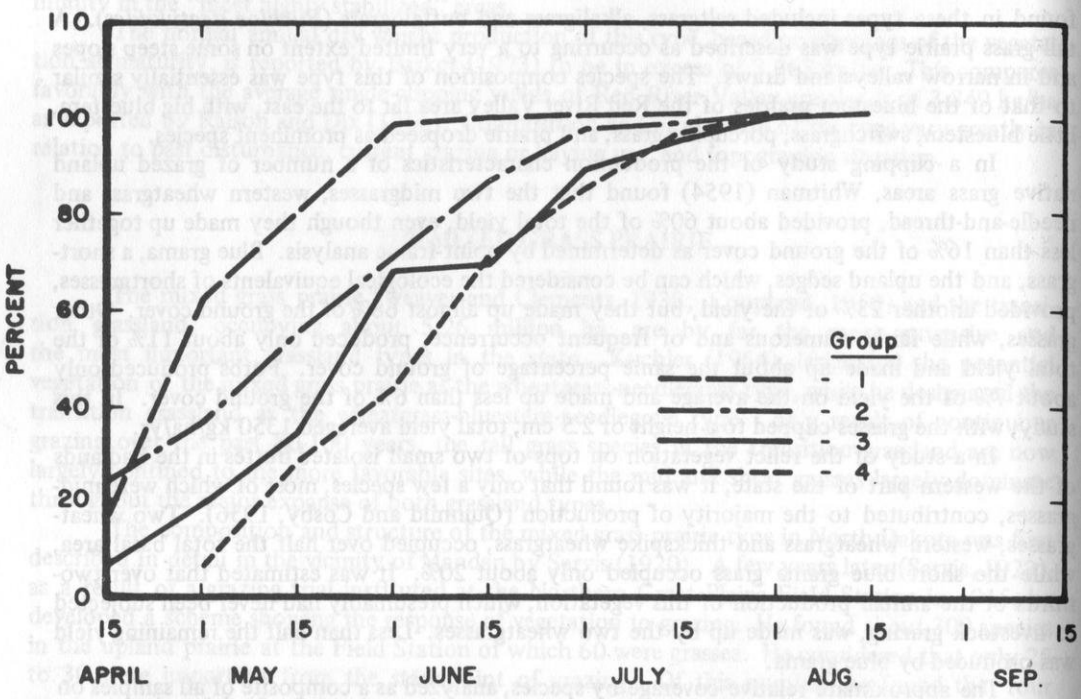

Fig. 7. An eight-year average in percent of leaf growth attained at dates indicated for four groups of grass and sedge species. Group 1 - needleleaf sedge, threadleaf sedge and sandberg bluegrass; Group 2 - western wheatgrass, needle-and-thread, prairie junegrass, green needlegrass, plains reedgrass and big needlegrass; Group 3 - blue grama; Group 4 - little bluestem, prairie sandreed, big bluestem, stonyhills muhly and red threeawn.

GROWTH AND PRODUCTION

The actual growing season for the grasses and sedges of the mixed grass prairie in this region is quite short, averaging for the most part from 90 to 100 days. Growth of the cool season species begins in late April or early May and by late July maximum height growth of these species has been achieved. Goetz (1963), as a result of an 8-year study of the phenology of the principal species in the mixed grass prairie at the Dickinson Experiment Station, found that the sedges and bluegrasses began growth first and were mature early in June. Western wheatgrass and the needlegrasses as well as others achieved maximum leaf length by July 1. Blue grama grass began growth later than the other species and maximum leaf length was reached about August 1 (Fig. 7). The growing period is terminated primarily by exhaustion of available soil moisture rather than by temperature relations (Wolters, 1968; Lauenroth, 1970; Whitman, 1971, 1972; Redmann, 1975). The observed fluctuations of available soil moisture over the growing season in the undisturbed mixed grass prairie is shown for a 3-year period in Fig. 8.

The course of production in the mixed grass prairie parallels very closely the height growth curves of the principal species. Whitman (1954) found that about 30% of the seasonal production was achieved by May 20, 80% by June 30, 93% by July 31, and approximately 97% by August 31. Late season growth does occur in some years when adequate precipitation

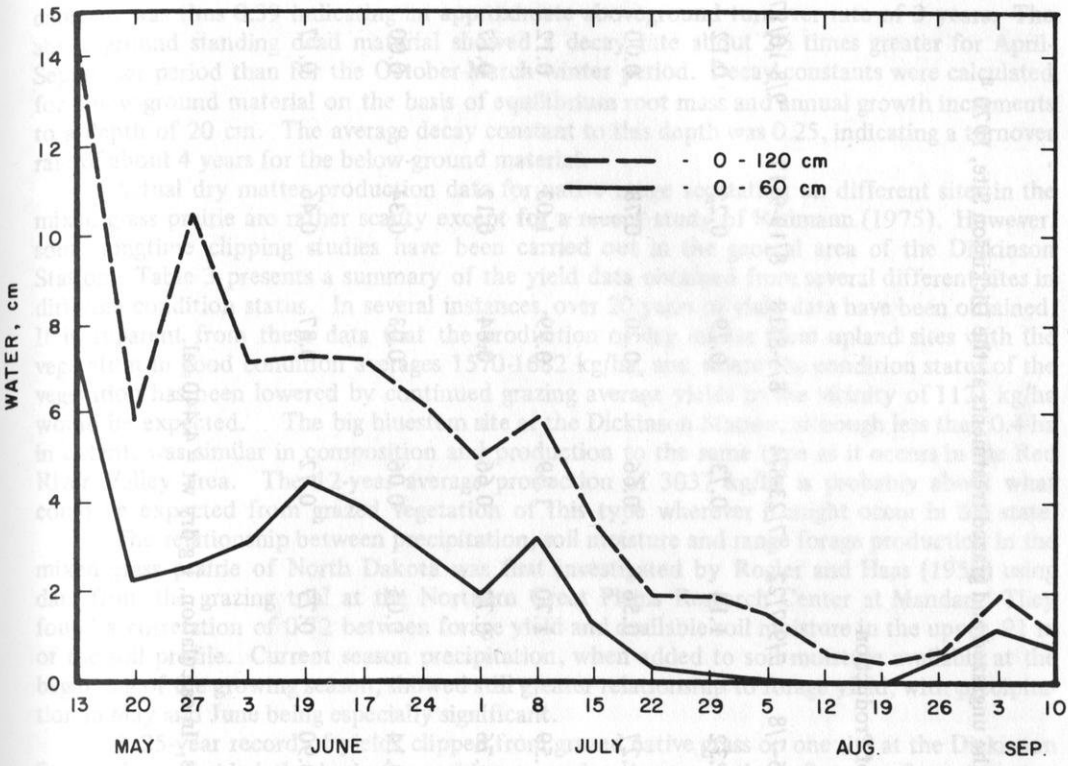

Fig. 8. Weekly average available water in the upper 60- and 120 cm layers of soil during the 1962-64 summer periods.

is received. In addition a number of the deep-rooted perennial forbs make additional growth and reach flowering and seed maturity stages in August and September. In most years the actual late-season dry-matter production by these species is quite small.

In recent years a number of studies of abiotic factors and production relations in the mixed grass prairie have been carried out at the Dickinson Experiment Station (Whitman and Wolters, 1967; Prasad, 1967; Wolters, 1968; Scoby, 1968; Lauenroth, 1970; Abouguendia, 1973). Maximum rates of aboveground dry matter production have been found to occur in June and very early July. In 1970, an average dry-matter production rate of 5.95 g/m^2/day was achieved over the period June 10-24. In 1971, the maximum production rate of 4.76 g/m^2/day was reached in the period June 21-July 7. The maximum production rate of 3.73 g/m^2/day in the 1972 season was reached in the period between June 2 and June 26. Maximum energy fixation on the ungrazed site averaged 2.46 cal/cm^2/day during June 11-24 in 1970 (Table 2).

Energy budgets were determined on both ungrazed and grazed sites in 1970 with the observation period beginning on May 15 and ending on October 20 (Whitman, 1972a). On the ungrazed site the following percentage utilization of measured net radiation occurred during this period: Plant production - 1.04%; evapotranspiration - 50.77%; soil heat flux - 0.42%; and sensible heat - 41.50%. On the grazed site less energy went into plant production and significantly more into evapotranspiration. Whitman (1974a) has discussed the influence of grazing on microclimatic relations in the mixed grass prairie in some detail.

Turnover rate in the mixed grass prairie was studied at the Dickinson site during the period 1970-72 (Abouguendia, 1973; Whitman, 1974). During this 3-year period above-ground biomass averaged 1125 g/m^2 and the average annual loss rate was 437 g/m^2. The average decay

Table 2: Mean rates of aboveground production (cal/cm^2/day) on the ungrazed and grazed treatments at the Dickinson Site, 1970 [a]

		Rates of Production								
Treatment	Group	-5/25	5/26-6/10	6/11-6/24	6/25-7/8	7/9-7/22	7/23-8/4	8/5-8/18	8/19-9/17	9/8-10/17
Ungrazed	All grasses and sedges	0.44	0.68	1.50	1.32	1.14	0.73	0.79	0.25	0.12
	All forbs	0.01	0.36	0.96	0.27	0.56	0.66	0.20	0.78	0.00
	Total community	0.45	1.04	2.46	1.59	1.70	1.39	0.99	1.03	0.12
Grazed	All grasses and sedges	0.61	1.23	1.43	0.76	0.72	0.66	0.84	0.12	0.17
	All forbs	0.09	0.24	0.33	0.14	0.05	0.06	0.03	0.34	0.00
	Total community	0.70	1.47	1.76	0.90	0.77	0.72	0.87	0.46	0.17

[a] Calculated from positive increments of growth on the treatments. In calculation, 1 g dry wt = 4,440 cal.

constant was thus 0.39 indicating an approximate aboveground turnover rate of 3 years. The above ground standing dead material showed a decay rate about 2½ times greater for April-September period than for the October-March winter period. Decay constants were calculated for below-ground material on the basis of equilibrium root mass and annual growth increments to a depth of 20 cm. The average decay constant to this depth was 0.25, indicating a turnover rate of about 4 years for the below-ground material.

Actual dry matter production data for native range vegetation on different sites in the mixed grass prairie are rather scanty except for a recent study of Redmann (1975). However, some longtime clipping studies have been carried out in the general area of the Dickinson Station. Table 3 presents a summary of the yield data obtained from several different sites in differing condition status. In several instances, over 20 years of yield data have been obtained. It is apparent from these data that the production of dry matter from upland sites with the vegetation in good condition averages 1570-1682 kg/ha, and where the condition status of the vegetation has been lowered by continued grazing average yields in the vicinity of 1121 kg/ha would be expected. The big bluestem site at the Dickinson Station, although less than 0.4 ha in extent, was similar in composition and production to the same type as it occurs in the Red River Valley area. The 12-year average production of 3037 kg/ha is probably about what could be expected from grazed vegetation of this type wherever it might occur in the state.

The relationship between precipitation, soil moisture and range forage production in the mixed grass prairie of North Dakota was first investigated by Rogler and Haas (1956) using data from the grazing trial at the Northern Great Plains Research Center at Mandan. They found a correlation of 0.72 between forage yield and available soil moisture in the upper .91 m of the soil profile. Current season precipitation, when added to soil moisture available at the beginning of the growing season, showed still greater relationship to forage yield, with precipitation in May and June being especially significant.

A 25-year record of yields clipped from grazed native grass on one site at the Dickinson Station has provided the basis for making a good estimate of the influence of precipitation on forage production in the mixed grass prairie (Whitman and Haugse, 1972). Yield data were taken over the period 1946-70. The average annual yield over this period was 1131 kg/ha, oven-dry material. The average annual precipitation was 406 mm. The best correlations between precipitation and yield were obtained for the total precipitation of September and October of the previous year plus April, May, June and July of the current year and for the total of April, May, June and July rainfall ($r = 0.84$). The regression coefficients for these two relations were 107.8 and 103.2. The conclusion seems justified that in general about 50 kg of plant material (oven-dry weight) would be produced per 25.4 mm of precipitation occurring in either of these periods. Lodge et al. (1971) reported that at Swift Current, Saskatchewan, the regression coefficient for yield and current season precipitation was 47 kg/2.5 cm, a value very similar to that obtained from the North Dakota data.

GRAZING INFLUENCES

Almost all of North Dakota's grassland is grazed by domestic livestock. The 1973 North Dakota Crop and Livestock Statistical Summary shows that there were 2,635,000 cattle and 265,000 sheep on North Dakota farms as of January 1, 1974. Considering that each head of cattle and every 5 sheep constitute one animal unit, this places the grazing load on North Dakota's grasslands in the vicinity of 2,688,000 animal units. Since there are 5,704,574 ha of grazable grasslands in the state, this makes 2.1 ha of grassland available per animal unit. Some of the livestock, of course, are grazed on cropland acres or are fed with materials produced on croplands and an estimate of this kind is bound to have considerable error in it. Nonetheless it is apparent that grazing pressure has had and will continue to have a profound influence on the grassland vegetation of the state. It is not the intent of this paper to examine the detailed

Table 3: Range clipping yields from different range sites in Stark and Billings Counties, North Dakota.[1]

Vegetation type	Period of clipping	Soil type	Range condition	Numerical rating - %	Avg. yield kg/ha
Sagebrush-grass	1950-70	Havre	Excellent	90	2116
"	1950-70	"	Good	75	1617
Grama-stipa-sedge-sandgrass	1951-70	Flasher	Excellent	90	1621
"	1951-70	"	Good	67	1094
Grama-wheatgrass sedge	1950-70	Grail	Excellent	90	1637
"	1950-70	"	Good	60	1025
Wheatgrass-green needle	1951-70	Searing	Excellent	85	1791
Wheatgrass-grama	1951-70	Patent	Excellent	85	1296
"	1950-63	Rhoades-Belfield	Good	65	881
Big bluestem	1946-57	Grail	Good	70	3037

[1]Yields obtained from clipping 10 1-m^2 plots on each site each year.

effects of grazing on the native grasslands of the state, but it seems apparent that a continued fairly heavy grazing pressure is likely to be maintained on the grasslands and may even be intensified in the future.

A development that has taken place in recent years is likely to produce rather drastic changes in composition and productivity of the mixed grass prairie should it become widespread. This is the use of nitrogen fertilizer on responsive sites in the grassland area. It has been shown that productivity and grazing capacity of native mixed grass pastures can be greatly increased by annual applications of nitrogen fertilizer (Rogler and Lorenz, 1965, 1969). The same type of response on certain pasture sites in the Dickinson area was reported by Goetz (1969). All of these workers point out that fertilization causes shifts in composition of the vegetation with the taller grasses increasing markedly in relative coverage, while the shorter grasses, especially blue grama grass, and the sedges show a corresponding decrease. Many of the more intricate aspects of the influence of fertilization on the native grass ranges and pastures still remain to be worked out. There seems little doubt, though, that the result of continued fertilizer use accompanied by more intensified grazing use will result in significant changes in ecological relationships in the mixed grass prairie.

OTHER INFLUENCES

Two other factors seem likely to affect the future status of North Dakota's grasslands. These are weather modification and strip mining. Weather modification procedures to augment precipitation have been underway for some time in the Northern Plains, and the last two or three years have seen the development of a more widespread and intensified effort in North Dakota. An evaluation of the probable effects of an additional 25-50 mm of precipitation received during the growing season (ARE Committee, 1974) indicate that production of the grasslands would be increased; internal changes in species composition would take place with those with higher moisture requirements tending to increase, while species more xeric in nature would tend to decrease. It was anticipated that initial changes would be gradual and there probably would not be a major change in dominants. Boundaries of natural vegetation are largely influenced by land use practices rather than natural influences in a predominantly agricultural area.

Strip mining for lignite coal has been underway for a number of years in North Dakota but with a relatively small amount of land disturbance thus far. The developing energy crisis has already resulted in increased mining, and projections for future activity indicate great increases by the 1980's. Most of the land in North Dakota that is projected for mining is in the mixed grass prairie area, but both grassland and cropland areas will be involved. Estimates of the amount of land that might be disturbed by surface mining in North Dakota range up to 809,720 ha, but a recent estimate by the Northern Great Plains Resources Program (1974) indicates that probably not much more than 28,340 ha would be affected.

The effect of strip mining on native grassland is complete and absolute, and the continuation of the area in grassland following the mining operation is dependent on reclamation procedures. The restoration of a native cover on strip mined lands is difficult (Dietrich, 1973), and as pointed out by Wali and Freeman (1973) cover developed by natural revegetation on mined land sites is significantly different from the cover on unmined native grass sites. It is possible to restore a grass cover on such sites more readily through the use of non-native grass species than through the use of native grass species (Sandoval et al. 1973). It seems quite likely that in the long run under present reclamation laws the mined lands will be regrassed largely with non-native species, which on an economic basis may well be as advantageous as would be their return to native prairie vegetation.

ACKNOWLEDGEMENT

Our sincere thanks are due Dr. Robert L. Burgess of the Oak Ridge National Laboratory for helpful comments.

ABSTRACT

North Dakota has about 35 million ha of native grass of which about 31 million ha are more or less in permanent grazing use as pasture and range. The bulk of the existing grassland is in the western two-thirds of the state and is considered to be mixed grass prairie, existing in a precipitation zone of 36-43 cm. In the eastern part, with somewhat higher rainfall, a tall grass type originally dominated. Both grassland types have sandy, alkaline, saline, and wet phases, and are also influenced in composition and structure by numerous other site factors. Studies of species distribution, diversity, major site influences, energy utilization, and mineral nutrient cycling in a number of representative grassland areas throughout the state, are discussed.

KEY WORDS

Tall grass prairie, mixed grass prairie, Sandhills prairie, North Dakota, grazing influences, primary production, prairie potholes.

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PLANT COMMUNITIES OF THE BLACKLAND PRAIRIE OF TEXAS

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INTRODUCTION

The Blackland Prairie (Godfrey et al. undated), one of 16 land resource areas of Texas, has been included in numerous treatments of North American midcontinental grasslands. Tharp (1926) referred to the Prairie as the *Andropogon-Stipa-Aristida* association, based on dominants of successional stages. Küchler (1964) recognized the Blacklands as an *Andropogon-Stipa* association and Carpenter (1940) considered *Sorghastrum avenaceum* the binding dominant. Livingston and Shreve (1921) described the Blackland Prairie as a grassland-deciduous forest transition while others include it as a component of the Coastal Prairie (Weaver and Clements, 1938; Clements and Shelford, 1939). Dodd (1968), in a general treatment of North American grassland associations, included the Blackland Prairie as an extension of the True Prairie, as did Allred and Mitchell (1954). The San Antonio Prairie, a large island of the Blackland Prairie within the Oak-Hickory forest association (Braun, 1950), has been identified as a part of the True Prairie (Launchbaugh, 1955) and similar to the Fort Worth Prairie as described by Dyksterhuis (1946). No quantitative studies of the climax vegetation of the Blackland Prairie have heretofore been published.

The purpose of this study is to provide a systematic, quantitative description of native grassland remnants of the Blackland Prairie of Texas. Specific objectives are: (1) to quantitatively describe the dominant species composition of these remnant prairies, (2) to relate this species composition to edaphic and climatic variables, and (3) to provide information to more objectively relate the Blackland Prairie to other North American grasslands.

STUDY AREA

The Blackland Prairie forms a narrow band bordered on the north by the Red River, the east by the East Texas Timberlands, the west by the Eastern Cross Timbers (Hill, 1901; Carter, 1931; Johnston, 1931) and extends southward into the Rio Grande Plain (Godfrey et al. undated) (Fig. 1). The Colorado River forms the southern boundary for this study. The Prairie is approximately 70 km across in the north and narrows southward to about 12 km. It covers an area of over 4,260,000 ha. Inventories often include with the main Prairie several outlier prairies, the largest of which are the Fayette and San Antonio Prairies (Johnston, 1931). Only the main belt is included in this discussion and will be referred to as the Blackland Prairie or Blacklands.

Approved by the Director, Texas Agr. Exp. Sta. as TA–11462.

Portions of this study were conducted as partial fulfillment for a Master of Science degree by the senior author.

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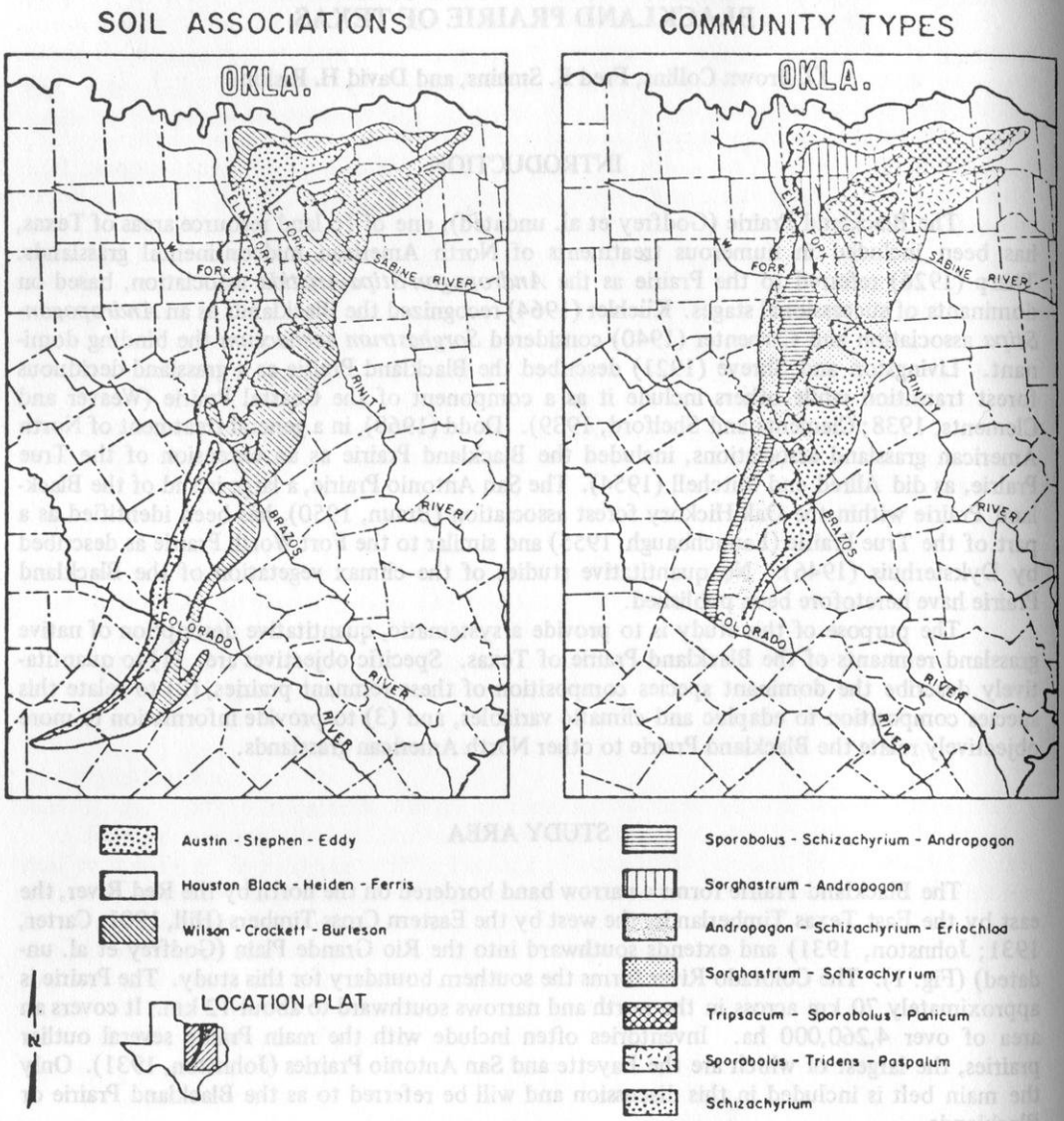

Fig. 1. Soil associations and plant community types of the Blackland Prairie of Texas.

Average annual precipitation varies from 115 cm in the north to 75 cm in the south. Virtually all precipitation occurs as rain with May and September peaks (Carr, 1967). Growing season increases from north to south and varies from 260 to 290 days (Blood and Hildreth, 1958). Average annual temperatures vary from 18 C in the northernmost portion to 21 C along the Colorado River (Carr, 1967).

The Blackland Prairie has a coastward or southeastward orientation. Relief is gently undulating and is marked by numerous mammillary hills with gently rounded slopes. Four major streams dissect the Blacklands. From north to south they are the Red, Trinity, Brazos and Colorado.

Geologically the Blackland Prairie may be longitudinally subdivided into five parallel north-south units. These divisions, from west to east are the Eagle Ford, Austin, Taylor, Navarro and Midway Groups (Hill, 1901). The Eagle Ford Group consists of well-laminated shales, the Austin and Taylor Groups are limestone, the Navarro is primarily calcareous shaly clays, sandy clays and sands and the Midway is characterized by calcareous sandstone, soft gypsiferous clays and limestone (Sellards et al. 1932).

Parent material variety results in associated soil diversity. Three major associations are recognized across the Prairie from west to east; the Austin-Stephen-Eddy, Houston Black-Heiden-Ferris and Wilson-Crockett-Burleson (Godfrey, 1964) (Fig. 1).

Austin-Stephen-Eddy Association

Derived from the Austin and Eagle Ford Groups, soils of this association are brown silty clay and clay loam Mollisols which are thermic, carbonatic and shallow. The "A" horizon has a maximum depth of 38 cm and the "C" horizon occurs within 75 cm of the surface. Differentiating characters are chalk fragments and $CaCO_3$ concentrations in lower portions of the solum.

Houston Black-Heiden-Ferris Association

This association, derived from the Taylor and Navarro Groups, covers the largest percentage of the Blackland Prairie and has long been considered typical of the region (Carter, 1931; Godfrey, 1964). This association also represents the largest continuous assemblage of Vertisols in the world (Dudal, 1965). These soils have no distinct "B" horizon. The transition is from "A" to "AC". They share fine montmorillonitic basic, thermic and ustertic properties.

This soil is characterized by shrink-swell properties which result in development of broad, deep cracks. Movement of the soil gives rise to a characteristic microrelief of low mounds and shallow depressions referred to as gilgai. On slopes of less than 5% gilgai topography is characterized by circular micro-depressions while on slopes greater than 5% it consists of continuous curving banks and depressions aligned approximately parallel to the maximum slope (Beckman et al. 1970).

Wilson-Crockett-Burleson Association

These soils, derived from the Midway Group, are dominant in the northern and eastern portion of the Prairie. The Wilson series (Alfisol) typifies soils in this association which are loamy in the surface; the Burleson series (Vertisol) typifies the ones which are clayey throughout (Godfrey, 1964). These are neutral to slightly acid gray, loamy and clayey soils usually characterized by massive, very hard fine sandy loam "A" horizon, a hard mottled clay "Bt" horizon and an olive "C" horizon.

METHODOLOGY

A survey was conducted in 1970 to determine the extent and distribution of remnant native vegetation in the Blacklands. All remnants reported were upland hay meadows. Each remnant was considered to be one stand unless topographic or edaphic factors warranted its division. To be selected a stand must: (1) have unbroken native sod; (2) be large enough that vegetation was not affected by agronomic treatments or other edge effects; (3) exhibit visual homogeneity of vegetation; (4) be ungrazed during the growing season; (5) not be mowed more than once during the growing season; (6) never have been interseeded; and (7) have no history of herbicide treatment. Of the 360 remnants reported, 83 satisfied these criteria. Stand size varied from 2 to 500 ha but most were about 20 ha.

These remnants were considered representative of climatic and edaphic variations across upland sites within the Blacklands. Many factors such as mowing, grazing and fire have differential effects upon vegetation composition and production (Dix, 1964; Smeins, 1972). However, there is little doubt that hay meadows are the best remaining approximation of the climax vegetation of the Blackland Prairie (Tharp, 1926; Johnston, 1931). All meadows are mowed annually in late June or early July. This time of cutting not only allows most of the vegetation to develop beyond the critical early spring growth period, but is prior to seedstalk formation of the major grasses so that after removal of hay, plants make new growth and complete their life cycle.

Basal cover and species frequency were measured in each stand. All samples were taken between May 10 and July 20, 1971. Sampling was initiated in the southernmost portion of the Blacklands and progressed northward to minimize phenological variation. Frequency of all species was determined by taking 30 rectangular 0.5 m^2 (100 x 50 cm) quadrats per stand similar to techniques employed by Nicholson and Hulett (1970). Basal cover was measured with 300 single vertical point quadrats per stand (Goodall, 1952). Quadrats and point quadrats were positioned in a stratified random manner throughout each stand. Samples of 30 quadrats and 300 points were arrived at by intensively sampling one stand to determine the adequate sample number for dominant species.

Taxonomic nomenclature follows (Correll and Johnston, 1970). Varietal appellations are only used for the genus *Sporobolus*.

Soil samples approximately 10 x 10 x 38 cm were taken of the solum from a representative location in each stand and analyzed for texture by the hydrometer method, pH and available water (1/3–15 bars) using the matrix suction method. Soil profiles for selected stands within each soil association were described in the field with the help of Soil Conservation Service soil scientists.

RESULTS

In addition to field observations, a number of measured vegetation variables were considered in an attempt to quantitatively delimit community types within the Blacklands. Percent composition of dominant species based on basal cover produced an effective single factor mechanism for consistent and rapid recognition of communities in the field. Frequency of dominant and secondary species and composition by weight for selected stands, although not reported here, provided additional support for identification of communities. A key was developed utilizing basal cover to distinguish seven community types which were named after dominant genera (usually only one species per genus) (Fig. 2).

Community types and species distribution related closely to edaphic, topographic and climatic variables. North-south boundaries are located on major streams since species distribu-

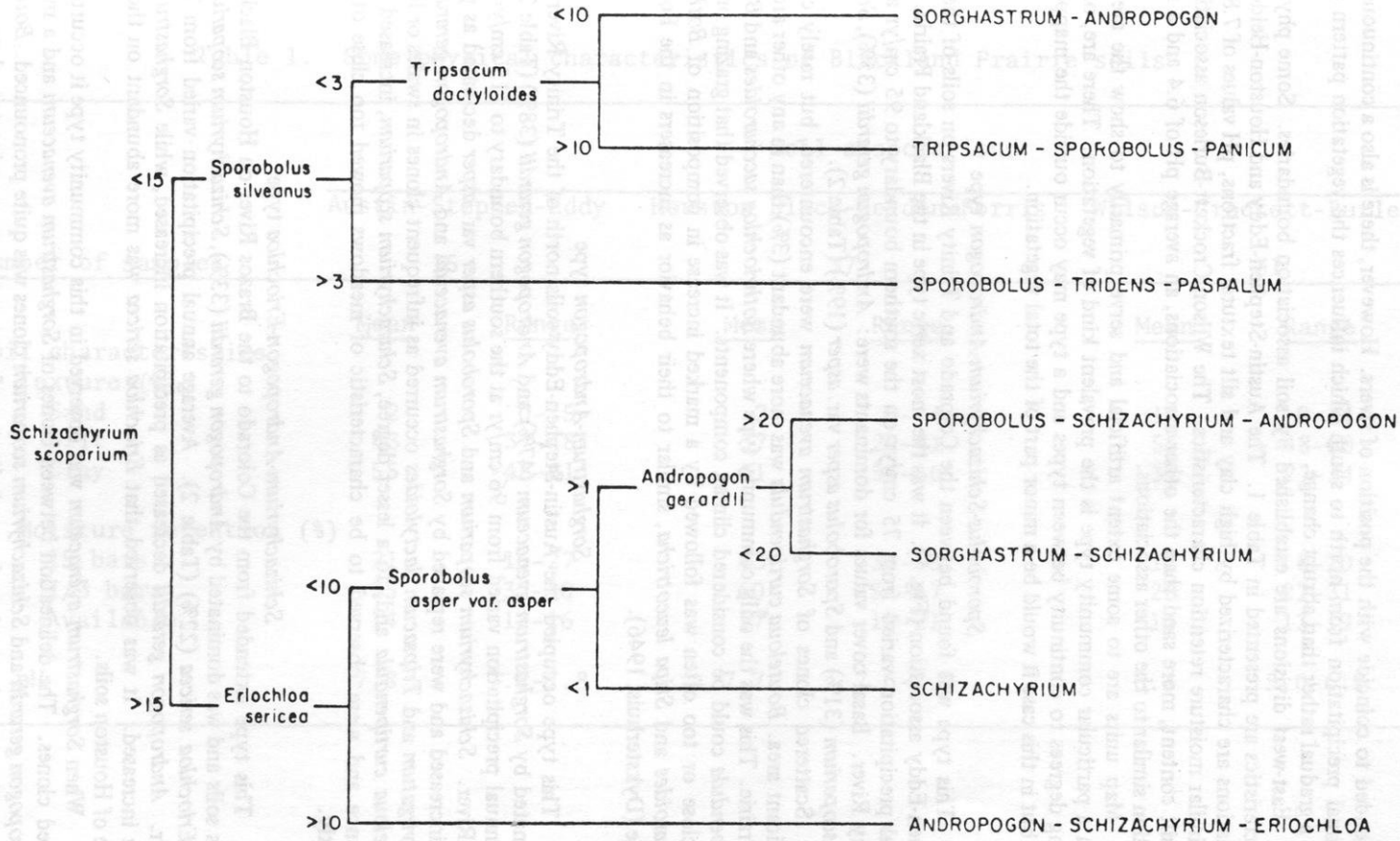

Fig. 2. Key to Blackland Prairie community types. Numbers represent percent composition based on basal cover.

tion tended to coincide with the position of rivers. However, there is also a continuous decline in annual precipitation from north to south which influences the vegetation pattern and produces a gradual rather than abrupt change.

East-west divisions are established by soil association boundaries. Some physical soil characteristics are presented in Table 1. The Austin-Stephen-Eddy and Houston-Heiden-Ferris associations are characterized by high clay and silt textural fractions, pH values of 7.8 and 7.7 and similar moisture retention characteristics. The Wilson-Crockett-Burleson association has a high silt content, more sand than the other associations, an average pH of 6.4 and a moisture retention similar to the other associations.

Map units are to some extent artificial and serve primarily to show the area within which a particular community type is the prevalent kind of vegetation. There are, of course, varying degrees to continuity between types and a type may occur outside the mapped boundary, but in this case it would be a minor part of the total vegetation.

Sporobolus-Schizachyrium-Andropogon type

This type was found between the Colorado and Trinity Rivers on soils of the Austin-Stephen-Eddy association (Fig. 1). It was the most xeric type in the Blackland Prairie. Average annual precipitation varied from 75 cm/yr on the southern boundary to 95 cm/yr along the Trinity River. Basal cover values for dominants were: *Andropogon gerardii* (35%), *Schizachyrium scoparium* (31%) and *Sporobolus asper* var. *asper* (19%) (Table 2).

Scattered clones of *Sorghastrum avenaceum* were encountered, but rarely covered a significant area. *Bouteloua curtipendula* was more abundant (3%) than in any other area within the Prairie. This was the only community type where *Bothriochloa saccharoides* and *Bouteloua curtipendula* could be considered climax components. It was observed that grazing or mowing too close or too often was followed by a marked increase in composition of *Bothriochloa saccharoides* and *Stipa leucotricha*, similar to their behavior as increasers in the Fort Worth Prairie (Dyksterhuis, 1946).

Sorghastrum-Andropogon type

This type occupied the Austin-Stephen-Eddy soils north of the Trinity River and was dominated by *Sorghastrum avenaceum* (47%) and *Andropogon gerardii* (38%) (Table 2). Average annual precipitation varied from 96 cm/yr at the southern boundary to 115 cm/yr near the Red River. *Schizachyrium scoparium* and *Sporobolus asper* var. *asper* decreased as precipitation increased and were replaced by *Sorghastrum avenaceum* and *Andropogon gerardii*. *Panicum virgatum* and *Tripsacum dactyloides* occurred as infrequent clones in swales or low areas. *Bouteloua curtipendula* and, to a lesser degree, *Schizachyrium scoparium*, increased with disturbance and were observed to be characteristic of meadows mowed too close ot too frequently.

Schizachyrium-Andropogon-Eriochloa type

This type extended from the Colorado to the Brazos River on Houston Black-Heiden-Ferris soils and was dominated by *Andropogon gerardii* (33%), *Schizachyrium scoparium* (37%) and *Eriochloa sericea* (22%) (Table 2). Average annual precipitation varied from 75 to 85 cm/yr. *Andropogon gerardii* decreased as precipitation increased, while *Sorghastrum avenaceum* increased. It was observed that *Eriochloa sericea* was more abundant on the gravelly phase of Houston soils.

When *Sorghastrum avenaceum* was observed in this community type it occurred as segregated clones. The delineation between clones of *Sorghastrum avenaceum* and a mixture of *Andropogon gerardii* and *Schizachyrium scoparium* clones was quite pronounced. *Bothriochloa saccharoides* was observed to be an indicator of overgrazing or mowing too close within this

Table 1. Some physical characteristics of Blackland Prairie soils

	Soil associations					
	Austin-Stephen-Eddy		Houston Black-Heiden-Ferris		Wilson-Crockett-Burleson	
Number of samples	15		37		31	
Soil characteristics	Mean	Range	Mean	Range	Mean	Range
Texture (%)						
Sand	2	0- 5	2	0- 4	14	9-24
Silt	43	37-48	37	29-41	55	48-60
Clay	55	48-61	61	56-66	31	27-34
Moisture retention (%)						
15 bars	21	16-27	43	34-50	13	8-20
1/3 bars	35	32-40	60	54-67	28	22-31
Available	14	12-16	17	15-21	15	13-19
pH	7.8	7.7-7.8	7.7	7.6-7.9	6.4	5.0-6.9

Table 2. Average species composition (%) based on basal cover in relation to soil associations and precipitation. Only species with greater than 20 percent basal cover in at least one stand are included.

	Soil associations											
	Austin-Stephen-Eddy				Houston Black-Heiden-Ferris				Wilson-Crockett-Burleson			
Average annual precipitation (cm)	75-85	86-95	96-105	106-115	75-85	86-95	96-105	106-115	75-85	86-95	96-105	106-115
Number of stands	3	4	3	5	11	12	10	4	5	6	6	14
SPECIES												
Andropogon gerardii												
Mean	31	39	32	44	33	9	-	1	4	-	-	-
Range	28-36	33-48	18-45	36-48	27-42	6-15	-	0- 3	0- 6	-	-	-
Eriochloa sericea												
Mean	-	-	-	-	22	4	-	-	-	-	-	-
Range	-	-	-	-	12-27	0-15	-	-	-	-	-	-
Panicum virgatum												
Mean	-	-	-	1	-	-	14	16	-	-	-	-
Range	-	-	-	0- 6	-	-	0-30	9-21	-	-	-	-
Paspalum floridanum												
Mean	-	-	-	-	-	-	-	-	5	9	9	17
Range	-	-	-	-	-	-	-	-	1- 9	3-18	0-24	6-27
Schizachyrium scoparium												
Mean	27	35	16	4	37	23	-	-	81	37	26	-
Range	21-33	30-42	6-24	0-9	30-48	9-36	-	-	64-92	33-48	21-30	-

Table 2 (continued)

	Soil associations											
	Austin-Stephen-Eddy				Houston Black-Heiden-Ferris				Wilson-Crockett-Burleson			
Average annual precipitation(cm)	75-85	86-95	96-105	106-115	75-85	86-95	96-105	106-115	75-85	86-95	96-105	106-115
Number of stands	3	4	3	5	11	12	10	4	5	6	6	14
SPECIES												
Sorghastrum nutans												
Mean	4	23	45	49	5	40	3	-	6	43	54	4
Range	0- 6	21-27	42-52	45-57	0-18	27-59	0-12	-	0-24	33-57	45-66	0-15
Sporobolus asper var. asper												
Mean	35	2	-	-	-	12	45	43	-	-	-	-
Range	27-42	0- 9	-	-	-	0-33	27-60	36-57	-	-	-	-
Sporobolus silveanus												
Mean	-	-	-	-	-	-	-	-	-	-	1	57
Range	-	-	-	-	-	-	-	-	-	-	0- 6	15-82
Tridens strictus												
Mean	-	-	-	-	-	-	-	-	-	-	3	21
Range	-	-	-	-	-	-	-	-	-	-	0- 6	12-33
Tripsacum dactyloides												
Mean	-	-	-	1	-	9	27	38	-	-	-	-
Range	-	-	-	0- 6	-	0-24	18-39	33-48	-	-	-	-

community type.

Sorghastrum-Schizachyrium type

This type extended from the Brazos to the Sabine River on the Houston Black-Heiden-Ferris soils and from the Trinity to the Sabine River on the Wilson-Crockett-Burleson soils. Basal cover values for *Sorghastrum avenaceum* and *Schizachyrium scoparium*, the dominant species in this type, were 39 and 32% on the acid soils. On basic soils their basal cover values were 40 and 23% (Table 2). This was the only type to cross two soil associations. Average precipitation on the Houston Black-Heiden-Ferris soils varied from 86 to 95 cm/yr and from 86 cm/yr to 105 cm/yr on the Wilson-Crockett-Burleson soils. The dominant species, *Sorghastrum avenaceum* and *Schizachyrium scoparium*, were of approximately equal importance on each soil association. The only striking difference between soil associations was that *Sorghastrum* did not occur as restricted clones on the Wilson-Crockett-Burleson soils while this segregated clonal pattern was common on Houston Black-Heiden-Ferris soils. *Tripsacum dactyloides* was observed in gilgai microlows in this type.

Tripsacum-Sporobolus-Panicum type

Dominated by *Tripsacum dactyloides* (38%), *Sporobolus asper* var. *asper* (29%) and *Panicum virgatum* (15%), this type was found on the Houston Black-Heiden-Ferris association north of the Sabine River. Average annual precipitation varied from 96 to 115 cm/yr. These three dominants were primary components throughout this type and all increased with increasing precipitation. All occurred equally throughout the area and showed little preference for gilgai microlows or knolls. This was in direct contrast with the distribution pattern of *Tripsacum dactyloides* and *Panicum virgatum* in other communities where they occurred in microlows. The vernal aspect of this community type was marked by *Elymus canadensis. Schizachyrium scoparium* was observed to increase with disturbance, responding much like *Bothriochloa saccharoides* in the *Sporobolus-Schizachyrium-Andropogon* type.

Maclura pomifera, a woody species, occurred on all community types in high precipitation areas, but was especially abundant in this community type.

Sporobolus-Tridens-Paspalum type

This type was situated on Wilson-Crockett-Burleson soils north of the Sabine River. Average annual precipitation varied from 106 to 115 cm/yr. Basal cover for dominants was *Sporobolus silveanus* (57%), *Tridens strictus* (21%), and *Paspalum floridanum* (17%) (Table 2). As *Sorghastrum avenaceum* and *Paspalum floridanum* decreased in percent basal cover with decreased precipitation, *Tridens strictus* and *Sporobolus silveanus* increased. This community type was dominated by species that in other types were subordinates.

Sporobolus silveanus has not previously been reported as an important grassland dominant but in the northeastern Blacklands it often formed monodominant stands. *Tridens strictus* often comprised over 20% of the composition. *Paspalum floridanum* contributed 17% of the vegetation in this type (Table 2). While *Tridens strictus* and *Paspalum floridanum* were often codominants with *Sporobolus silveanus* they seldom grew together in abundance. There was a distinct strata of low-growing species dominated by *Panicum linearifolium, P. angustifolium* and *P. oligosanthes, Aira elegans, Eragrostis hirsuta* and the rare (in Texas) *E. capillaris*.

Mima mounds were abundant in many portions of the area covered by this community type and vegetation on these mounds differed markedly from the general community. Where the mounds were not mowed, an almost zonal 3-part community was observed. Dominating the upper one-third of the mound was *Andropogon gerardii*. This was unusual because the only other habitat it was observed to frequent in the *Sporobolus-Tridens-Paspalum* type were microlows running perpendicular to the slope. The center section of the mounds was dominated by

Tridens strictus and the lowest section of the mound did not deviate noticeably from the majority of the meadow.

When the mounds were mowed yearly a different vegetation type occurred probably because it was impossible to control correct cutting height when traversing the mima mounds. Again a 3-part zonal vegetation was observed. The upper section of the mounds was dominated by *Chloris verticillata, Aristida oligantha* and *Cenchrus incertus*. The central part of the mound was dominated by *Andropogon ternarius* while the bottom again differed little from the rest of the meadow.

Andropogon ternarius was a characteristic indicator of mowing severity or overgrazing. *Juniperus virginiana* was a woody species observed to be associated with communities in the early stages of succession and *Maclura pomifera* occurred as scattered motts in native hay meadows within this type.

Schizachyrium type

This community type was found on Wilson-Crockett-Burleson soils between the Trinity and Colorado Rivers. Average annual precipitation varied from 75 cm/yr along the Colorado River to 95 cm/yr at the Trinity. *Schizachyrium scoparium* was the sole dominant here, composing 81% of the vegetation based on basal cover (Table 2). *Andropogon gerardii, Sorghastrum avenaceum, Paspalum floridanum* and *Manisuris cylindrica* were found in all stands. *Bouteloua curtipendula, Eriochloa sericea* and *Stipa leucotricha* often were found within this type.

DISCUSSION

The grassland formation of North America is generally divided into seven major associations (Dodd, 1968). The Blackland Prairie, due to its location, climate and vegetational characteristics, could be considered part of either the True Prairie or Coastal Prairie associations.

Climatically, the True Prairie, in its southern extension, receives between 75 and 100 cm/yr precipitation; the Coastal Prairie receives 65 to 85 cm/yr. The Blacklands receive 75 to 115 cm/yr and thus could be considered within the precipitation range of either of the associations. Geographically the Blackland Prairie is situated at the very southern end of the True Prairie, but it is also, through a series of outlier grasslands (Godfrey et al. undated), continuous southward to the Coastal Prairie.

Vegetationally the True Prairie is characterized by 7 major dominant species: *Stipa spartea, Sporobolus heterolepis, Schizachyrium scoparium, Andropogon gerardii, Panicum virgatum, Elymus canadensis* and *Spartina pectinata* (Weaver, 1954). The Coastal Prairie, although not thoroughly investigated, is characterized by *Bothriochloa saccharoides, Stipa leucotricha, Schizachyrium scoparium* var. *littoralis, Andropogon gerardii, Sorghastrum avenaceum* and several species of *Panicum* and *Paspalum* (Weaver and Clements, 1938).

The Blacklands have most dominants of the True Prairie except *Stipa spartea, Sporobolus heterolepis* and *Spartina pectinata* and they contain all species of the Coastal Prairie, however, *Bothriochloa saccharoides* and *Stipa leucotricha* are considered disturbance, not climax, species in the Blacklands.

Species of minor significance as dominants in either the True or Coastal Prairies, but which become major dominants in the Blacklands are *Eriochloa sericea, Paspalum floridanum, Sorghastrum avenaceum, Sporobolus asper* var. *asper,* and *Tripsacum dactyloides*, while *Sporobolus silveanus* and *Tridens strictus* are unique as major dominants within portions of the Blacklands. Thus, the Blackland Prairie has elements of both associations and also contains species combinations and certain species that make it a distinctive grassland.

An apparent factor in comparing dominant species of the Blacklands with the True and Coastal Prairies is that nearly all species are tall grasses and the communities are physiognomically similar to lowlands of the True and Coastal Prairie. In terms of precipitation and soil moisture retention characteristics, the Blacklands are humid in nature. Consequently, the Prairie takes on a lowland grassland appearance even on upland, well-drained situations. Also, the gilgai microtopography influences this relationship by acting to retain water. The influence is well illustrated by *Tripsacum dactyloides* which is a dominant in the northern, high precipitation *Tripsacum-Sporobolus-Panicum* community type but southward into drier portions of the grassland it becomes more restricted to gilgai microlows until it eventually disappears.

To place the Blackland Prairie into either the True or Coastal Prairie association is still somewhat questionable. If the most extensive community type is used as the main criterion, this type, the *Sorghastrum-Schizachyrium* type, doesn't fit well into either of the associations. Launchbaugh (1955) considered the San Antonio Prairie, which lies between the Blacklands and the Coastal Prairie and which is dominated by *Schizachyrium scoparium*, to be part of the True Prairie. If so, the Blacklands might also logically be placed in the True Prairie.

Data available do not adequately help to properly classify the Blacklands. Lack of data from the Coastal Prairie makes comparisons with it difficult. Presence of certain community types within the Blacklands, particularly the *Sporobolus-Tridens-Paspalum* type, which are unique to this grassland, tend to separate it from the other Prairies while many communities would present logical ties to both the True and Coastal Prairies.

Another possibly is that some of the northern more humid types, particularly the *Tripsacum-Sporobolus-Panicum* type, may be part of the Tall Grass Prairie as described by Weaver and Clements (1938). They included as dominants *Andropogon gerardii, Sorghastrum avenaceum, Schizachyrium scoparium, Elymus canadensis, Panicum virgatum* and less frequently *Sporobolus asper*. This then also closely resembles at least portions of the Blacklands.

It appears the Blackland Prairie has elements of the True and Coastal Prairies, of the Tall Grass Prairie and some unique elements of its own. Further investigations of the total floristics of the Blacklands, and more complete data from the Coastal Prairie may ultimately provide the necessary information for placement of the Blacklands. Nonetheless, the Blackland Prairie of Texas was once an extensive grassland region of North America and today has been nearly erased as a vegetation type. Continued investigation of the ecology of its remnants may not only elucidate its ecological ties to other grassland, but provide understanding for more proper management and maintenance of this grassland.

ABSTRACT

The Blackland Prairie of Texas is described with emphasis focused upon relationship of major community types, soil associations and precipitation pattern. The authors recognize three major soil associations, upon which are distributed seven major community types. East-west community boundaries are primarily defined by soil associations, while north-south boundaries tend to coincide with divisions produced by major streams and a precipitation gradient. A key to community types of the Blackland Prairie is presented. The Blacklands are compared to other grasslands of North America and are shown to have characteristics of the True, Coastal and the Tall Grass Prairies, as well as some unique communities not previously reported.

KEY WORDS

Blackland Prairie, Coastal Prairie, plant communities, grasslands, Tall Grass Prairie, Texas, True Prairie.

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ECOLOGICAL STUDY OF FRIENDLY PRAIRIE, MISSOURI

Richard M. Hurd and Donald M. Christisen

INTRODUCTION

Friendly Prairie is a 16 ha remnant of upland tall grass prairie in west central Missouri, 19.2 km south and 2 km west of Sedalia, Pettis County, lat. 38° 42' N, long. 93° 20' W. It is near the northeastern edge of the unglaciated prairie section which is sometimes referred to as the Osage Plains (Fig. 1). Occasional tracts, comparable to Friendly Prairie, still exist in the locality and are grazed or hayed. Most of the state's 6 million ha of prairie have been plowed and are now in cultivation.

Surface soils on the more level uplands of the rolling to sometimes steep topography of Friendly Prairie are derived from a 60-150 cm mantle of silty, wind-deposited material (loess) underlain by shales, sandstones, and limestones. The soil is deepest on the flat east-west ridge and rock-free to at least 90 cm. Interior drainage is fair to poor. The upper 45 cm is black to dark brown silt loam changing to yellowish tan with reddish mottling below and becoming a silt at 75 to 90 cm. Stones are common at 37.4 to 45 cm on mid-and-lower gentle, north facing slopes; some drainages are cut to a stony bottom. A narrow line of shrubs and trees has apparently advanced up the central drainage from the brushy pasture to the north. Occasional patches of shallow soils with sparse plant cover are present.

The average annual precipitation approximates one m and the mean annual temperature is 12.2 C. The precipitation pattern and amount, the temperature regime plus water demand by plants, produces a soil moisture deficiency in the summer season for the area (Fig. 2). Moisture stored in winter and early spring is drawn upon during the summer to meet total evapotranspiration demands. Lack of summer rain and/or unusual distribution patterns can and does produce a moisture stress for the plant cover.

Present management consists of mowing for hay, in either July or early August, alternate halves of the prairie (Fig. 3). This practice began in 1964 and has continued since 1969 when the prairie was purchased by the Missouri Prairie Foundation. From 1957 to 1964 the entire 16 ha were mowed annually and the aftermath grazed lightly. Unfortunately no specific information on management before 1954 is available other than the prairie was hayed and/or grazed.

Initially, periodic visits were made to Friendly Prairie in 1971 to build a plant species list and to determine the flowering sequence of tall grass prairie species. This objective was expanded in 1972 and 1973 to include estimates of herbage production and soil moisture. Miscellaneous observations believed useful in characterizing this particular prairie were recorded.

NUMBER OF SPECIES

Two hundred and sixty-eight plant species were identified on Friendly Prairie excluding mosses, lichens, and fungi. Forbs were most numerous, 179 species, (67%); grasses and grass-like plants, 51 species, (19%); and woody plants, 38 species, (14%). The latter were generally

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FIG. 1 MISSOURI PRAIRIE REGION AND FRIENDLY PRAIRIE

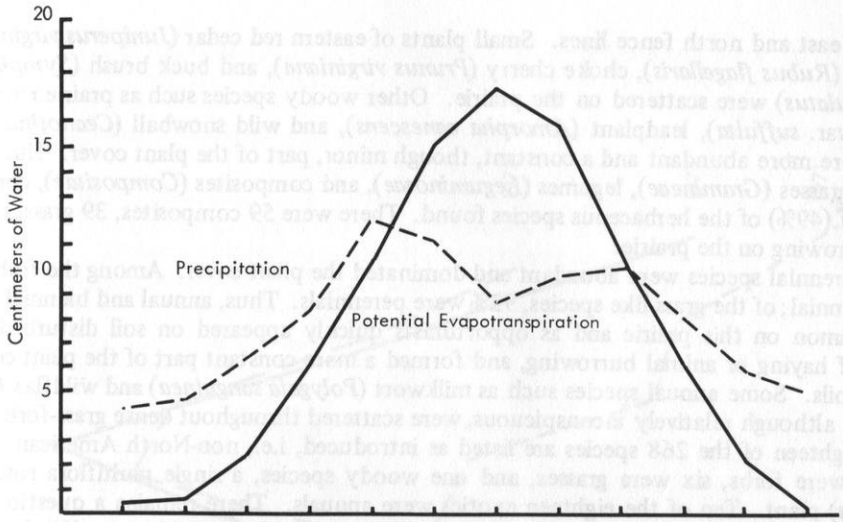

Fig. 2. WATER BALANCE AT COLUMBIA, MO.

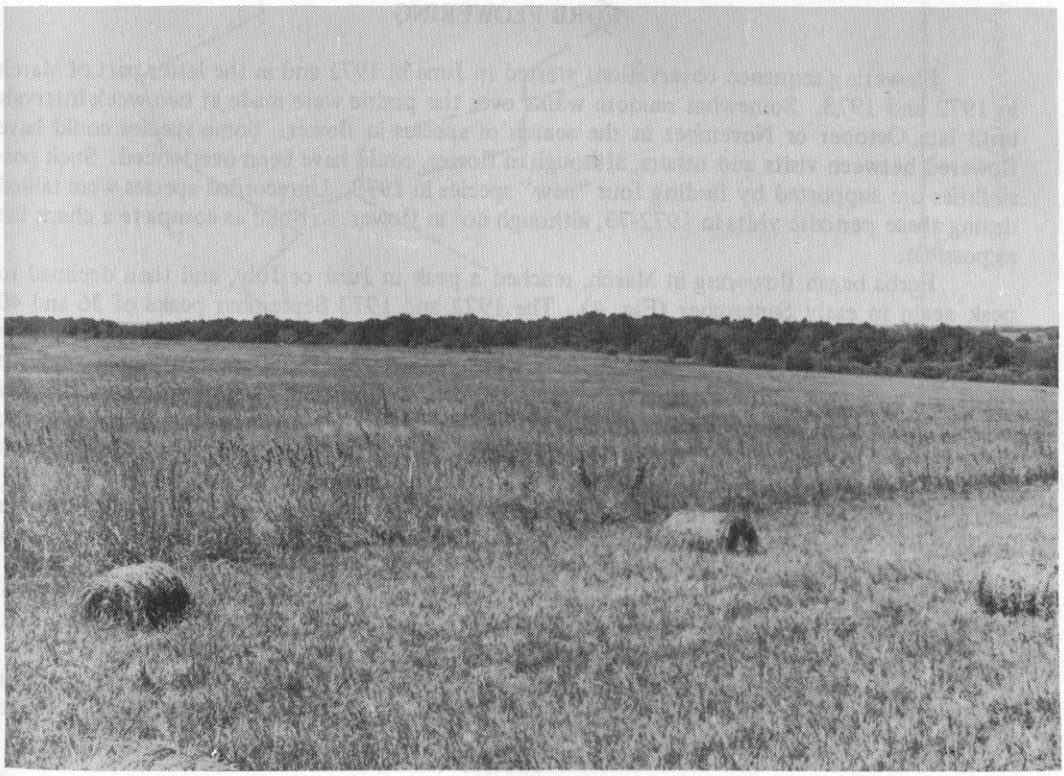

Fig. 3. Present management of Friendly Prairie consists of mowing for hay alternate halves of this 40 acre meadow.

along the east and north fence lines. Small plants of eastern red cedar (*Juniperus virginiana*)[1], dewberry (*Rubus flagellaris*), choke cherry (*Prunus virginiana*), and buck brush (*Symphoricarpos orbiculatus*) were scattered on the prairie. Other woody species such as prairie rose (*Rosa arkansas* var. *suffulta*), leadplant (*Amorpha canescens*), and wild snowball (*Ceanothus americanus*) were more abundant and a constant, though minor, part of the plant cover. Three plant families, grasses (*Gramineae*), legumes (*Leguminosae*), and composites (*Compositae*), contained about half (49%) of the herbaceous species found. There were 59 composites, 39 grasses, and 15 legumes growing on the prairie.

Perennial species were abundant and dominated the plant cover. Among the forbs, 75% were perennial; of the grass-like species, 92% were perennials. Thus, annual and biennial species were common on this prairie and as opportunists quickly appeared on soil disturbed in the process of haying or animal burrowing, and formed a more constant part of the plant cover on shallow soils. Some annual species such as milkwort (*Polygala sanguinea*) and wildflax (*Linum medium*), although relatively inconspicuous, were scattered throughout dense grass-forb stands.

Eighteen of the 268 species are listed as introduced, i.e., non-North American. Eleven of these were forbs, six were grasses, and one woody species, a single multiflora rose (*Rosa multiflora*) plant. Ten of the eighteen exotics were annuals. There remains a question about the origin of some species: Kentucky bluegrass (*Poa pratensis*) and field pansy (*Viola kitaibeliana* var. *rafinesquii*). The introduced species, singly or as a group, were minor contributors to the plant cover.

FORB FLOWERING

Flowering sequence observations started in June in 1971 and in the latter part of March in 1972 and 1973. Somewhat random walks over the prairie were made at two-week intervals until late October or November in the search of species in flower. Some species could have flowered between visits and others, although in flower, could have been overlooked. Such possibilities are supported by finding four "new" species in 1973. Unrecorded species were tallied during these periodic visits in 1972-73, although not in flower, to build as complete a check list as possible.

Forbs began flowering in March, reached a peak in June or July, and then declined to peak again in early September (Fig. 4). The 1972 and 1973 September peaks of 36 and 40 species were slightly higher than the early summer peaks for these years. A lower September peak was noted in 1971. Although there were year-to-year variations in number of forbs flowering on a given date or period, the same pattern of early peak, decline, and late peak was apparent. This may be a visual contradiction in that tall grass prairies in early summer appear to be more floriferous than at any other season. Late flowering forbs, (especially if short stemmed) were less conspicuous in the tall, warm season grasses. Certainly the fall flowering, low growing, downy gentian (*Gentiana puberula*) and common ladies' tresses (*Spiranthes cernua*) were much less conspicuous in September than Indian paintbrush (*Castilleja coccinea*), ragwort (*Senecio paupercalus*), and violets in spring.

Prominent forb species, those most conspicuous to a person walking through a prairie, are either abundant and/or have showy flowers or inflorescences. Prominence, so judged, changes from month-to-month and often from week-to-week. By way of illustration:

March - White dog-toothed violets (*Erythronium albidum*), bluets (*Houstonia minima*).

April - White dog-toothed violet, birds foot violet (*Viola pedata*) and sagittate-leaved violet (*Viola saggittata*).

[1]Nomenclature follows Steyermark, J. A. 1963. Flora of Missouri.

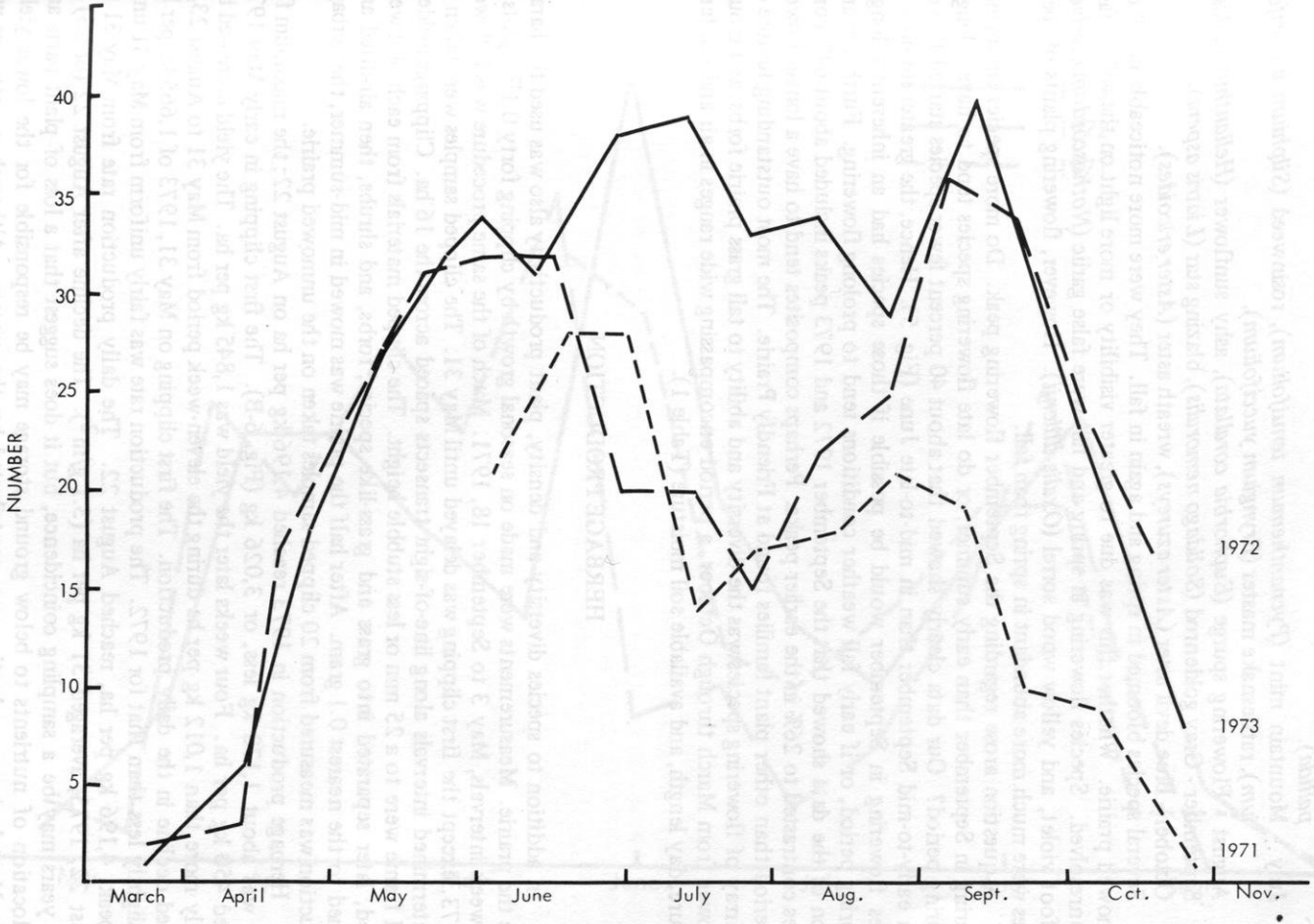

FIG. 4 FORB SPECIES IN FLOWER AT FRIENDLY PRAIRIE

May - Ragwort, golden alexanders (*Zizia aurea*), Indian paintbrush, phlox (*Phlox pilosa*).
June - Coreopsis (*Coreopsis grandiflora* and *C. palmata*), pale coneflower (*Echinacea pallida*).
July - Mountain mint (*Pycnanthemum tenuifolium*), rosinweed (*Silphium integrifolium*), rattlesnake master (*Eryngium yuccifolium*).
August - Flowering spurge (*Euphorbia corallata*), ashy sunflower (*Helianthus mollis*).
September - Gray goldenrod (*Solidago nemoralis*), blazing star (*Liatris aspera*).
October - Blue devil aster (*Aster azureys*), wreath aster (*Aster ericoides*).

Several species bloomed in spring and again in fall. They were more noticeable in fall on the mowed prairie. Whether this was due to greater visibility or more light on the soil surface was unresolved. Species flowering in spring and fall were false garlic (*Nothoscordum bivalve*), birdsfoot violet, and yellow wood sorrel (*Oxalis dillenii*). However, flowering plants of these species were much more abundant in spring than fall.

A question arose regarding the September flowering peak. Do more species commence flowering in September than early summer, or do late flowering species tend to have a longer flowering period? Our data clearly showed that about 40 percent fewer species started flowering in early-to-mid September than in mid-to-late June (Fig. 5). Hence, the greater number of species flowering in September would be possible if those species had an inherently longer flowering period, or if early fall weather conditions tend to prolong flowering. Further examination of the data showed that the September 1972 and 1973 peaks included about 64% composites contrasted to 26% in the earlier peaks. Perhaps composites tend to have a longer flowering period than other plant families found at Friendly Prairie. The most outstanding feature of this array of flowering species was the diversity and ability to tall grass prairie forbs, as a group, to flower from March through October, a period encompassing wide ranges in air and soil temperature, day length, and available soil moisture (Table 1).

HERBAGE PRODUCTION

In addition to species diversity and density, plant productivity also was used to characterize the prairie. Measurements were made on seasonal growth by clipping forty 0.1^{m2} plots at four week intervals, May 3 to September 18, 1971. Much of the same procedure was followed in 1973, except the first clipping was delayed until May 31. The clipped samples were taken at predetermined intervals along line-of-sight transects spaced across the 16 ha. Clippings inside a metal frame were to a 25 mm or less stubble height. The clipped materials from each plot were bagged, later separated into grass and grass-like species, forbs, and shrubs, then air-dried and weighed to the nearest 0.1 gram. After half the prairie was mowed in mid-summer, the herbage production was measured from 20 clipped samples taken on the unmowed prairie.

Herbage production in 1973 reached 4,196 kg per ha on August 22; the maximum for 1972 was about 1,170 kg less, or 3,026 kg (Fig. 6-B). The first clipping in early May 1972 yielded 450 kg per ha. Four weeks later the yield was 1,845 kg per ha. The yield increased by slightly more than 1,012 kg per ha during the eleven-week period from May 31 to August 23, a marked decline in the daily production. The first clipping on May 31, 1973 of 1,665 kg per ha was slightly less than that for 1972. The production rate was fairly uniform from May 31 until the peak, 4,196 kg per ha, reached August 22. The daily production rate from May 31 to August 22, 1973, averaged 31 kg per ha ($3.1\ g/m^2$). The decline after August 22 (or 23) in both years may be a sampling coincidence, but it does suggest that a loss of plant parts and translocation of nutrients to below ground storage may be responsible for the lower yield.

Most herbage production was contributed by the grasses. Although no attempt was made to separate grasses from grass-like species, primarily sedges, visual evidence supported

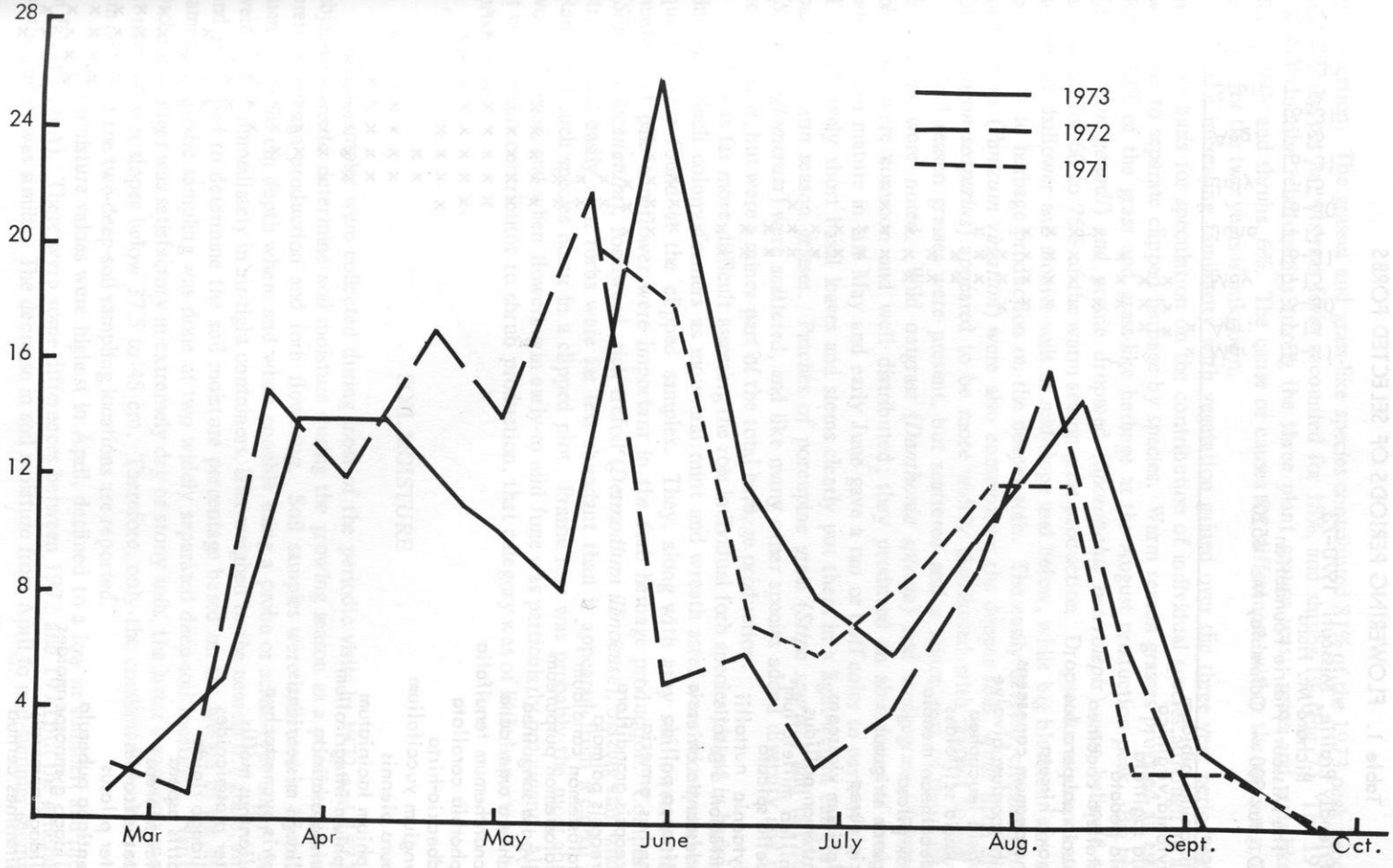

FIG. 5 FORB SPECIES EARLIEST DATE OF FLOWERING AT FRIENDLY PRAIRIE

Table 1. FLOWERING PERIODS OF SELECTED FORBS

Friendly Prairie, Missouri 1970-73
Richard M. Hurd
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P.O. Box 200 - Columbia, Mo 65201

Species	Mar. 15-31	Apr. 1-15	Apr. 16-30	May 1-15	May 16-31	June 1-15	June 16-30	July 1-15	July 16-31	Aug. 1-15	Aug. 16-31	Sept. 1-15	Sept. 16-30	Oct. 1-15	Oct. 16-31
Erythronium albidum	x	x													
Claytonia virginica		x	x	x											
Viola sagittata		x	x	x											
Viola pedata				x	x	x									
Castelleja coccinea				x	x	x	x								
Senecio pauperculus				x	x	x	x								
Hypoxis hirsuta				x	x	x	x								
Lithospermum canescens				x	x	x	x								
Nothoscordum bivalve				x	x	x									
Baptisia leucophea					x	x	x								
Camassia scilloides					x	x									
Dodecatheon meadia					x	x									
Phlox pilosa					x	x	x								
Erigeron strigosus						x	x	x	x	x					
Zizia aurea						x	x								
Delphinum virescens						x	x								
Penstemon pallidus						x	x								
Achillea millefolium						x	x	x							
Lobelia spicata						x	x								
Polytaenia nuttallii						x	x								
Penstemon digitalis						x	x								
Tradescantia ohiensis						x	x								
Echinacea pallida							x	x	x						
Dianthus armeria							x	x	x	x	x				
Coreopsis grandiflora							x	x	x						
Coreopsis palmata								x	x						
Petalostemon candidum								x	x						
Petalostemon purpureum								x	x						
Polygala sanguinea								x	x	x	x	x			
Buchnera americana								x	x	x	x	x	x		
Pycnanthemum tenuifolia								x	x	x	x	x	x	x	x
Euphorbia corollata								x	x	x	x	x	x	x	
Rudbeckia-hirta							x	x	x	x					
Eryngium yuccifolium									x	x					
Gaura biennis									x	x	x	x	x	x	
Silphium laciniatum									x	x	x	x			
Silphium integrifolium									x	x	x	x	x		
Vernonia crinita									x	x	x	x	x		
Solidago missouriensis										x	x	x	x		
Liatris pycnostachya										x	x	x			
Helianthus mollis											x	x	x	x	
Aster ptarmicoides												x	x		
Solidago rigida												x	x	x	
Liatris aspera												x	x		
Aster azureus													x	x	x
Aster ericoides													x	x	x
Aster pilosus													x	x	x
Gentiana puberula													x	x	x
Solidago gymnospermoides													x	x	x
Solidago nemoralis													x	x	x
Spiranthes cernua															x

this assertion. The grasses and grass-like species contributed 81% of the 1973 peak production of 4,196 kg per ha, whereas forbs accounted for 18%, and shrubs 1% (Fig. 7). The 1972 herbage production relationships among the three plant groups was: grass and grass-like, 68%; forbs, 26%; and shrubs, 6%. The cause or causes for differences within the species group percentages for the two years is unknown.

The increasing familiarity with vegetation gained over the three year period may be a reasonable basis for speculation on the contribution of individual species although no attempt was made to separate clipped herbage by species. Warm season grasses provided an estimated 80 to 90% of the grass and grass-like herbage at the August production peak. Big bluestem (*Andropogon gerardi*) and prairie dropseed (*Sporobolus heterolepis*) were believed to have accounted for 60 to 75% of the warm season grass production. Dropseed was abundant on the somewhat shallower and stonier soils at mid-slope and below, while big bluestem was a major contributor to herbage production on the deeper soils. The easily defined, circular patches of switch-grass (*Panicum virgatum*) were also common on the deeper soils, while little bluestem (*Andropogon scoparius*) appeared to be more widely distributed with respect to soil depth.

Cool season grasses were present, but scattered and a minor part of the plant cover. Exceptions were noted. Wild oatgrass (*Danthonia spicata*) and wedgegrass (*Sphenopholis obtusata*) were common and well distributed; they produced an abundance of seed stalks, which when mature in late May and early June gave a tan or buff color to parts of the prairie. Their relatively short basal leaves and stems clearly put them in a light-weight category compared to warm season grasses. Patches of porcupine grass (*Stipa spartea*) and tall nut grass (*Scleria triglomerata*) were scattered, and like many other species added diversity and interest to the prairie, but were a minor part of the total herbage production.

It was far more difficult assessing the role individual forb species played in herbage production. Such colony formers as mountain mint and wreath aster were widespread and frequently were found in the clipped samples. They, along with ashy sunflower, rattlesnake master and pale coneflower were important in the forb herbage production. Compass plant (*Silphium laciniatum*), rosinweed, tick trefoil (*Desmodium illinoense*), blazing star, and other striking and easily seen forbs were far less abundant than it appeared from a casual glance. Rarely did such species occur in a clipped plot. Prairie rose was probably the most abundant woody species, and when flowering in early-to-mid June was particularly prominent. Although it was a major contributor to shrub production, that category was of little importance to total production.

SOIL MOISTURE

Soil samples were collected during most of the periodic visits in 1972 and 1973. The objective was to determine soil moisture during the growing season as a possible aid in interpreting herbage production and forb flowering. Soil samples were collected at 15 cm increments to a 90 cm depth where and when possible using a probe or screw-type auger. Samples were placed immediately in air-tight containers, later weighed to the nearest 0.1 gram, air dried, and reweighed to determine the soil moisture percentage based on the weight of the air-dried sample. Periodic sampling was done at two widely separated deep-soil locations. Neither the probe nor auger was satisfactory in extremely dry or stony soils, the latter a common condition at mid-to-lower slopes below 37.5 to 45 cm. Therefore, only the combined results from 0-60 cm depths at the two-deep-soil sampling locations are reported.

Soil moisture values were highest in April, declined to a low in summer, and increased in fall (Fig. 6-A). There were some differences between 1972 and 1973 but the general shape of the curves was similar. The decrease in soil moisture from April to mid-summer seems a nat-

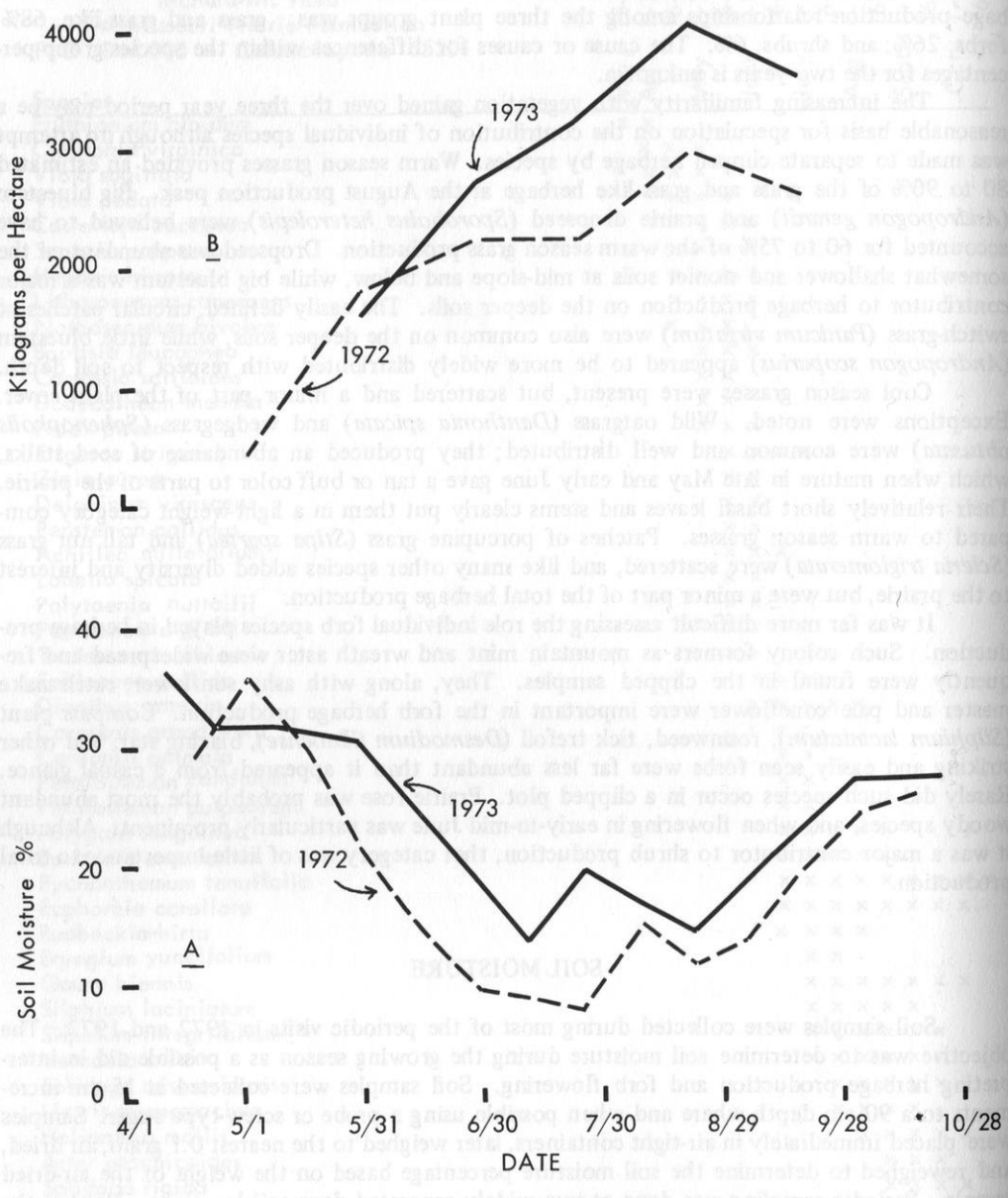

Fig. 6. A SOIL MOISTURE PERCENTAGES 0-60 CENTIMETERS
B HERBAGE PRODUCTION

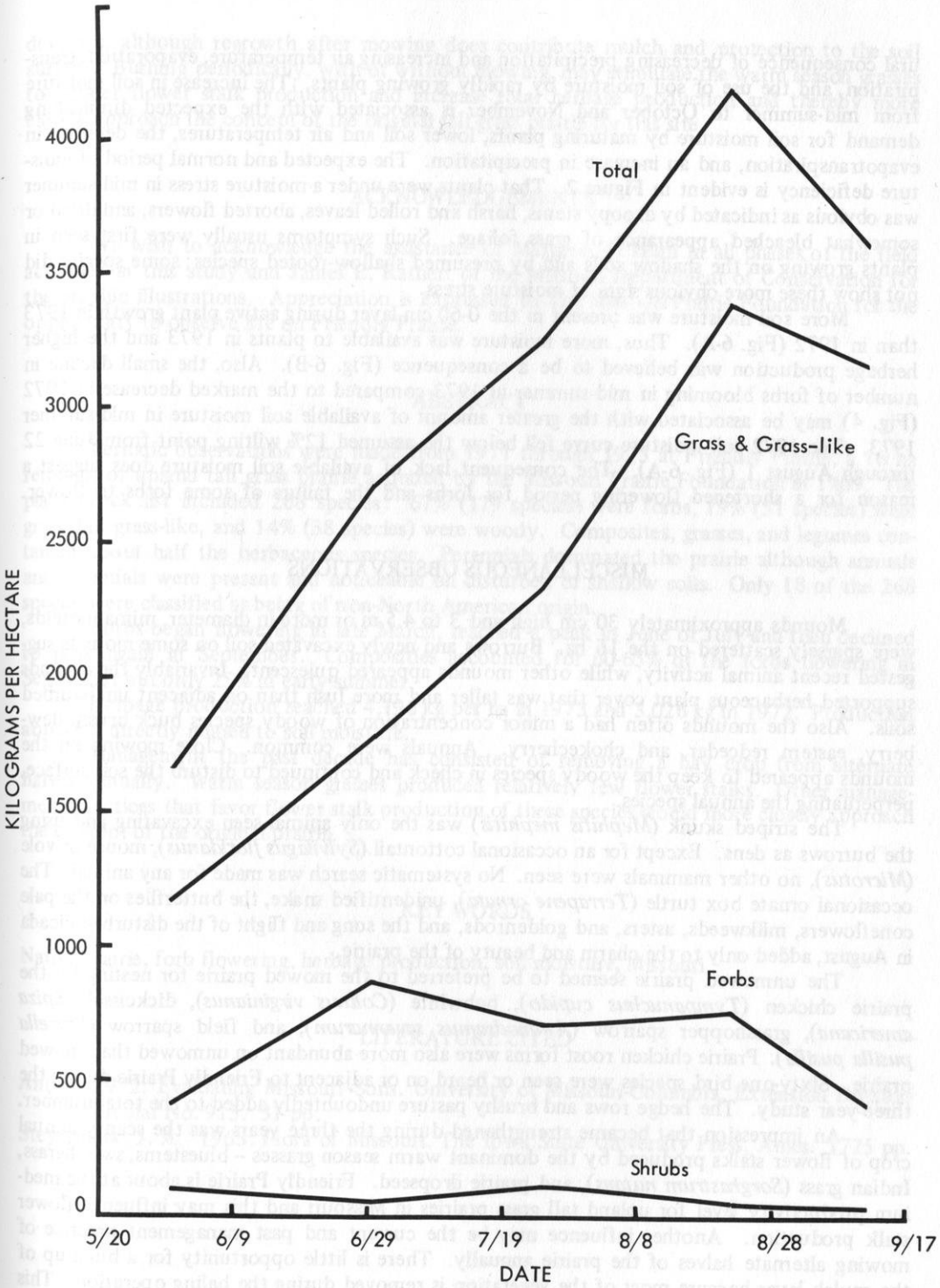

Fig. 7. HERBAGE PRODUCTION BY SPECIES GROUPS AT FRIENDLY PRAIRIE

ural consequence of decreasing precipitation and increasing air temperature, evaporation, transpiration, and the use of soil moisture by rapidly growing plants. The increase in soil moisture from mid-summer to October and November is associated with the expected diminishing demand for soil moisture by maturing plants, lower soil and air temperatures, the decrease in evapotranspiration, and an increase in precipitation. The expected and normal period of moisture deficiency is evident in Figure 2. That plants were under a moisture stress in mid-summer was obvious as indicated by droopy stems, harsh and rolled leaves, aborted flowers, and dried or somewhat bleached appearance of grass foliage. Such symptoms usually were first seen in plants growing on the shallow soils and by presumed shallow-rooted species; some species did not show these more obvious signs of moisture stress.

More soil moisture was present in the 0-60 cm layer during active plant growth in 1973 than in 1972 (Fig. 6-A). Thus, more moisture was available to plants in 1973 and the higher herbage production was believed to be a consequence (Fig. 6-B). Also, the small decline in number of forbs blooming in mid-summer in 1973 compared to the marked decrease in 1972 (Fig. 4) may be associated with the greater amount of available soil moisture in mid-summer 1973. The 1972 soil moisture curve fell below the assumed 12% wilting point from June 22 through August 1 (Fig. 6-A). The consequent lack of available soil moisture does suggest a reason for a shortened flowering period for forbs and the failure of some forbs to flower.

MISCELLANEOUS OBSERVATIONS

Mounds approximately 30 cm high and 3 to 4.5 m or more in diameter, mima mounds, were sparsely scattered on the 16 ha. Burrows and newly excavated soil on some mounds suggested recent animal activity, while other mounds appeared quiescent. Invariably the mounds supported herbaceous plant cover that was taller and more lush than on adjacent undisturbed soils. Also the mounds often had a minor concentration of woody species buck brush, dewberry, eastern redcedar, and chokecherry. Annuals were common. Close mowing on the mounds appeared to keep the woody species in check and continued to disturb the soil surface, perpetuating the annual species.

The striped skunk (*Mephitis mephitis*) was the only animal seen excavating and using the burrows as dens. Except for an occasional cottontail (*Sylvilagus floridanus*), mouse or vole (*Microtus*), no other mammals were seen. No systematic search was made for any animal. The occasional ornate box turtle (*Terrapene ornata*), unidentified snake, the butterflies on the pale coneflowers, milkweeds, asters, and goldenrods, and the song and flight of the disturbed cicada in August, added only to the charm and beauty of the prairie.

The unmowed prairie seemed to be preferred to the mowed prairie for nesting by the prairie chicken (*Tympanuchus cupido*), bobwhite (*Colinus virginianus*), dickcissel (*Spiza americana*), grasshopper sparrow (*Ammodramus savannarum*), and field sparrow (*Spizella pusilla pusilla*). Prairie chicken roost forms were also more abundant on unmowed than mowed prairie. Sixty-one bird species were seen or heard on or adjacent to Friendly Prairie during the three-year study. The hedge rows and brushy pasture undoubtedly added to the total number.

An impression that became strengthened during the three years was the scanty annual crop of flower stalks produced by the dominant warm season grasses -- bluestems, switchgrass, Indian grass (*Sorghastrum nutans*), and prairie dropseed. Friendly Prairie is about at the medium productivity level for upland tall grass prairies in Missouri and this may influence flower stalk production. Another influence may be the current and past management practice of mowing alternate halves of the prairie annually. There is little opportunity for a build-up of the mulch layer because most of the vegetation is removed during the baling operation. This leaves much of the surface soil exposed from mid-summer until the next year's standing crop

develops, although regrowth after mowing does contribute mulch and protection to the soil surface. Burning periodically, with or without mowing, may stimulate the warm season grasses to greater flower stalk production and increase total herbage production and thereby more closely approach the concept of the original tall grass prairie for this site.

ACKNOWLEDGEMENTS

We wish to acknowledge the assistance of Margaret P. Hurd in all phases of the field activities in this study and James E. Rathert of the Missouri Department of Conservation for the graphic illustrations. Appreciation is expressed to The Missouri Prairie Foundation for the opportunity to observe life on Friendly Prairie.

ABSTRACT

Periodic observations were made from 1971 through 1973 at Friendly Prairie, a 16 ha remnant of upland tall grass prairie acquired by the Missouri Prairie Foundation in 1969. The plant check list included 268 species: 67% (179 species) were forbs, 19% (51 species) were grass and grass-like, and 14% (38 species) were woody. Composites, grasses, and legumes contained about half the herbaceous species. Perennials dominated the prairie although annuals and biennials were present and noticeable on disturbed or shallow soils. Only 18 of the 268 species were classified as being of non-North American origin.

Forbs began flowering in late March, reached a peak in June or July and then declined to peak again in September. Composities accounted for 60-65% of the forbs flowering in September but only 25% in early summer.

Herbage production reached 4,196 kg per ha in 1973 and 3,026 kg in 1972. Production appeared directly related to soil moisture.

Management the past decade has consisted of removing a hay crop from alternate halves annually. Warm season grasses produced relatively few flower stalks. Other management practices that favor flower stalk production of these species would more closely approach the concept of the original prairie.

KEY WORDS

Native prairie, forb flowering, herbage production, soil moisture, Missouri.

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SOME EFFECTS OF FIRE UPON A TALL GRASS PRAIRIE PLANT COMMUNITY IN NORTHWESTERN IOWA

Gerald R. Hill and William J. Platt

INTRODUCTION

Although it is not known to what extent fire was important in the maintenance of tall-grass prairie communities (cf. Shimek, 1928), numerous investigations have demonstrated that fire alters the plant community (Curtis and Partch, 1948; Aikman, 1955; Ehrenreich and Aikman, 1957, 1963; Kucera and Ehrenreich, 1962; Hadley, 1970). In the present study, some effects of fire upon certain prairie species were studied quantitatively. Changes at the community level of organization (production, dominance, diversity) were measured over the growing season on burned and unburned prairie. The responses of certain species of grasses also were measured by comparisons of production over the season on burned and unburned prairie.

METHODS

The study was conducted on the Cayler Prairie Preserve, a 64 ha prairie in Dickinson County, Iowa. It is part of the Altamont glacial moraine of the Wisconsin drift area (Riecken and Smith, 1949). Aikman and Thorne (1956) noted that most of Cayler Prairie was upland prairie with moderate ($<15\%$) slopes. This region was described by Shimek (1931) as "very rough ridges ... which represent the most extreme xerophytic conditions in Iowa". Climax prairies in this region would be considered tall-grass prairies (Weaver, 1954).

On April 10, 1972, the Iowa Conservation Commission conducted the first recorded burning of the prairie. Subsequently, two homotactic areas were established on burned and unburned regions. Four 60 x 60 m quadrats were located on each; two in the burned region and two in the unburned region. The effects of burning were measured for both upland and lowland prairie by establishing sampling sets in the respective categories.

Six sets of plant samples were collected at roughly three week intervals from May through September, 1972. Each set consisted of four randomly selected samples from each of the eight quadrats. All forbs within a 0.20 m^2 wire hoop were cut at ground level and sorted to species. Grasses and sedges within a 0.05 m^2 hoop placed in the center of the larger hoop were collected in a similar manner. All species in each sample were weighed to obtain the above ground dry weight biomass. A ratio of dry/wet weight biomass, combining all species, was calculated to obtain an index to water content. Nomenclature used followed that of Gleason and Cronquist (1963). A list of species collected in samples is presented in Hill (1973).

Measurements of community organization were obtained using the plant samples collected. Indices used in this study included species richness (s), the Shannon-Weiner information theory function (H'), equitability (J), and dominance (c). These were calculated in the following manner: s = the number of species in a sample; $H' = -\Sigma P_i \log_2 P_i$; $J = H'/H(max)$; and $c = \Sigma P_i^2$. In these calculations, P_i was the fraction of the total wet or dry weight biomass represented by the i^{th} species, and $H(max) = -\log_2 s$, the maximum diversity obtainable by s species

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in a sample (Pielou, 1966). These indices were calculated using all species collected in each of the samples. Analysis of variance was conducted for treatment (burned and unburned prairie), block (upland and lowland prairie), and interaction effects. The response of forb and grass in general, and certain grass species (*Poa pratensis, Andropogon gerardi, Sorghastrum nutans*) were measured by comparison of seasonal production on burned and unburned prairie.

RESULTS

Production and Moisture Content

No significant difference in the total dry weight biomass of upland and lowland areas of burned and unburned prairie were recorded at any time during the summer. Consequently, samples from upland and lowland areas were pooled for analysis of burn effects.

Over most of the summer, the production was higher on burned than on unburned prairie (Table 1). Immediately after burning, mean wet and dry weight biomasses of samples from the burned region were significantly lower ($P<0.001$) than those from the unburned region. However, by early June the difference had diminished and in late summer the wet and dry weight biomasses were significantly higher ($P<0.05$) on the burned region. The difference in mean biomass continued to increase throughout the season ($P<0.001$ in September).

The ratio of dry/wet weight biomass (Table 1) indicated that during May and June plants on the burned region of the prairie had a higher moisture content than plants on the unburned prairie. The lower moisture content of plants on the unburned region was due primarily to overwintering *Poa pratensis*. The water content of plants from both regions decreased during the growing season, there being no significant difference between burned and unburned areas from July through September.

Species Richness, Species Diversity, Equitability, and Dominance

Comparisons of diversity indices based upon wet and dry weight biomass produced similar results. All data presented were calculated using dry weight biomass.

The species richness (s) of the plant community on burned and unburned regions of the prairie were not significant throughout the growing season. Thus, fire did not effect the number of species present per unit area.

The species diversity (H') was higher on the burned area than on the unburned area during three sampling periods (Figure 1). The two regions were very similar in May, but in June the diversity was significantly higher ($P<0.05$ - $P<0.01$) on the burned area. The diversity on the burned area decreased during June and the diversity on the unburned area increased. The diversity was similar on both areas and remained relatively constant from July through September.

Equitability (J) of plant communities was significantly higher ($P<0.001$) on the burned region during May and early June (Figure 2). From July through September the equitability of the burned area was slightly lower than that of the unburned prairie. This difference was significant ($P<0.01$) in July and September.

Dominance (c) of plant communities on the burned and unburned regions was significantly different in early June ($P<0.001$) but was not significantly different the rest of the growing season (Figure 3). Dominance declined more rapidly on the burned region than on the unburned region. Dominance stabilized at levels of 0.30-0.40 during the latter part of the summer (July-September).

Table 1. Plant production and moisture content on burned and unburned prairie during the summer of 1972. $\overline{WWB}$ is mean wet weight biomass ± standard error. $\overline{DWB}$ is mean dry weight biomass ± standard error. Ratio is $\overline{DWB}/\overline{WWB}$ ± standard error.

Sampling Times	$\overline{WWB}$		$\overline{DWB}$		Ratio	
	Burned	Unburned	Burned	Unburned	Burned	Unburned
May	18.6 ± 2.5	112.0 ± 15.8	4.5 ± 0.7	37.3 ± 6.4	0.23 ± 0.01	0.35 ± 0.01
Early June	536.9 ± 49.4	409.2 ± 39.1	127.9 ± 14.8	111.9 ± 9.6	0.24 ± 0.10	0.28 ± 0.13
Late June	982.5 ± 70.9	757.7 ± 63.4	310.3 ± 21.9	269.5 ± 20.3	0.32 ± 0.09	0.36 ± 0.01
July	2244.02± 215.1	1482.65± 170.5	794.0 ± 70.1	520.2 ± 46.3	0.35 ± 0.08	0.35 ± 0.06
August	2198.6 ± 204.2	1311.1 ± 79.5	851.2 ± 79.4	520.5 ± 33.8	0.39 ± 0.08	0.40 ± 0.10
September	1332.2 ± 103.4	720.9 ± 48.6	562.4 ± 39.5	312.6 ± 29.8	0.43 ± 0.01	0.43 ± 0.02

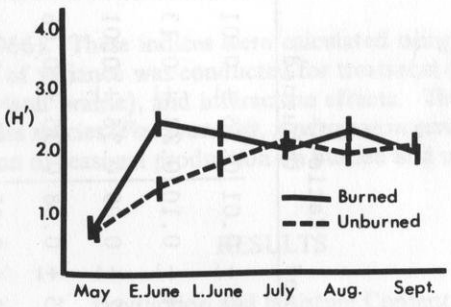

Fig. 1. Mean species diversity (H′) ± standard errors (vertical lines) on burned and unburned prairie during the summer.

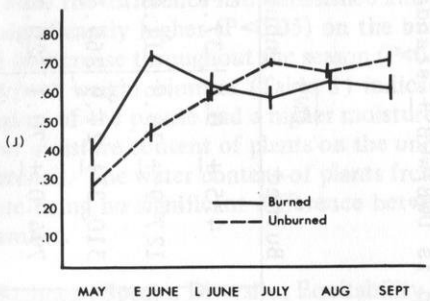

Fig. 2. Mean equitability (J) ± standard errors (vertical lines) on burned and unburned prairie during the summer.

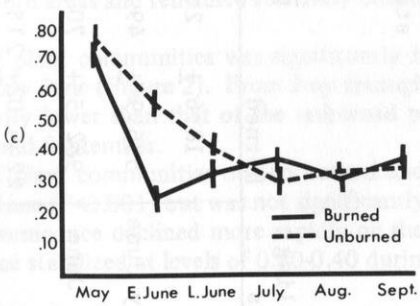

Fig. 3. Mean dominance (c) ± standard errors (vertical lines) on burned and unburned prairie during the summer.

Plant Species Biomass on Burned and Unburned Prairie

The biomasses of forbs on burned and unburned regions of the prairie were not significantly different at any time during the summer (Figure 4). Although the mean dry weight biomass of forbs was greater on the burned region at all times except July, the large variance between samples obscured any statistical differences.

The mean dry weight biomasses of grasses on burned and unburned prairie (Figure 5) showed similar increases during May and June. From July to September mean dry weight biomasses of grasses on burned and unburned prairie were significantly different ($P<0.01$). The burned region had a peak mean dry weight biomass of grasses of 566.8 ± 66.4 gr/m^2 in July. A peak mean dry weight biomass of grasses of 375.0 ± 30.1 gr/m^2 occurred in the unburned region in July.

The composition of the grass biomass was very different on the burned and unburned prairie. *Poa pratensis* contributed a lesser proportion of the total mean dry weight biomass in the burned region than in the unburned region (Figure 5). The mean dry weight biomass of *P. pratensis* on the unburned region was significantly higher ($P<0.001$) the entire growing season (Figure 6). *Poa pratensis* reached a peak mean dry weight biomass of 57.8 ± 77.3 gr/m^2 on the burned region in July and 214.5 ± 14.6 gr/m^2 in August on the unburned region. In the late summer (July-September) grasses other than *Poa pratensis* had a much higher biomass on the burned than on the unburned prairie (Figure 5). *Poa pratensis* peak mean dry weight biomasses of 507.8 ± 77.3 gr/m^2 (burned region) and 175.4 ± 38.7 gr/m^2 (unburned region) occurred in August.

Andropogon gerardi (big bluestem) was the most abundant grass on the burned area. The mean dry weight biomass of *A. gerardi* increased significantly ($P<0.001$) following burning (Figure 7). The peak mean dry weight biomass of *A. gerardi* occurred in July, with 418.9 ± 82.4 gr/m^2 on the burned region and 124.4 ± 31.8 gr/m^2 on the unburned region.

DISCUSSION

The Effects of Environmental Factors on Production

Increased plant production occurred on Cayler Prairie following burning. Similar increases in production have been recorded (Curtis and Partch, 1950; Aikman, 1955; Ehrenreich and Aikman, 1957; Kucera and Ehrenreich, 1962; Hadley and Kieckhefer, 1963; Penfound, 1964). In other studies (Dix, 1960; Hadley, 1970) production of some prairies decreased after burning. Kucera et al. (1967) suggested that increased production following burning might occur where rainfall is dependable and in excess of 530 mm per year. The region of Iowa in which Cayler Prairie is located receives an average of 688 mm precipitation annually (U.S. Weather Bureau, Climatological Data, Iowa: 1950-1969). Thus observed production increases were consistent with the hypothesis of Kucera et al. (1967).

Biomass production on both burned and unburned areas of Cayler Prairie was higher than that measured for other prairies in Iowa (Aikman, 1955) and in Missouri (Kucera and Ehrenreich, 1962).

The Effects of Fire on Community Organization

During the early growing season, species diversity was higher on burned than unburned prairie. This resulted from the great reduction in *P. pratensis* on the burned prairie. The opening of sites allowed other species, especially the warm season grasses, to increase production. This resulted in a more equitable distribution of biomass among species and a lower dominance.

During June the species diversity and equitability decreased and dominance increased on burned prairie. These changes resulted from the greatly increased production of warm season

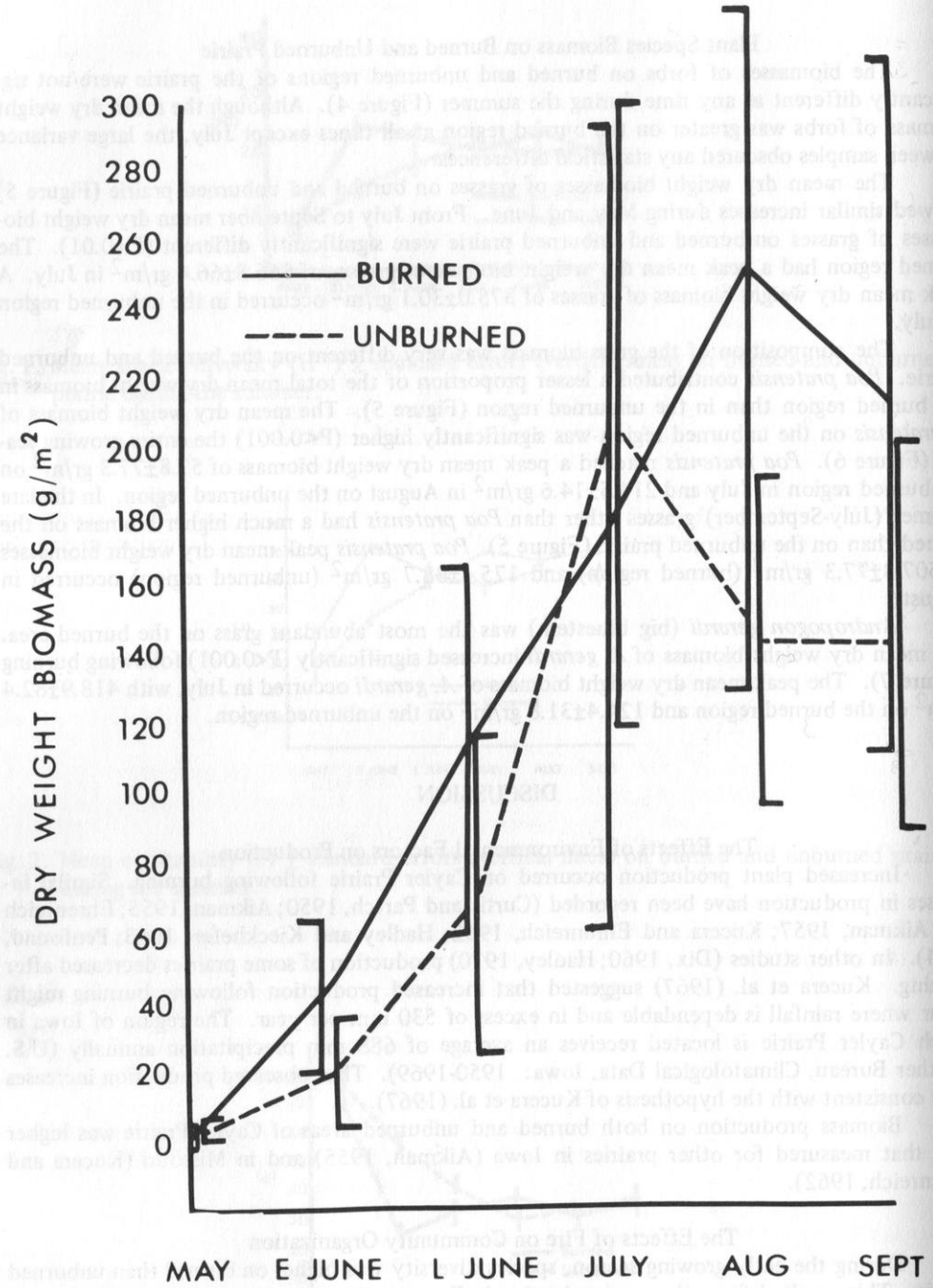

Fig. 4. Mean dry weight biomass ± standard errors (vertical lines) of forbs on burned and unburned prairie during the summer.

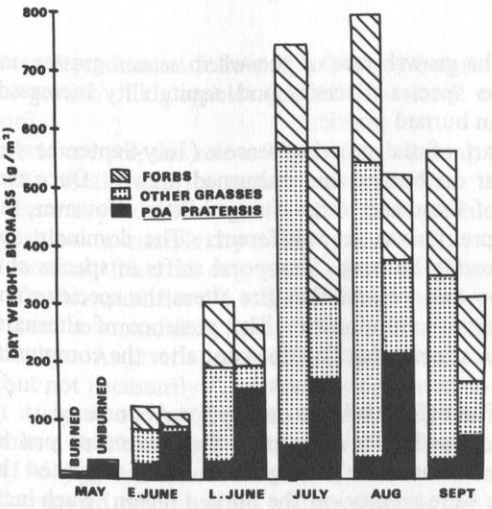

Fig. 5. A histogram of the relative contributions of forbs, *Poa pratensis* and other grasses to the mean dry weight biomass of burned (left) and unburned (right) prairie during the summer.

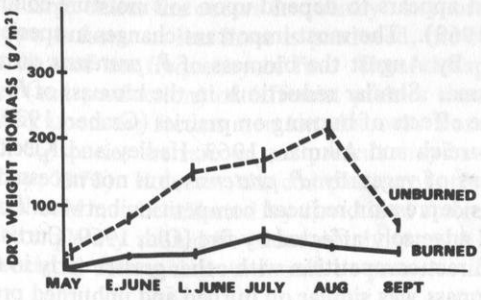

Fig. 6. Mean dry weight biomass ± standard errors (vertical lines) of *Poa pratensis* on burned and unburned prairie during the summer.

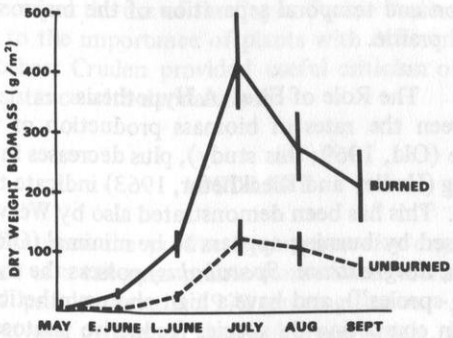

Fig. 7. Mean dry weight biomass ± standard errors (vertical lines) of *Andropogon gerardi* on burned and unburned prairie during the summer.

grasses during this time. The growth rate of the warm season grasses on unburned prairie was much slower, and thus the species diversity and equitability increased, and dominance decreased, more slowly than on burned prairie.

During the latter part of the growing season (July-September) diversity, equitability, and dominance were similar on burned and unburned prairie. Once the warm season grasses matured, the organization of the community changed little. However, the species composition of burned and unburned prairie was very different. The dominant species shifted from *P. pratensis* to *A. gerardi* following burning. Temporal shifts in species abundance were evident on the burned prairie. The data suggest that fire alters the species composition, but not the complexity of tall-grass prairie communities. The presence of alternate states of equivalent organization (resonance) also suggest that fire does not alter the community structure ofprairies.

The Effects of Fire on Species Abundance

The biomass of forbs was higher on burned than unburned prairie, but the differences were not significant. Observations made during the summer suggested that flowering and seed production of many species were greater on the burned region. Such increases following burning have been recorded (Kucera and Ehrenreich, 1962; Hadley and Kieckhefer, 1963; Old, 1969). Long term changes in forb abundance may result from increases in seed production after a fire.

The biomass of grasses was much higher on burned than unburned prairie. The response of grasses to fire is variable and appears to depend upon soil moisture conditions of the particular site (Zelder and Loucks, 1969). The most important changes in species composition were those of the dominant grasses. By August the biomass of *P. pratensis* on the burned area was 27% of that in the unburned area. Similar reductions in the biomass of *P. pratensis* have been recorded in other studies of the effects of burning on prairies (Graber, 1926; Curtis and Partch, 1948; Ehrenreich, 1959; Enrenreich and Aikman, 1963; Hadley and Kieckhefer, 1963). Fire apparently decreases the amount of vegetative *P. pratensis*, but not necessarily seed production (Curtis and Partch, 1948). This depression reduced competition between *P. pratensis* and other grasses, since the latter are not adversely affected by fire (Old, 1969; Curtis and Partch, 1948). *Poa pratensis* appears to be in direct competition with other grasses early in the growing season. During June the total grass biomass was similar on burned and unburned prairie. *Poa pratensis* comprised 80% of the biomass of grasses on unburned prairie, but only 25% on burned prairie. The depression of *P. pratensis* and removal of litter enabled warm season grasses, such as *A. gerardi*, to grow much more rapidly, since they were not shaded and soil temperatures were warmer. The biomass of *A. gerardi* on the burned area was 33% greater than on the unburned area. Vegetative reproduction and temporal separation of the major warm season grasses also were most evident on burned prairie.

The Role of Fire: A Hypothesis

The difference between the rates of biomass production of warm season grasses on burned and unburned prairie (Old, 1969; this study), plus decreases in production occurring in successive years after burning (Hadley and Kieckhefer, 1963) indicate that inhibition of growth occurs when litter is present. This has been demonstrated also by Weaver and Rowland (1952). The effect of nutrients released by burning appears to be minimal (Old, 1969). The warm season grasses (e.g. *Andropogon, Sorghastrum, Sporobolus*) possess the C_4-dicarboxylic acid pathway of carbon fixation ("C_4-species"), and have a high photosynthetic capacity (Black, 1971). When litter is removed, when competing C_3 species (reductive pentose phosphate cycle only) such as *P. pratensis* are removed, and when soil temperatures are warmer, these species cannot only initiate growth earlier, but can grow more rapidly and produce more biomass. However, when substantial litter is present, the soil temperatures are lower, and shade tolerant C_3 species

are favored. Thus, increased production following a fire may be primarily a result of depression of factors inhibiting the growth of C_4 species (assuming that soil moisture is sufficient to permit increased production).

If this hypothesis is correct, the role of fire in maintaining prairie communities should be reevaluated. The data obtained in the present study indicate that fire alters the temporal sequence of events in seasonal production and total biomass production. However, it does not alter the species composition or complexity of the community. Alterations occurring after fire can be considered to result from the depression of the dominant C_3 species, which permits C_4 species to increase if other conditions (i.e. soil moisture) are appropriate. Fire thus induces a resonance in prairie plant communities. Immediately following fire, the community shifts to a C_4 dominated community. As litter accumulation occurs and reaches a steady state, there is a shift towards a C_3 (but not necessarily *P. pratensis*) dominated community. Such shifts were observed in the present study, in a *Stipa* (C_3) - *A. scoparius* (C_4) dominated community studied by Hadley (1970), and in a *Solidago* (C_3) - *A. gerardi* (C_4) dominated community studied by Kucera and Koelling (1964). Periodic recurrence of fire would result in a continual shifting between C_3 and C_4 dominated communities. The extent to which such a resonance might occur would depend upon the total equilibrium litter accumulation (Koelling and Kucera, 1965), time to reach equilibrium between production and decomposition, and the frequency of fire. Thus, in more northern prairies where litter accumulation is greater and the time to reach equilibrium is longer (Koelling and Kucera, 1965), the biomass of the C_3 components of the community should be large unless fire occurs frequently. In more southern and western prairies where litter breakdown is faster or less litter is produced, the biomass of the C_4 components should be large regardless of the frequency of fire. Thus, the species composition and relative abundance of species (and production) of different prairies should be influenced by fire in different ways, depending upon the factors mentioned above. For example, C_3 dominated northern prairies in which C_4 species are rare or not present may have production decreased by fire (cf. Dix, 1960; Hadley, 1970). However, the complexity of any one community containing C_3 and C_4 components should not be affected by fire due to the resonance. Those prairies which exhibit the greatest complexity should be those which resonate between C_3 and C_4 dominated states, since flora associated with each state should be present.

ACKNOWLEDGEMENTS

We are indebted to the Iowa State Preserves Board and Conservation Commission for their support of this project and the use of the Cayler Prairie Preserve. Discussions with Patricia Werner provided insight to the importance of plants with different photosynthetic capacities. Richard Bovbjerg and Robert Cruden provided useful criticism of the study and manuscript. Michael Weis provided assistance with data analysis.

ABSTRACT

Some effects of fire upon the production, community organization, and relative abundance of dominant grasses of a tall-grass prairie in northwest Iowa were studied by comparison of burned and unburned prairie over the 1972 growing season. Above ground standing crop biomass production was greater on burned than unburned prairie. Due to the depression of *Poa pratensis* by fire, the species diversity and equitability were higher and dominance lower on burned than unburned prairie during the early growing season. After the warm season grasses increased greatly in biomass (July), the complexity (as measured by species diversity, equit-

ability and dominance) changed little and was similar on burned and unburned prairie. *Poa pratensis* was the dominant species on unburned prairie, but was reduced in abundance by 73% on burned prairie. *Andropogon gerardi* increased greatly in abundance and was the dominant species on burned prairie. Temporal separation of species such as *A. gerardi* and *Sorghastrum nutans* was more noticeable on burned prairie. Fire was hypothesized to alter factors inhibiting C_4 species (removal of litter, depression of C_3 species, and the subsequent warming of the soil). This results in changes in the relative abundance of species and increases the production of warm season (C_4) species (but does not affect the community complexity). Resonance between C_3 and C_4 dominated states may be a characteristic of tall-grass prairies, and would depend upon variables capable of depressing the production of C_4 species.

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SOME INTERACTIONS OF FIRE, PRAIRIE AND ASPEN IN NORTHWEST MINNESOTA

W. Daniel Svedarsky and Philip E. Buckley

INTRODUCTION

The Red River Valley Natural History Area was established as an environmental education and research facility by the University of Minnesota in 1971 under the direction of the Northwest Agricultural Experiment Station at Crookston. A major portion of the area contains stands of trembling aspen (*Populus tremuloides*) interspersed throughout grassland and prairie remnants and forms what Bird (1961) termed "aspen parkland". The Natural History Area was grazed in the past which regulated the spread of aspen into the openings and also altered the composition of the prairie. This paper discusses the use of fire as an effective technique in regulating aspen encroachment and in changing the composition of bluegrass (*Poa pratensis*) dominated prairie to favor warm season native species, notably, big bluestem (*Andropogon geradi*).

THE ASPEN PARKLAND

Throughout the prairie-forest transition region in North America, a complex of factors interact to determine the rate and extent to which prairies are invaded by woody vegetation. Along the transition zone in the northern great plains, one of the principal woody invaders is trembling aspen, which, in the absence of fire, grazing or mowing, will actively encroach into prairies and where moisture is sufficient will eventually develop dense forest stands, thereby replacing the prairie species.

In this aspen parkland region, which extends from northwest Minnesota through the prairie provinces of Canada, aspen typically occurs in groves or "aspen islands" in a prairie expanse. These groves expand into the prairie (Fig. 1) by developing root sucker shoots which are capable of penetrating up through the grassland where it would be difficult for a seedling to become established under most conditions. Buell (1959) examined one of these sucker producing roots near Waubun, Minnesota. In tracing it to its origin he noted that the distance from the young shoot to the parent tree was 31.7 m and the root was 1 cm or less in diameter for most of its length and occurred mainly in the black A horizon within 10 cm of the surface. The characteristic of having this type of feeder root plus the ability to vigorously resprout after fire makes aspen an especially persistent woody species of the prairie where it occurs. The interaction between aspen and prairie has been discussed by Ewing (1924), Buell and Buell (1959), Bird (1961) and Tester and Marshall (1962) and intensively investigated by Maini (1960).

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STUDY AREA

The Red River Valley Natural History Area is located one mile north of Crookston, Minnesota on a slight rise in the Red River Valley. The soil is a Sioux loam underlain by a thin layer of gravel deposited on lacustrine silts and clays which occur 1 m below the surface.

After the establishment of the Natural History Area in 1971, it became clear that the prairie openings would soon disappear unless the aspen sucker shoots were controlled. To evaluate the effectiveness of fire as a control means, 60 x 25 foot (18.29 x 7.62 m) plots were established along the south edge of an aspen stand with the long dimension extending out into the prairie which contained a good population of sucker shoots and also big bluestem and little bluestem (*Schizachyrium scoparium*).

The main treatment applied to date has been annual spring burning with efforts made to burn against the wind so as to achieve better consumption of the litter and prolong the high temperature at the base of the sucker shoots.

RESULTS

Aspen Control

Changes in the density of aspen sucker shoots have been measured by counting the number of living stems in late August. Virtually all of the aboveground portion of sucker shoots less than 5 cm at the base are killed by a spring fire but most are quick to resprout and grow up to 1 m in height by fall. Repeated spring burning appears to reduce the number of shoots in approximate proportion to the number of years burned (Table 1).

In a biennial spring burn plot the number of shoots present was reduced to 31% of the original number which suggests that effective aspen control might be accomplished with less frequent burning. Annual burning, however, has the advantage of speeding the rejuvenation of certain prairie species as will be discussed later. Limited observations on the effects of a summer burn (July 5, 1973) indicated a reduction of shoots to 57% of the original number after only one burn in a well-drained area dominated by bluegrass. We hope to clarify these effects of different burning rotations and timing in further studies.

Changes in herbaceous vegetation

When the spring burn plots were initiated in 1971, one of the most striking effects was the increased flowering response of big and little bluestem. Little flowering occurred in the unburned areas having a matted accumulation of bluegrass litter. Flower production in big bluestem has been examined by Curtis and Partch (1950) in which they noted that the most important factor in stimulating flowering was the removal of the dead litter by either clipping or burning.

Another apparent effect of the spring burning was in decreasing the vigor of bluegrass since fewer flowering stalks were noted in burn plots. The differential response of cool-season bluegrass and warm-season prairie grasses to spring burning has been noted by Curtis and Partch (1948), Zedler and Loucks (1969), and Troester (1970). To evaluate compositional changes in dominant species, the burn plots were sampled using a ten-point frame (NAS-NRC 1962). These observations were recorded in late August each year following late April or early May burns (Table 2). Burn dates varied depending on fuel moisture and wind conditions.

These data indicate that spring burning tends to reduce bluegrass cover and increase the cover of big bluestem by enhancing the growth of individual clumps (Fig. 2 and 3) and by preparing a bare-ground seedbed which is suitable for the establishment of new plants. Clumps of little bluestem appear much more vigorous in the burn plots compared to the no-burn controls

Table 1. Effect of Annual Spring Burning on Aspen Sucker Shoots[1]

	Percent Live Shoots Remaining		
	After 1 Burn	After 2 Burns	After 3 Burns
Plot A	81.6%	45.6%	
Plot B	90.7%		
Plot C		50.2%	7.3%

1. Values expressed as a percentage of the original number of sucker shoots

Table 2. Effect of Spring Burning on Plant Composition (By Major Species)[1]

Species	I. No-Burn Control	II. After 1 Burn	III. After 2 Annual Burns	IV. After 3 Annual Burns	V. After 1 Bien. Burn
Bluegrass (*Poa pratensis*)	82.4%	56.1%	68.6%	53.9%	73.4%
Big bluestem (*Andropogon geradi*)	5.5%	6.6%	14.2%	29.2%	13.2%
Little bluestem (*Schizachyrium scoparium*)	3.5%	5.0%	1.9%	3.9%	3.7%
Many flowered aster (*Aster ericoides*)	2.9%	3.0%	4.7%	6.1%	5.0%
Black medick (*Medicago lupulina*)		24.7%			
Total Basal Cover	37.1%	40.7%	29.3%	35.6%	31.6%

1. Data expressed as percent composition with treatments I, II, and III being the means of 2 plots each and treatments IV and V being data from 1 plot each.

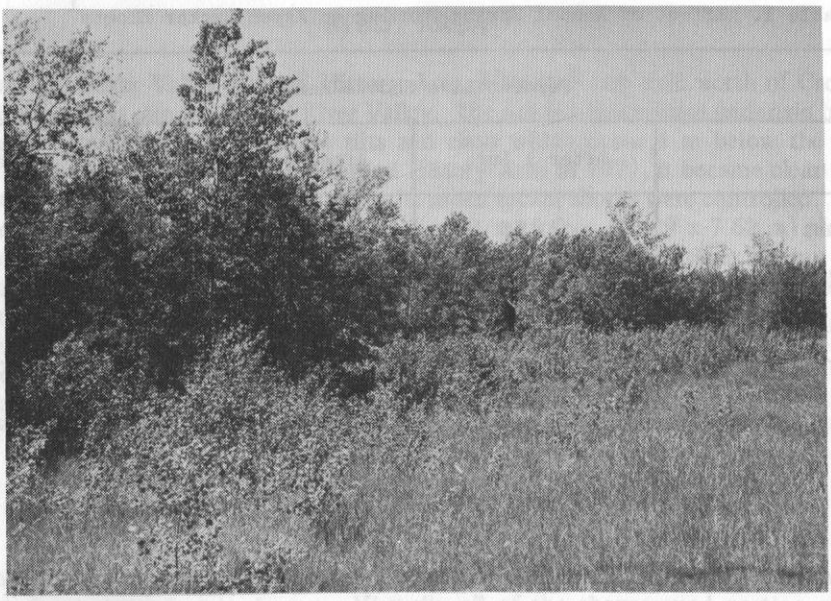

Fig. 1. Aspen invasion of prairie. Younger sucker shoots in foreground have developed in three seasons following the cessation of grazing in 1971. July 5, 1974.

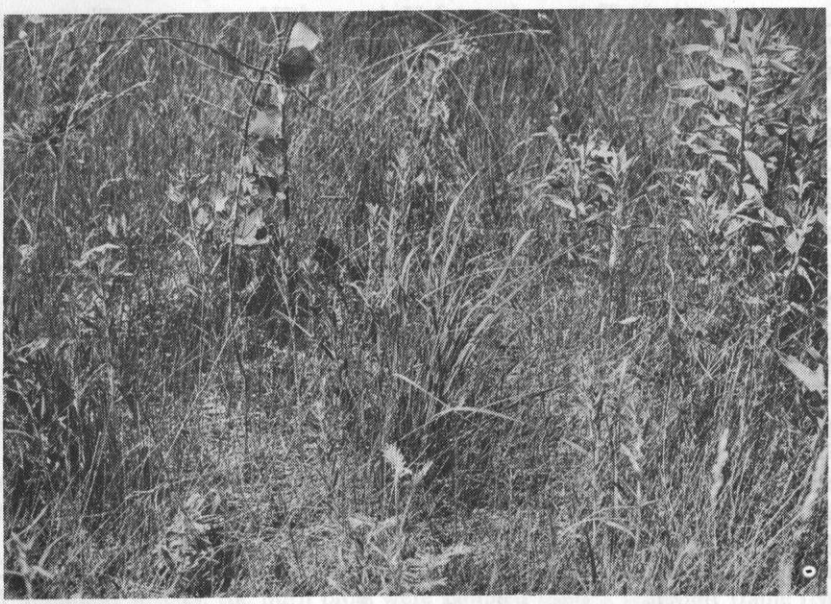

Fig. 2. Unburned prairie. Note clump of big bluestem in center weakened by accumulation of bluegrass litter. To left of bluestem is newly established cottonwood (*Populus deltoides*) seedling. July 5, 1974.

Fig. 3. Prairie after 3 spring burns. Note vigorous clumps of big and little bluestem with top-killed aspen sucker shoots in center. Needlegrass (*Stipa spartea*) is shown flowering in left-center of photo. July 5, 1974.

but the data do not indicate any overall change in its cover. After spring burning in central Wisconsin, Zedler and Loucks (1969) noted a dramatic increase in the flowering of bluegrass in mesic depressions and a negative effect only on nearby dry ridges. Little bluestem, also present in their study area, was stimulated only in the mesic depressions while no change in standing crop was observed on the dry ridges, which emphasizes the importance of local site conditions in accounting for differing responses of species to burning.

DISCUSSION

Although the duration and intensity of the study are not sufficient at this point to be conclusive, some trends seem apparent. Spring burning is useful in maintaining prairie in the aspen parkland region by the control of woody vegetation. The parkland character - with scattered aspen groves throughout prairie - may be preserved by burning at a time when the moisture content of the fuel is higher in the forest than the prairie so that the fire does not burn much beyond the ecotone. Most of the burning carried out by the authors did not carry into the adjacent aspen stand.

Spring burning is also beneficial in rejuvenating certain prairie species such as big bluestem and purple prairie clover (*Petalostemum purpureum*) in grazed prairies dominated by bluegrass. This rejuvenation not only increases the aesthetic appeal but adds to overall wildlife values as well. Kirsch and Kruse (1972) noted that one year following spring burning, grasslands in their North Dakota study area had a greater variety of upland nesting birds with a higher percentage of nesting success than an unburned grassland in comparable setting. Whitetail deer (*Odocoileus virginianus*) fawns were also more abundant on the burned grasslands.

Degraded prairie vegetation in conjunction with brush invasion is associated with population declines of the greater prairie chicken (*Typanuchus cupido pinnatus*) particularly in the northern and eastern segments of its range (Kirsch, 1974). In Minnesota, the range of the prairie chicken is restricted to the northwestern part of the State in which both trembling aspen and willow (*Salix* spp.) are capable of invading prairies. Kirsch (1973) recommends burning at intervals of three to five years for chicken habitat management but more frequent burning may be in order in situations where brush has become trees and requires setting back to an earlier successional stage. Hamerstrom (1973) suggests that 15% brush, 85% grassland is perhaps near optimum for prairie chicken habitat in Wisconsin and that the same is probably true for Minnesota. However, throughout much of the present chicken range in Minnesota the proportion of brush (mainly trembling aspen) is considerably higher than 15% of the habitat and is in need of intensive management to secure the remnant flocks of this rare species in the State.

The use of fire in the management of prairie species and in brush control also has implications for range management in northwestern Minnesota. However, the occurrence of fire in this region is frequently viewed by the general public as a totally destructive force as evidenced by a newspaper account of spring prairie fires in early April of 1973. It was "estimated that fires had damaged grassland for approximately 10 miles long and about as wide in the Mentor area" and one rancher reportedly "lost more than 3,200 acres of grass" (Anon., 1973). The grassland referred to was primarily bluestem prairie with scattered clumps of brush. Later observations of the area by the senior author indicated up to 50% top-kill of the aspen and willow which greatly stimulated the growth of herbaceous forage as well as aspen regrowth within the reach of livestock and deer. Smith (1972) points out, "aspen itself is palatable to big game and livestock and provides considerable forage". Improvements in the quality of grass resulting from the burns were also likely as the protein and ash content of little bluestem has been reported to increase significantly due to burning (Neal and Becker, 1933; Greene, 1935; Smith and Young, 1959).

Wright (1974) notes the importance of the amount of fuel, fuel moisture, wind velocity, soil moisture stress and other factors in predicting what the effects of fire are in terms of meeting range management objectives. In practical range management, can a rancher afford to defer grazing long enough for an adequate fuel supply to accumulate? Would the use of herbicides for brush control be less expensive? These are management decisions that have to be made on a specific situation basis.

Although this study is of a preliminary and exploratory nature, our results would indicate that in some areas of northwest Minnesota, fire is an effective control of aspen encroachment of prairie and is a useful tool in rejuvenating grazed prairies for livestock use, wildlife habitat, and human enjoyment.

ABSTRACT

Prairies occurring in regions receiving sufficient rainfall to support tree growth usually require periodic disturbances such as fire, grazing or mowing to retard the invasion of woody species. This paper presents the results of a study in northwest Minnesota using annual spring burning as an effective technique in retarding trembling aspen (*Populus tremuloides*) sucker shoot growth in prairie and in favoring the growth of warm season native grasses over introduced cool season grasses, especially Kentucky bluegrass (*Poa pratensis*). Many tracts of prairie in the "aspen-parkland" region of northwest Minnesota are degrading due to lack of appropriate management which is resulting in diminished habitat for prairie plants and wildlife species, notably the greater prairie chicken. Management problems and opportunities are discussed.

KEY WORDS

Prairie management, spring burning, aspen, aspen parkland, bluegrass, big bluestem, northwest Minnesota.

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BURNING A PROTECTED TALLGRASS PRAIRIE TO SUPPRESS SWEETCLOVER, *MELILOTUS ALBA* DESR.

Mark E. Heitlinger

INTRODUCTION

The tract known as Schaefer Prairie was mowed annually for hay from about 1880 until shortly before 1967, when it was purchased by the Minnesota Chapter of The Nature Conservancy. Burning was included in the management plan of the unplowed portion of this land because fire had been present in this vicinity for the past 10,000 years (Waddington, 1969), and it is considered by most authorities to be an integral part of grassland ecology and thus prairie preserve management (Curtis, 1959; Smiley, 1961; Christianson, 1972; Richards, 1972; Ownsby and Smith, 1973; and Lawrence, 1974). The first prescribed burn, however, produced an unexpected and undesirable result. In the years following a spring 1969 burn, dense stands of the Eurasian plant white sweetclover occurred over much of the upland. Mature sweetclover overtopped native vegetation, competing for available light, moisture, and nutrients. Its presence detracted from the visual quality of native prairie. The sweetclover was mowed 16 July 1971 to prevent the production of new seed.

This paper is a report of research to determine the relationship between sweetclover and fire, and to test several strategies for controlling sweetclover through prescribed burning, the technique most compatible with natural area preservation.

SWEETCLOVER

Members of the genus *Melilotus* are legumes, all native to the Old World. The two most common in the United States today are the biennial white, *M. alba*, referred to in this paper as sweetclover, and the biennial yellow, *M. officinalis*. The latter differs from the former only slightly in morphology and life cycle, being somewhat smaller, earlier to flower, and more xeric (Coe, 1917; Martin, 1934). In rare instances sweetclover may be encountered that flowers the first year of growth, but this is a rare exception to the general condition of flowering the second year only (Martin and Leonard, 1949; T. Stevenson, 1937; G. Stevenson, 1969).

Sweetclover spread to the New World by 1739. Its dispersion was hastened by beekeepers and agriculturalists, though it pioneers readily on disturbed soil in many cases. By 1911 it could be found thriving in waste areas throughout Minnesota (Lloyd, 1912). It was actively promoted after about 1915 as a forage crop and soil builder, reaching its peak acreage during the drought years of the 1930's. Sweetclover is sometimes used to stabilize fresh road cuts, and this may be the major source of its migration onto natural areas today. Sweetclover evidently spread onto Schaefer Prairie following work on adjacent roads in the 1950's.

METHOD

The data in Table 1 were collected from study areas A, B, and C, each of which is 0.5 ha and located within a different management unit at Schaefer Prairie. Each study area has the

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same soil (Clarion loam), elevation, and slope aspect. Each had received the same management treatment prior to 1973, including a spring burn in 1969 and mowing on 16 July 1971 (Fig. 1). Area A is part of a section burned 1 May 1974, area B has not been burned since 1969, and area C was burned 21 April 1973 (Figs. 1 and 2).

Data were obtained by randomly tossing a hoop and counting the sweetclover individuals inside to determine average densities. On 5 September 1974, first year sweetclover densities were determined by tossing a 0.5 m^2 hoop 40 times in area A and 40 times in area B. On 8 July 1974 a 2.0 m^2 hoop was tossed 20 times in each of the study areas, A, B, and C, to determine densities of the second year sweetclover plants. Identification of young plants was aided by Anna Krummer's Weed Seedlings (1951).

SWEETCLOVER AND FIRE

Several hypotheses about the relationship between sweetclover and fire were tested on the native grassland of Schaefer Prairie.

1) A spring fire about early May increases the number of first year sweetclover following the burn.

The few references to fire in the sweetclover literature all indicate that burning aids in the establishment of sweetclover on grassland (Graber, 1927, 1928; Anon., 1930; Crosby, 1933). Whether this is due to increased germination, better conditions for seedling survival, decrease in competition pressure, or some combination remains unclear.

As much as 99 per cent of sweetclover seed may be covered with a hard, impermeable shell that permits it to remain dormant in the soil for years to decades (T. Stevenson, 1937; Stevens, 1943). Fluctuating temperatures due to freezing and thawing are said to weaken the shell of "hard" seed (Cleavinger and Willoughby, 1955; Stewart and Gross, 1932). The heat from a prairie fire may similarly break down the outer shell, and increase the amount of seed that is capable of germination the spring and summer after the fire. It is also possible that fire aids seedling survival by increasing available phosphorus, a nutrient released after grassland fires and one often limiting sweetclover growth (Thomas et al., 1952). Decreasing the competition from cool season plants, especially Kentucky bluegrass (*Poa pratensis*), may also be important.

Data from Schaefer Prairie (Table 1) show that study area A supported first year sweetclover at densities more than four times greater than in area B. This is attributed to the fact that area A was burned 1 May 1974, a few months before sampling, and area B had not been burned since 1969 (Figs. 1 and 2).

The densities of first year sweetclover recorded for area A in Table 1 might have been considerably higher were it not for a drought that occurred in this region in June and July 1974. Since area C had 6.5 second year sweetclover individuals in 1974 it must have had at least this number and probably more the months following the spring 1973 burn. The large number of second year plants in area C further substantiates the positive effect of a spring burn on first year sweetclover.

2) A spring fire about early May decreases the number of second year sweetclover following the burn.

A fire can damage the tissues of sweetclover plants that are capable of growth. Above ground growth of young second year sweetclover plants begins with the enlargement of crown buds, located at the summit of the root. Only in spring of the second year can a crown bud develop into a stem. In this sense sweetclover differs from alfalfa which can produce new stems from crown buds during most of the growth season (Stewart and Gross, 1932). If crown buds are damaged by a spring fire, sweetclover plants will not be able to send up stems and complete their life cycle.

Once the crown buds have expanded, sweetclover growth originates from the tips of the branches, and possibly from buds in the branch axils (Martin and Leonard, 1949). There can be no additional top growth once the stems are severed beneath the axil of the lowest lateral branch (Fig. 3). Burning injures sweetclover stems at the base or removes the top much lower than could be accomplished with a mower.

Study area A, within the unit burned 1 May 1974 (Fig. 2), was found to be virtually free of second year sweetclover in July 1974 (Table 1). By 1 May young second year sweetclover stems were 5-15 cm high, though many sweetclover plants may have still been in the bud stage. The fire was probably critical because of its affect on crown buds, though the close removal of young stems may have been a factor.

On a few low, wet spots outside the study area, considerable numbers of second year sweetclover did survive the 1 May burn. The development of these plants may have lagged behind those on more elevated sites, and it is possible that a combination of being in a less mature stage and being insulated somewhat by the moist soil and litter allowed these plants to survive the 1 May fire. Those who wish to suppress sweetclover should be aware that a burn in early May may not be as effective on low or poorly drained ground. If possible, delay the fire until young second year plants have begun shoot growth on even the wetter sites at which they may occur.

3) A summer fire about early July decreases the number of both first and second year sweetclover following the burn.

Study area C and much of the section burned 21 April 1973 supported dense stands of sweetclover in the flowering stage in 1974 (Table 1). First year sweetclover plants were numerous in the area but difficult to sample early in July because of their small size. Prairie with sweetclover in it was burned in July (Fig. 2). Inspection on 5 September revealed that sweetclover scorched by the July fires had not recovered. New sweetclover germination or resprouting was not observed. Sweetclover survived only on those few spots where fresh gopher mounds had shielded vegetation from the flames.

The July fires crept close to the ground, fueled by litter that had accumulated since the previous burn on 21 April 1973 (Fig. 1). Weak stems and low foliage were consumed by fire, producing dense, pungent smoke. Stouter stems, including those of second year sweetclover, remained standing after the fire. These plants were apparently killed by the heat of the fire at the base of their main stems.

Perennial herbs and grasses quickly recovered. Many that had flowered already flowered a second time after the July burns. Among this group were butterfly weed (*Asclepias tuberosa*), northern bedstraw (*Galium boreale*), stiff tickseed (*Coreopsis palmata*), purple prairie clover (*Petalostemum purpureum*), prairie rose (*Rosa blanda*), and even the pasque flower (*Anemone patens*). At Schaefer Prairie, the usual practice was to mow hay on the uplands the second or third week of July. The ability of many prairie remnants to survive decades of annual mowing suggests that they should be able to tolerate a few years of summer burns.

I was somewhat surprised at the ease of burning prairie in July. Our success may have been due in part to the drought mentioned earlier, though one of the July burns was conducted less than 24 hours after a rain shower that soaked the mulch. The dense smoke from these burns produced a definite hazard on the roads adjacent to the prairie, and was troublesome to the crew managing the fire.

4) An early fall burn between the first and second years of sweetclover growth will increase winter mortality and decrease vitality of second year plants (untested).

In Ohio, Willard (1927b) found that 75 per cent of first year sweetclover plants clipped September 9 died over the winter, compared to 5 per cent winter kill among plants not clipped. Mortality of clipped plants continued to be high, approaching 100 per cent by mid summer. Martin (1934) reports similar results from Iowa.

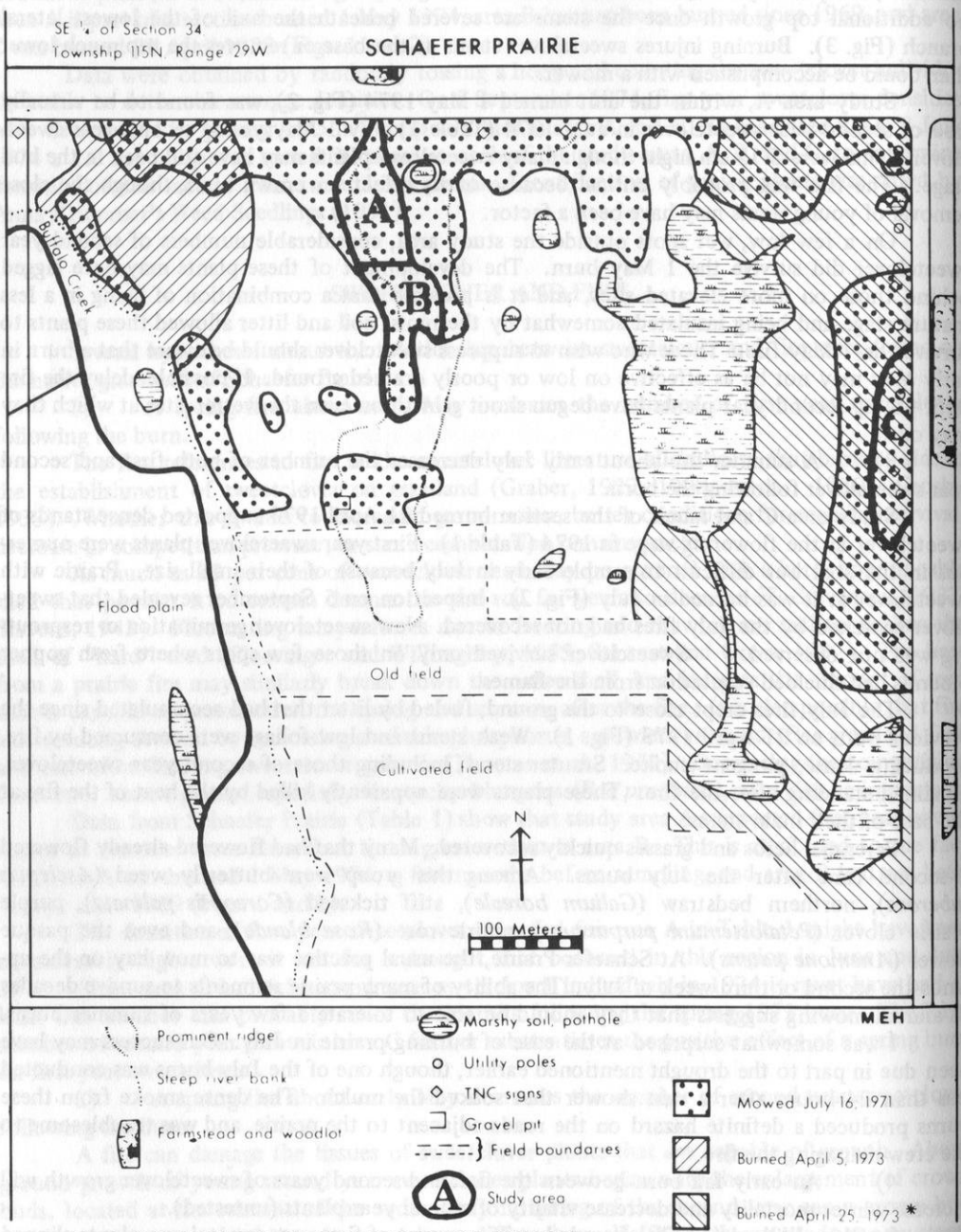

Fig. 1 MANAGEMENT OF SCHAEFER PRAIRIE, 1971-1973

* should read 21 April 1973.

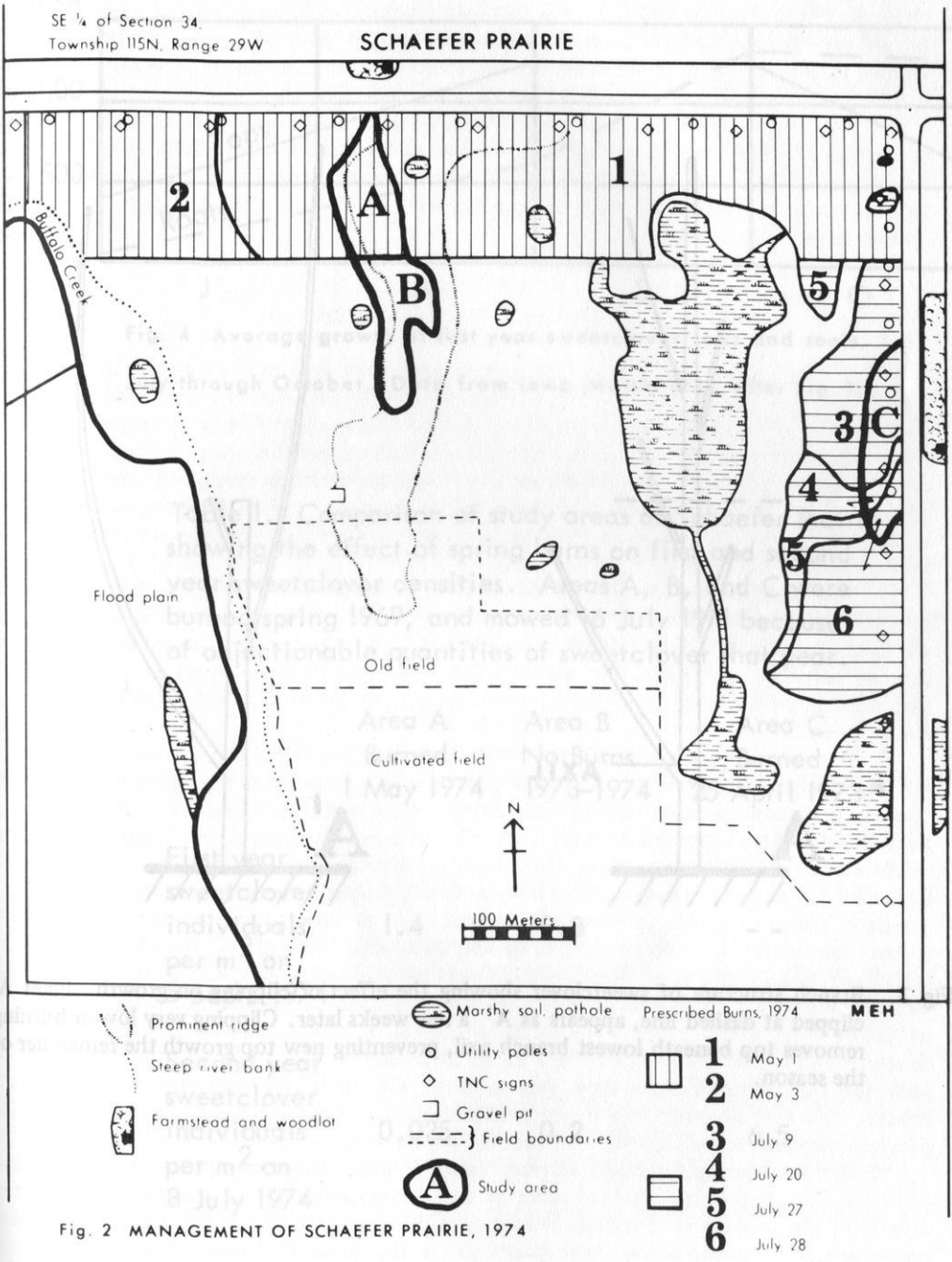

Fig. 2 MANAGEMENT OF SCHAEFER PRAIRIE, 1974

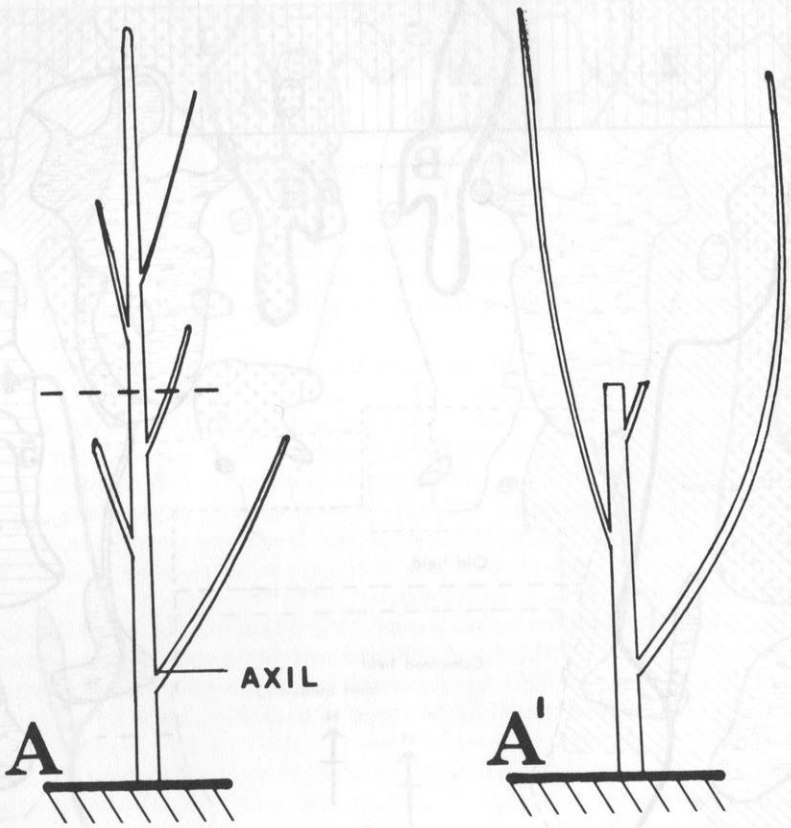

Fig. 3. Branch structure of sweetclover showing the effect of clipping on growth. Plant A, clipped at dashed line, appears as A' a few weeks later. Clipping very low or burning removes top beneath lowest branch axil, preventing new top growth the remainder of the season.

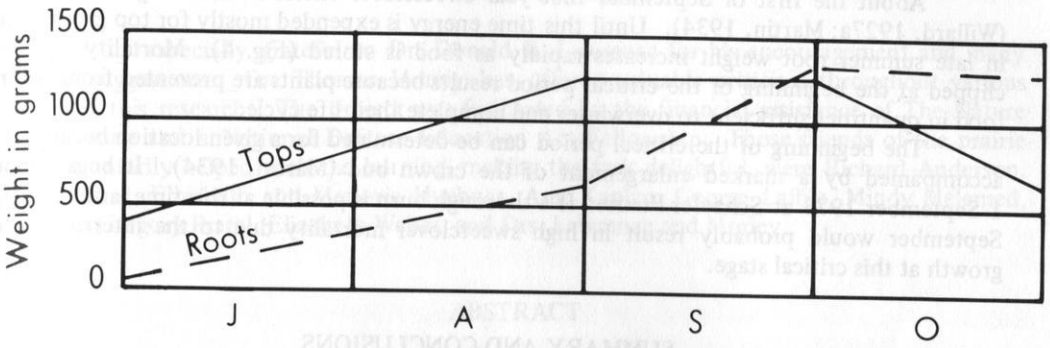

Fig. 4 Average growth of first year sweetclover tops and roots, July through October. Data from Iowa (Martin 1934, after Fig. 1).

Table 1. Comparison of study areas at Schaefer Prairie showing the effect of spring burns on first and second year sweetclover densities. Areas A, B, and C were burned spring 1969, and mowed 16 July 1971 because of objectionable quantities of sweetclover that year.

	Area A Burned 1 May 1974	Area B No Burns 1973-1974	Area C Burned 25 April 1973*
First year sweetclover individuals per m^2 on 5 Sept. 1974	1.4	0.3	- -
Second year sweetclover individuals per m^2 on 8 July 1974	0.025	0.2	6.5

* should read 21 April 1973.

About the first of September first year sweetclover enters a "critical growth period" (Willard, 1927a; Martin, 1934). Until this time energy is expended mostly for top growth, but in late summer root weight increases rapidly as food is stored (Fig. 4). Mortality in plants clipped at the beginning of the critical period results because plants are prevented from storing food in quantities sufficient to overwinter and complete their life cycle.

The beginning of the critical period can be determined for a given location because it is accompanied by a marked enlargement of the crown bud (Martin, 1934). It began about 1 September 1973 at Schaefer Prairie. If a thorough burn is possible at this time, a fire in early September would probably result in high sweetclover mortality due to the interruption of growth at this critical stage.

SUMMARY AND CONCLUSIONS

The results of this study indicate that sweetclover suppression on native prairie is possible through any one of the following strategies: burning annually about early May once second year shoots are clearly visible; burning every second year in early July before second year plants ripen seed; and possibly by burning annually in early September near the beginning of the critical growth period. Each procedure should reduce seed reserves in the soil while largely preventing the addition of new seed. Any second year sweetclover surviving a treatment must be hand pulled or clipped right at the base before it can produce seed, since a single large plant may yield 350,000 seeds (Coe, 1917, 1920).

The earliest date after which sweetclover germination is either not possible or cannot produce a viable plant remains to be discovered. It might be several weeks earlier than 8 July, the date of a fire at Schaefer Prairie after which no new sweetclover germination was observed. A burn between this critical but undetermined date and the time sweetclover produces seed would be an effective control for two years, since it would destroy both first and second year sweetclover.

Prescribed burns to suppress sweetclover will surely affect other plants and animals as well. The question worth careful consideration is whether the act of suppressing an undesirable species may produce more damage than its continued presence? There are two ways to possibly minimize the undesirable impact from a suppression management program. One is to divide the tract into several management units so that all stands of a community type are not subjected to the same management treatment in a given year. A second approach is to alter the timing of management burns from year to year. For example, a five year program to suppress sweetclover could be: year 1 - burn early May after second year growth begins; year 2 - burn early July, before seed is produced; year 3 - no burn necessary; year 4 - burn about early June; year 5 - probably no burn necessary, but if second year plants are present burn about early July or before they produce seed. The safest method is to both divide the tract into ecologically similar management units employing a different prescribed fire schedule on each, and for each unit alter the timing of burns from year to year. This is the approach being taken at Schaefer Prairie. It is also advisable to attempt to determine negative effects arising from a management program through monitoring plant and animal populations.

It should be emphasized that many generalizations have been made based on inferences from the literature and only two years of fire experimentation on a single prairie. Several aspects of the sweetclover life cycle need more study, particularly the affect of fire on seed germination and on young second year plants still in the crown bud stage. The ecological consequences of various management programs should be carefully studied.

ACKNOWLEDGEMENTS

I am especially grateful to Dr. Donald B. Lawrence for his encouragement and many helpful suggestions. Dr. Thomas Morely has offered valuable criticism throughout various stages of this research. The project was facilitated by the financial assistance of The Nature Conservancy and a National Defense Education Act Fellowship. Those friends of the prairie who voluntarily helped with the burning, making the task delightful, were Richard Anderson, Sid Howard, Elizabeth and Marjorie Huebner, Ann Kaplan, George Laible, Mindy Melemed, Eric and Gregory Praml, Elizabeth Weber, and Drs. Lawrence and Morley.

ABSTRACT

At Schaefer Prairie in southcentral Minnesota, control of the Eurasian biennial white sweetclover (*Melilotus alba*) has been a major management concern. The height and abundance of this plant detract from the esthetic and ecological quality of what is otherwise an exceptional prairie remnant. Field studies support the hypotheses that (1) a spring fire about early May increases the number of first year sweetclover following the burn, (2) a spring fire about early May decreases the number of second year sweetclover following the burn, and (3) a summer fire about early July decreases the number of both first and second year sweetclover following the burn. New sweetclover germination or resprouting were not observed in the weeks after the July burn. With very rare exception, only second year individuals of this species flower and produce seed. The regular application of prescribed burns either every year in spring after second year growth is under way, or every second year shortly before seed is produced, should largely prevent the addition of new sweetclover seed and reduce existing seed reserves.

KEY WORDS

Melilotus alba Desr., sweetclover, natural area, prairie management, fire, weed control, prescribed burning, tallgrass prairie, Minnesota, grassland management.

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SEASONAL VARIATION IN BODY COMPOSITION OF THE MEADOW VOLE (*MICROTUS PENNSYLVANICUS*)

Stuart L. Iverson and Brian N. Turner

INTRODUCTION

The observation that many northern small mammals have a definite annual cycle in weight, involving a fall and winter weight loss and a pre-reproductive weight gain, is well documented (Iverson and Turner, 1974; Brown, 1973; Whitney, 1973; Fuller, Stebbins and Dyke, 1969; Mezhzherin, 1964). It has been suggested that the adaptive advantage of being small in the winter is a lesser individual food requirement (Mezhzherin, 1964; Fuller, Stebbins and Dyke, 1969). It does not appear that a food shortage in the fall causes the decrease in weight, but rather that weight decreases as a preparation for the winter (Iverson and Turner, 1974). The adaptive significance of this preparation may be the ability to forestall or survive a late winter food shortage, or to decrease exposure to predators or inclement conditions by minimizing winter foraging time. Considering the relatively large loss in body mass of some of the voles (Iverson and Turner, 1974), and its apparently well controlled, adaptive character, it is of interest to determine which body components contribute to the weight changes. This investigation therefore describes an annual weight cycle in terms of body composition, with the purpose of demonstrating the difference between the summer and winter states, and identifying which body components change.

METHODS

Voles were trapped in a previously described old-field (Turner, Iverson and Walley, 1972) at Atomic Energy of Canada's Whiteshell Nuclear Research Establishment at Pinawa in southeastern Manitoba. Trapping methods follow Iverson and Turner (1974). Whenever possible, five males and five females were randomly selected from the day's capture. The animals were individually killed with ether, and total length, tail length, hind foot length, and ear length were measured. An incision was made in the ventrum of the animal, and the length and position of the testes, or presence of embryos or placental scars, was noted. The stomach was excised, washed clean of its contents, blotted and returned to the body cavity. The animal was weighed to the nearest 0.001 g, wrapped in plastic and frozen until the end of the collection period when all the tissue analyses were done. The maximum time between death and weighing of the animal was 5 minutes, and care was taken during autopsy to minimize loss of body fluids.

When all samples had been collected, the animals were dried to constant weight at 95C, to determine water content. Ether-extractable lipid (fat) was determined by ether extraction of the dried specimen in a Soxhlet apparatus for 16 hours. Nitrogen content was determined by the Kjelhdahl method, and the nitrogen value was multiplied by 6.25 to give protein content. All analytical techniques employed were those of the Association of Official Agricultural Chemists (1960).

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RESULTS

Total length varied both with season, longer animals being present in the summer, and over the course of the study, longer animals being present during the second winter (Fig. 1). Only the August sample showed a significant difference in length between the sexes, with the males being shorter in that month. Live weight showed variation similar to that of length, but the differences in live weights between the two winters were not as great as the difference in lengths (Fig. 2). Males were significantly heavier than females in February, June and July. Lean dry body mass showed variation similar to live weight, although the only significant differences between sexes were in June and July (Fig. 3). Water as a per cent of lean dry body mass was significantly higher in females from May through September, and appeared to be generally higher in both sexes in the summer than in the winter (Fig. 4). Protein as a per cent of lean dry body mass did not show any clear annual variation (Fig. 5), but males had significantly higher percentages in February and December 1969, and January 1970. There was also a suggestion that protein content was higher in the second winter than in the first. Fat as a per cent of lean dry body mass tended to increase during the course of the study, with the only significant differences being higher percentages in the females in May and June (Fig. 6).

Since significant differences were present between males and females, further analyses were done with the sexes separate. Samples were divided into two groups, summer (April through September) and winter, and weights of the different body components examined by covariance analysis. Correlation analyses were also performed using the same season and sex groupings.

When the variation attributable to length was removed by covariance analysis, both males and females had significantly greater lean dry body masses in the summer than in the winter (Table 1). Both sexes also had significantly greater masses of water, protein, and residue in the summer than in the winter. Males had significantly more fat in the winter, while females had more in the summer. With lean dry body mass as the covariate, both sexes had significantly greater amounts of water in the summer than in the winter (Table 1). Males had a significantly greater amount of fat in the winter, but the seasonal difference in the amount of fat in the females was not significant, nor were differences in amounts of protein or residue in either sex.

The correlations between length, or lean dry body mass, and the body components were significant in all but one of the tests (Table 2). The relationship between length and lean dry body mass explained more of the variation in the data in the summer than it did in the winter. This was also true of the relationship between length and residue, and lean dry body mass and residue. The variation in the amount of fat was poorly explained by either length or lean dry body mass except in winter males, in which case the relationship between length and fat explained 0.55 of the variation.

DISCUSSION

A difficulty encountered with this type of study is that although body weight can be measured repeatedly, and a fall and winter weight loss documented in a free ranging animal (Iverson and Turner, 1974), the body composition of an animal can only be estimated once. This study therefore relied on taking a representative sample from the population each month for analysis. Since the age structure of the population, and therefore of the sample, varied from month to month, the weights of various body components were affected by changes in age, and did not accurately reflect changes within individuals.

Mezhzherin (1964) reported that some shrews in northern USSR apparently decrease in length during the winter, but Brown (1973) presents data which indicate that in Minnesota,

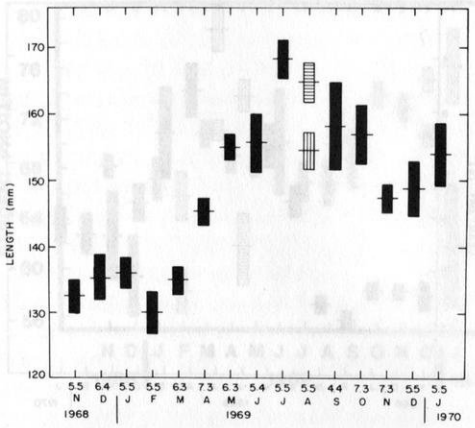

Fig. 1. Total length ($\bar{x} \pm$ S.E.) of monthly *M. pennsylvanicus* samples. Sexes (numbers of males - females shown) were t-tested within each month, and where significantly different ($p < 0.05$) are plotted separately (males: vertical hatch; females: horizontal hatch).

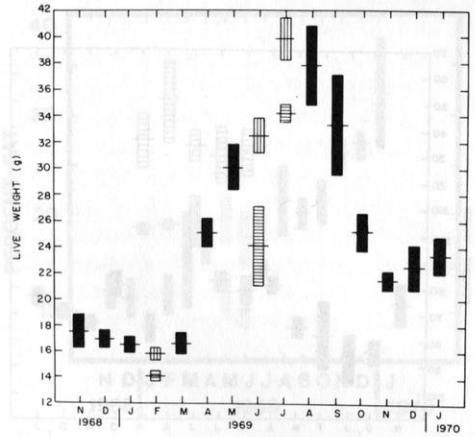

Fig. 2. Live weight ($\bar{x} \pm$ S.E.) of *M. pennsylvanicus*. Males are shown (vertical hatch) where significantly different from females (horizontal hatch) (t-test, $p < 0.05$). Sample sizes as in Figure 1.

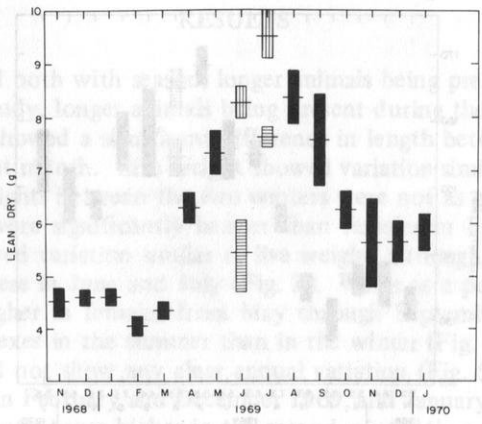

Fig. 3. Lean dry weight ($\bar{x} \pm$ S.E.) of *M. pennsylvanicus*. Males are shown (vertical hatch) where significantly different from females (horizontal hatch) (t-test, $p < 0.05$). Sample sizes as in Figure 1.

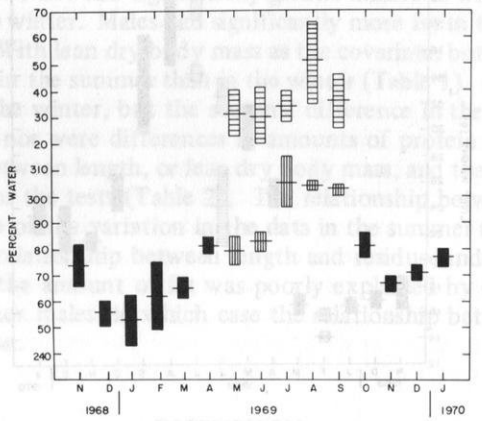

Fig. 4. Water ($\bar{x} \pm$ S.E.) as a percent of lean dry weight. Males are shown (vertical hatch) where significantly different from females (horizontal hatch) (t-test, $p < 0.05$). Sample sizes as in Figure 1.

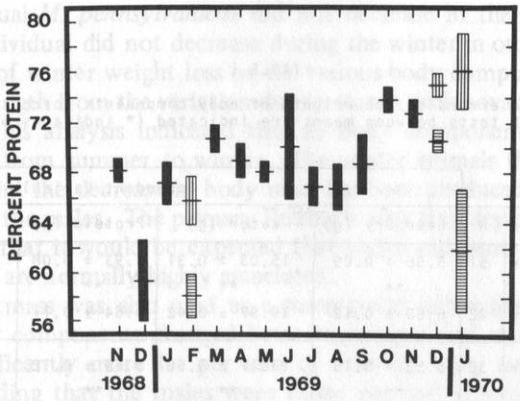

Fig. 5. Protein ($\bar{x} \pm$ S.E.) as a percent of lean dry weight. Males are shown (vertical hatch) where significantly different from females (horizontal hatch) (t-test, $p < 0.05$). Sample sizes as in Figure 1.

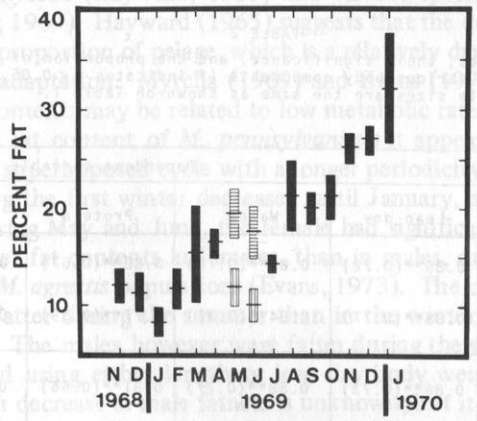

Fig. 6. Fat ($\bar{x} \pm$ S.E.) as a percent of lean dry weight. Males are shown (vertical hatch) where significantly different from females (horizontal hatch) (t-test, $p < 0.05$). Sample sizes as in Figure 1.

TABLE 1

Means and standard errors of the weights of body components corrected by covariance. The significance of F tests between means are indicated (* indicates $p \leq 0.05$, ** $p \leq 0.01$).

				Dependent Variable				
Covariate	Sex	Season	N	Lean Dry (g)	Water (g)	Protein (g)	Fat (g)	Residue (g)
Length	Male	winter	51	5.56 ± 0.09	15.03 ± 0.31	3.93 ± 0.08	1.12 ± 0.06	1.63 ± 0.07
				**	**	**	**	**
		summer	32	6.89 ± 0.12	19.97 ± 0.42	4.64 ± 0.11	0.81 ± 0.08	2.25 ± 0.09
	Female	winter	38	5.52 ± 0.15	15.17 ± 0.60	3.69 ± 0.12	0.93 ± 0.10	1.77 ± 0.11
				**	**	**	*	*
		summer	24	6.51 ± 0.19	21.67 ± 0.77	4.41 ± 0.15	1.29 ± 0.13	2.14 ± 0.14
Lean dry	Male	winter	51		16.58 ± 0.18	4.27 ± 0.07	1.18 ± 0.07	1.80 ± 0.07
					*		**	
		summer	32		17.49 ± 0.25	4.10 ± 0.10	0.71 ± 0.10	1.98 ± 0.10
	Female	winter	38		16.48 ± 0.30	3.93 ± 0.09	1.01 ± 0.10	1.86 ± 0.11
					**			
		summer	24		19.59 ± 0.39	4.02 ± 0.11	1.16 ± 0.13	2.00 ± 0.14

TABLE 2

Correlation coefficients, their significance, and the proportion of the variation explained (r^2) for the various body components (* indicates $p \leq 0.05$, ** $p \leq 0.01$). Sample sizes are the same as shown on Table 1.

			Dependent Variable				
Independent Variable	Sex	Season	Lean dry	Water	Protein	Fat	Residue
Length	Male	winter	0.85**(0.72)	0.85**(0.72)	0.82**(0.67)	0.74**(0.55)	0.31*(0.10)
		summer	0.88**(0.77)	0.84**(0.71)	0.77**(0.59)	0.40*(0.16)	0.64**(0.41)
	Female	winter	0.86**(0.73)	0.88**(0.77)	0.81**(0.66)	0.44**(0.19)	0.31*(0.10)
		summer	0.91**(0.83)	0.86*(0.73)	0.87**(0.76)	0.44*(0.19)	0.64**(0.41)
Lean dry	Male	winter		0.96**(0.92)	0.91**(0.83)	0.66*(0.44)	0.49**(0.24)
		summer		0.96**(0.92)	0.88**(0.77)	0.45**(0.20)	0.70**(0.49)
	Female	winter		0.96**(0.92)	0.89**(0.79)	0.44**(0.19)	0.21 (0.04)
		summer		0.97**(0.94)	0.92**(0.85)	0.60**(0.36)	0.78**(0.61)

body length of individual *M. pennsylvanicus* did not decrease in the winter. Assuming that total length in each individual did not decrease during the winter in our population, it is possible to find the effects of winter weight loss on the various body components by separating the variation due to body length from the variation due to season with covariance analysis.

The results of this analysis indicated that all body components, except fat in males, decreased significantly from summer to winter. The winter animals therefore have less body mass per unit length, and the decrease in body mass has been produced by a loss in all components, except for fat in the males. The primary finding is that lean dry body mass decreases per unit length, and from that it would be expected that water and protein would also decrease, since these components are normally highly associated.

Lean dry body mass was also used as a covariate to determine if the relationship between the various body components changed between summer and winter. It was found that winter males had significantly more fat per unit of lean dry body mass than summer males. This reinforces the finding that the males were fatter per unit length. The other significant result of this analysis was that both males and females contained less water, per gram of lean dry body mass, in the winter than in the summer.

The variation in water content in *M. pennsylvanicus* observed in this study is similar to that reported by Evans (1973) in *Microtus agrestis*. She found significantly higher water contents in females than in males during the reproductive season, and suggested that the high water content was associated with lactation. The results of the present study indicate that females have significantly elevated water contents during all but the first month of the reproductive season. Both sexes show significantly decreased water content in the winter. A similar decrease has been reported in *M. agrestis* (Evans, 1973), *Clethrionomys rutilus* and *Microtus oeconomus* (Whitney, 1973), *Peromyscus* (Hayward, 1965) and various species of shrews (Pucek, 1965; Gorecki, 1965; Myrcha, 1969). Hayward (1965) suggests that the decreased water content may be due to an increased proportion of pelage, which is a relatively dry tissue, while Pucek (1965) suggests it is a winter adaptation. Myrcha (1969) and Evans (1973) refer to work indicating that low winter water contents may be related to low metabolic rates.

Considering the fat content of *M. pennsylvanicus* it appears that there is not only an annual cycle but also a superimposed cycle with a longer periodicity. The per cent of fat in the samples collected during the first winter decreased until January, and then increased until the onset of breeding. During May and June, the female had significantly greater amounts of fat than the males. Greater fat contents in females, than in males, during the breeding season is also a characteristic of *M. agrestis* populations (Evans, 1973). The covariance analysis indicated that the females were fatter during the summer than in the winter, which is also similar to *M. agrestis* (Evans, 1973). The males however were fatter during the winter than they were in the summer, when analyzed using either length or lean dry body weight as a covariate. The significance of the summer decrease in male fatness is unknown, but it may be related to increased intermale aggression at the time (Turner and Iverson, 1973). The observed increase in fat during the second winter of the study, as well as greater lengths, live weights and fat free dry weights, indicates that a fluctuation with a period greater than a year was observed. The under-snow temperature in the second November to January period was lower (Iverson and Turner, 1974) showing that the larger size was not entirely due to a more favorable energy balance. The density of animals on the grid (Turner and Iverson, 1973) approximately doubled during this period, and the larger size of the animals may be related to high population densities, as was found by Keller and Krebs (1970). If a high fat content is found to be characteristic of high population densities, it will be a good indication that energy, or food, is not the factor limiting density.

The decrease in residue is difficult to interpret. Since it was determined by subtraction of the other three body components from the total weight of the animal, it can be considered

to be composed of two components: ash, and error in the other analyses. Unless ash, which is mainly located in the skeleton, was being lost, this component would not be expected to decrease. Since the magnitude of the error component would be proportional to the mass of the component being analyzed, the error component of residue would be expected to decrease in absolute magnitude in the winter. Thus the apparent decrease in residue may be due to a decrease in the magnitude of the errors. Further studies should determine ash by analysis rather than by subtraction.

The body composition data can be interpreted in the context of winter weight loss by comparing the weights of the body components standardized to total length by covariance analysis. In males the total weight decreased from a mean of 27.7 g in the summer to 21.7 in the winter, with a 5.0 g loss in water, a 0.7 g loss in protein, a 0.3 g gain in fat and a 0.6 g loss in residue. The females decreased from 29.5 g to 21.6 g with a 6.5 g loss in water, a 0.7 g loss in protein, a 0.4 g loss in fat and a 0.3 g loss in residue. Stated in this way it is apparent that the major contribution to weight loss was the result of a decrease in body water. This loss in water can be attributed to two factors: 1. the decrease in body mass, and 2. the fact that winter animals contain less water per unit body mass. These factors can be separated by considering the amount of water present per g of lean dry body weight in the summer, and then calculating how much water would be present in the winter if the ratio was the same. When this is done, it is found that in the males 3.6 g of the 5.0 g decrease is due to weight loss, and 1.4 is due to winter dehydration. In the females 3.6 g of the 6.5 g loss is due to weight loss, while 2.8 g is due to winter dehydration. Therefore although the major component decreasing from summer to winter is water, much of the water-loss is associated with a decrease in body mass.

Therefore, the fall and winter decrease in body weight is produced by small losses of protein and residue, and associated body water, plus the loss of water associated with changing to the more dehydrated winter condition. Considering that most of the weight lost is water, it does not appear that the significance of the weight cycle involves metabolism of body mass to fulfill energy requirements, nor does it appear that very large supplies of energy would be necessary in the spring to gain back the lost weight. The results of this investigation reinforce the suggestion that loss of body weight is a controlled adaptive response. They also indicate that changes in the amount of fat are not important in this response in comparison to changes in protein and water. The meadow vole in Manitoba can be thought of as having the ability to alternate on an annual basis between a state of true growth in the spring and summer, and a state of negative growth in the fall and winter.

ABSTRACT

A population of *Microtus pennsylvanicus* in southeastern Manitoba, Canada was sampled monthly for 15 months to study variations in body composition. When corrected for body length, both sexes had significantly greater lean dry body mass, protein, water and residue contents in the summer than in the winter. Males and females showed different patterns of fat content, with the males being fatter in the winter than in the summer, while the females contained more fat in the summer. When corrected for lean dry body mass, both sexes had less water in the winter than in the summer. The previously described fall and winter weight loss in this vole population is produced by losses of protein, residue, and associated water, plus a change to a more dehydrated state in the winter. Changes in fat content play a minor role. Since most of the weight lost is water, it does not appear that the tissue lost is important in filling energy requirements, nor does it appear that large supplies of energy are necessary in the spring to gain back the lost weight. The weights of the animals and of various body components were cycling not only on an annual basis, but also on a longer cycle which may be correlated with population fluctuations.

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ARTHROPOD FOOD CHAIN ENERGETICS IN A MISSOURI TALL GRASS PRAIRIE

N. David Schmidt and C. L. Kucera

INTRODUCTION

Since the classic work of Lindeman (1942), the field of ecology has taken on the additional dimension of function. Prior to that time, the emphasis of most ecological studies was on the description and classification of the natural biotic units of the earth. Since then there has been a thrust toward the discovery of the functional relationships between the organisms within these biotic units (ecosystems).

When the functional relationships (namely energy degradation patterns and mineral cycles) are known for a given ecosystem, the efficiency of that ecosystem can be evaluated. Evans (1967) points out the following two weaknesses in the energy flow-nutrient cycle approach. "--(1) that these phenomena are mediated by the activities of organisms, which are themselves discrete 'packets' of matter and energy, and (2) that these activities differ according to the species of organism, so that the pattern of energy and material distribution depends upon the biotic composition of the ecosystem under consideration. The world of life which we observe and deal with involves the bodies of organisms and their excretory and decay fragments, and these organisms act within the framework of population systems which must be studied from a great many aspects that do not require energy or matter concepts at all." These aspects include changes in population parameters such as numbers, age and sex ratios, and changes in organismal parameters like physiological condition (Schwartz, 1967).

Basically this is a plea to understand ecosystems at the species population level prior to analysis at the ecosystem level. It would be nice to understand a natural ecosystem at an even lower level of organization than the individual organism but the time and instrumentation (where proven field analysis techniques exist) involved plus the lack of analysis facilities and techniques precludes realizing a goal of this nature in the near future. Energy flow and nutrient cycles are two measurable, analyzable properties that all ecosystems share and they provide a basis for the comparison of otherwise quite dissimilar systems. Another important consideration is that if any meaningful predictions are to be made about a particular level of organization, the data on which any predictions are based should be gathered from the same level.

The purpose of this study is to determine and evaluate the energy flow through the arthropod food chain component of a native tall grass prairie ecosystem. This information will add to that already amassed about the University of Missouri Prairie Research Station and will hopefully contribute toward a more thorough understanding of how this and similar ecosystems work.

METHODS AND MATERIALS

The field work in this study was carried out at the University of Missouri Tucker Prairie Research Station approximately 32 km east of Columbia, Missouri. The topography is flat to gently rolling. The soils are deep and typically have a clay pan which makes the A horizon

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poorly drained and water logged in the spring. The soils are placed in the Mexico-Putnam group by Scrivner et al. (1966). The dominant grasses are big bluestem (*Andropogon gerardi*), little bluestem (*A. scoparius*), prairie dropseed (*Sporobolus heterolepis*) and Indian grass (*Sorghastrum natans*). Switch grass (*Panicum virgatum*) and prairie cordgrass (*Spartina pectinata*) form occasional dense stands. The most obvious forbs are members of the Compositae and more specifically members of the genera *Solidago, Eupatorium, Aster* and *Helianthus*. More detailed descriptions of the floristics and plant composition are contained in works of Brown (1962), Kucera (1956) and Koelling (1964). Other studies on the arthropods of the study area include Kopp and Yonke (1970) and Cancelado and Yonke (1969, 1970).

Arthropods were collected by vacuuming them out of hand-thrown traps. They were collected with a D-Vac portable collection device. The trap was constructed from a 15 cm length of 75 cm diameter corrugated steel tube and a net made from organdy with a muslin base. The net tended to stabilize the trap in a horizontal position while it was in the air. After some practice the trap could be thrown some 10 m to capture arthropods with a minimum of disturbance by the sampler. The net was subsequently vacuumed out and the arthropods were killed in a jar containing cotton soaked in ethyl acetate. The samples were transported to the laboratory, dried to constant weight at 70 C and weighed to the nearest 0.1 mg. It was originally planned to weigh each sample individually but due to the small size of many of the organisms the samples were pooled for each collection date to gain more weighing accuracy. Fourteen 0.456 m^2 samples were taken at each sampling time. The first samples were taken May 1, 1970, and five other samples were taken periodically throughout the growing season with the last on October 5.

In September, collection efficiency of the D-Vac was estimated in three heights of vegetation which simulated the resistance to collection the vegetation offered throughout the growing season. The correction factor for collection efficiency was calculated using the formula below:

$$\text{Correction factor} = \frac{\text{Number released in the trap}}{\text{Number recovered with the D-Vac}}$$

Grasshoppers, leafhoppers and spiders were used in the determinations (Table 1).

A computer program was written to calculate community energetics based on arthropod biomass and average weekly air temperature of the study area. The models used are shown in Figure 1. Respiration rate of invertebrates (at constant temperature and pressure) is closely related to the size of the organism. Smalley (1960), Wiegert (1965), Reichle (1968) and Van Hook (1971) have looked at this relationship in terrestrial arthropods. The relationship usually plots as a straight line on a log-log plot and the general formula that describes the relationship best is:

$$Y = aX^b$$

where Y = respiration in $mm^3 O_2/hr$; a = a constant; X = body weight of the organism and b = the slope of the line. The function $5.0X^{0.83}$ was selected for use in this study because it is in close agreement with the literature.

Respiration was calculated as:

$$R = (5.0b_i^{0.83} x 2(\frac{t-20}{10}) x .1152 x n_i)$$

where R = the weekly respiration of the *ith* species or group, b = the average dry weight in mg of members of the *ith* group, 5.0 is a constant mentioned above, $2(\frac{t-20}{10})$ corrects respiration

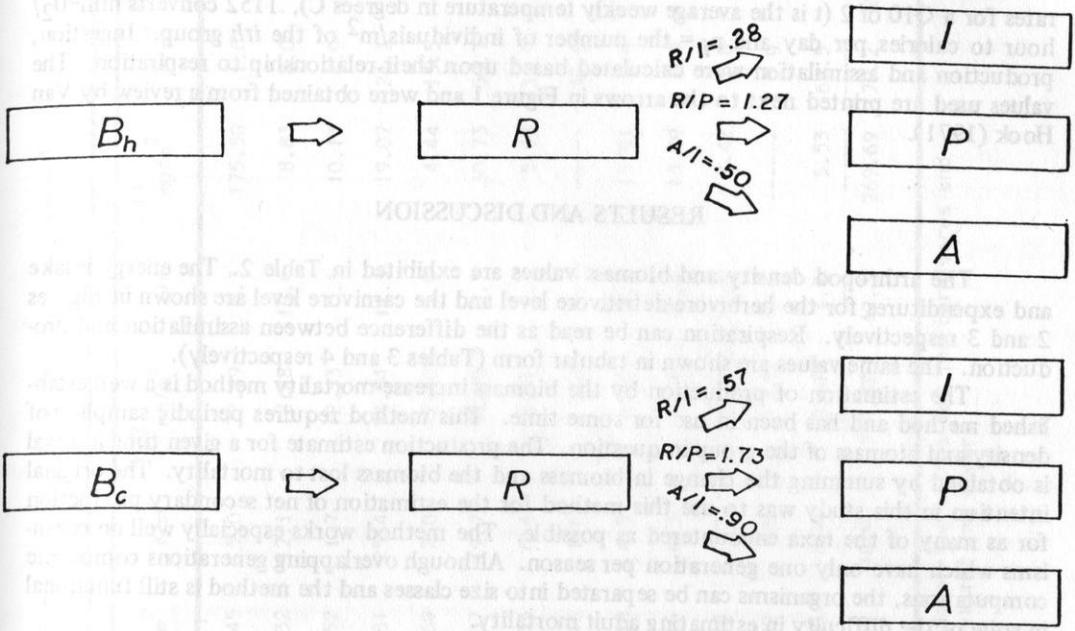

Fig. 1. Mathematical models used to calculate herbivore-detritivore and carnivore energetics. B, R, I, P and A represent average biomass of a group of arthropods, respiration, ingestion, net production or growth, and assimilation respectively. The calculation of respiration hased upon arthropod size and study area temperature is described in the text. The subscripts h and c stand for herbivores and carnivores respectively.

Table 1. Vegetation height versus sampling efficiency[a]

	High	Med	Low
Grasshoppers	.72	.73	.100
Leafhoppers	.68	.77	.100
Spiders	.54	.57	.65
Crawl	.54	.57	.65
Jump Flying	.70	.75	1.00

[a]The number put in was usually 10 but it varied from 8 to 12. The values of the upper rows are the average of these determinations. The bottom two rows are the correction factors used in the study.

rates for a Q10 of 2 (t is the average weekly temperature in degrees C), .1152 converts $mm^3 O_2$/ hour to calories per day and n_i = the number of individuals/m^2 of the *ith* group. Ingestion, production and assimilation were calculated based upon their relationship to respiration. The values used are printed next to the arrows in Figure 1 and were obtained from a review by Van Hook (1971).

RESULTS AND DISCUSSION

The arthropod density and biomass values are exhibited in Table 2. The energy intake and expenditures for the herbivore-detritivore level and the carnivore level are shown in Figures 2 and 3 respectively. Respiration can be read as the difference between assimilation and production. The same values are shown in tabular form (Tables 3 and 4 respectively).

The estimation of production by the biomass increase-mortality method is a well established method and has been in use for some time. This method requires periodic sampling of density and biomass of the group in question. The production estimate for a given time interval is obtained by summing the change in biomass and the biomass lost to mortality. The original intention in this study was to use this method for the estimation of net secondary production for as many of the taxa encountered as possible. The method works especially well on organisms which have only one generation per season. Although overlapping generations complicate computations, the organisms can be separated into size classes and the method is still functional in spite of the difficulty in estimating adult mortality.

The combination of several factors made it necessary to use an alternate method for the total study. It was not possible in most cases to identify immature stages of the insects in the study (there are no keys available in most cases so organisms would have to be reared to maturity for accurate determination). The sample interval was too long to catch the developmental stages of many of the taxa (eg. leafhoppers). The individual samples were too small to contain sufficient numbers for analysis of all but the most common taxa.

Another factor affecting this and other similar studies of relatively mature ecosystems is that of complex life cycles. Many Hymenopterans are flower feeders as adults and are parasitic as larvae. No attempt was made to estimate herbivory by gall inhabiting larvae. Fortunately the most significant herbivore groups in the study (62% of the herbivore ingestion) were in the paurometabolous orders Orthoptera and Homoptera. The ultimate description and analysis of energy flow would have to include detailed studies of all the relatively common species in the tall grass prairie ecosystem.

Immigration is also a factor worthy of note. In the fall of 1970 many redlegged grasshopper adults (*Melanoplus femur-rubrum femur-rubrum*) were observed in the study area but the nymphs had not been that apparent. It is probable that the adult forms moved in from adjacent agricultural areas. This idea was strengthened when grasshoppers were captured for a feeding study in 1971. While the densities of grasshoppers in the study area were quite low, large numbers were collected with ease from a nearby, essentially monospecific stand of the successional species *Setaria faberii*. The *Setaria* stand was in the fencerow of a cornfield across the road from the study area.

Cancelado and Yonke (1970) found significantly more insects (Hemiptera and Homoptera) in the earlier part of the growing season on a portion of the study area which was burned annually. Based upon the marked effect annual burning had upon insect populations of the above two orders it is highly probable that burning also affects the abundance of many other arthropod populations. Burning history probably did not affect this study since the sampling covered numerous burning treatments.

Assumption of too low a Q10 (2.0) to correct for field temperature could be a source of

TABLE 2. 1971 ARTHROPOD DENSITY AND STANDING CROP AT THE VARIOUS SAMPLE TIMES IN THE STUDY[a]

GROUP	5/1 #/m^2	5/1 mg/m^2	6/5 #/m^2	6/5 mg/m^2	6/30 #/m^2	6/30 mg/m^2	7/22 #/m^2	7/22 mg/m^2	8/19 #/m^2	8/19 mg/m^2	10/5 #/m^2	10/5 mg/m^2
ORTHOPTERA	1.0	16.65	8.9	26.95	13.1	43.45	5.0	72.89	4.3	175.50	1.6	75.92
HYMENOPTERA[b]	24.8	10.07	25.0	9.78	38.6	14.32	12.1	12.28	10.6	8.83	8.0	2.59
LEPIDOPTERA	1.5	21.15	1.5	10.87	.2	11.52	1.7	12.53	.5	10.13	4.9	15.88
HOMOPTERA	.5	2.02	11.1	14.05	32.6	64.81	25.4	57.34	11.3	19.07	24.3	29.00
DIPTERA	2.7	.50	11.0	3.72	10.2	5.69	2.0	2.40	1.0	4.44	13.5	4.49
COLEOPTERA	43.6	48.05	30.5	59.63	21.5	35.97	19.7	37.29	8.7	30.73	50.7	74.12
HERBIVOROUS	23.4	25.34	9.4	13.95	5.0	6.03	6.4	18.61	1.7	5.53	35.9	43.26
CARNIVOROUS	17.8	8.31	15.8	6.29	1.6	.46	1.6	.70	----	-----	30.6	10.20
HEMIPTERA	2.1	9.28	1.7	.56	1.4	2.78	4.5	8.63	4.2	15.91	3.8	5.65
HERBIVOROUS	1.9	9.12	1.7	.56	1.0	2.56	4.3	7.31	2.4	13.49	2.0	1.48
CARNIVOROUS	.2	.16	---	-----	.4	.22	.2	1.32	1.8	2.42	1.8	4.17
PHALANGIDA	2.3	6.37	1.8	17.23	1.6	27.92	.5	12.65	---	------	5.9	9.79
ARANEIDA	41.2	33.65	25.2	20.24	6.6	6.49	8.0	19.31	1.7	5.53	66.5	53.46
Totals	119.7	147.74	116.7	163.03	125.8	212.95	78.9	235.32	42.3	269.69	179.2	270.90

[a]For orders with various feeding habits (e.g. Coleoptera and Hemiptera) the values for the carnivores and herbivore-detritivores in the group are immediately below the total for the order.

[b]Three fourths of the ants were considered carnivorous

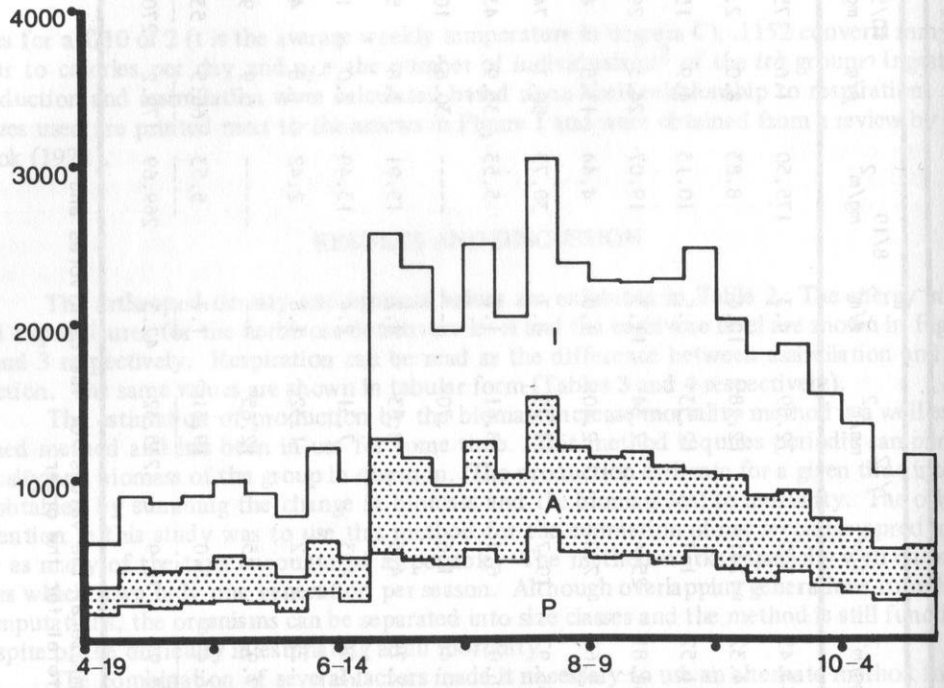

Fig. 2. Estimated ingestion (I), assimilation (A), net production (P), and respiration for the herbivore-detritivore level expressed as calories per week. Respiration can be read as the difference between assimilation and production.

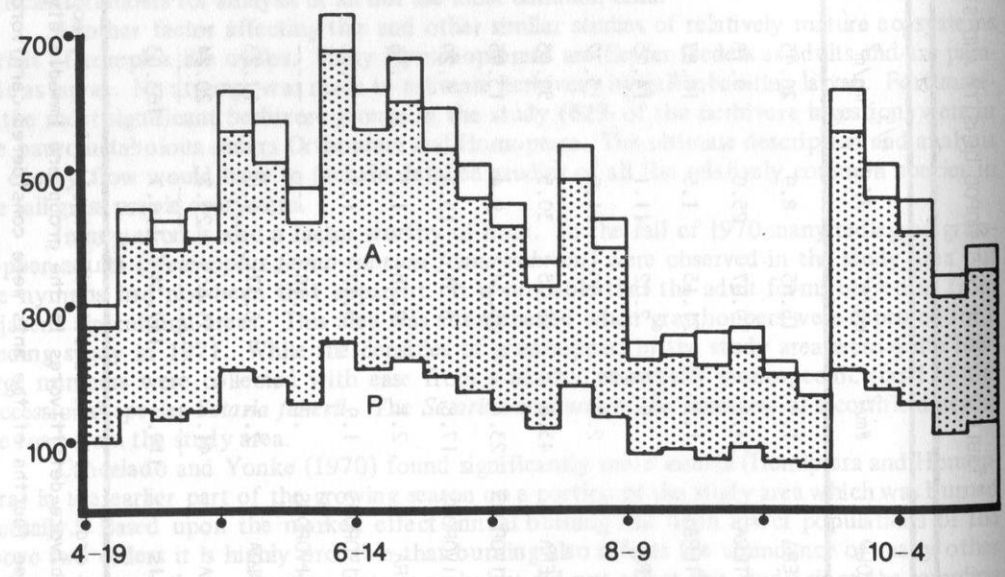

Fig. 3. Estimated ingestion (I), assimilation (A), net production (P), and respiration for the carnivore level expressed as calories per week. Respiration can be read as the difference between assimilation and production.

TABLE 3. WEEKLY CALORIES/M^2 OF INGESTION (I), EGESTION (E), ASSIMILATION (A), NET PRODUCTION (P) AND RESPIRATION (R) FOR THE HERBIVORE-DETRITIVORE TROPHIC LEVEL

	I	E	A	P	R
4/19	598	297	297	131	167
4/26	881	438	438	192	245
5/3	855	420	420	185	235
5/10	881	438	438	201	245
5/17	997	491	491	217	277
5/24	914	457	457	201	256
5/31	759	377	377	166	211
6/7	1197	599	599	263	342
6/21	2542	1271	1271	560	718
6/28	2365	1132	1132	498	641
7/5	1942	972	972	427	513
7/12	2794	1246	1246	548	701
7/19	2053	1027	1027	452	567
7/26	3021	1511	1511	665	851
8/2	2396	1199	1199	528	689
8/9	2272	1136	1136	500	636
8/16	2262	1181	1181	520	661
8/23	2286	1093	1093	481	612
8/30	2454	1026	1026	540	687
9/6	2023	1011	1011	445	567
9/13	1802	901	901	396	501
9/20	1874	437	437	412	525
9/27	1545	783	783	330	433
10/4	1375	688	688	303	385
10/11	1051	525	525	231	294
10/18	1180	590	590	260	331

TABLE 4. WEEKLY CALORIES/M^2 OF INGESTION (I), EGESTION (E), ASSIMILATION (A), NET PRODUCTION (P) AND RESPIRATION (R) FOR THE CARNIVORE TROPHIC LEVEL

	I	E	A	P	R
4/19	302	30	272	100	172
4/26	443	45	399	147	253
5/3	427	42	385	141	243
5/10	443	45	399	147	353
5/17	620	62	559	205	354
5/24	574	58	517	189	327
5/31	474	48	426	156	270
6/7	751	75	677	248	249
6/14	620	63	559	205	354
6/21	665	66	600	220	380
6/28	593	59	535	196	338
7/5	508	51	458	168	290
7/12	447	45	420	148	255
7/19	368	37	332	121	210
7/26	542	55	488	179	309
8/2	429	42	388	142	245
8/9	246	25	222	81	141
8/16	255	26	230	84	146
8/23	257	24	214	78	135
8/30	266	27	240	88	152
9/6	220	22	198	72	125
9/13	196	20	176	65	112
9/20	615	61	554	203	350
9/27	508	50	458	168	290
10/4	453	45	408	150	258
10/11	346	34	311	114	197
10/18	388	39	350	129	221

underestimation of arthropod energy flow. Mason (1971) determined the oxygen consumption rates for 20 species of woodland snails. He found Q10 values varying from 1.20 to 4.27 with an average value of 2.21. The species which attained greater size were associated with the higher values. Menhinick (1967) determined O_2 consumption and Q10 (22 C - 32 C) for over 50 groups of arthropods and the average Q10 based on O_2 consumption was 2.99. He observed no relation between arthropod size and Q10 values. The value of 2.0 was used in this study. If it is in error, it is probably too small.

No correction was made that compensates for increased organism activity under field conditions. To our knowledge there are no data on this for poikilothermic organisms. For homeothermic organisms the difference between oxygen consumption at rest and during vigorous exercise is in excess of 10 fold (Schmidt-Nielsen, 1970).

The models used in the generation of community energetics values are shown in Figure 1. When the various compartments are viewed in trophic level sequence (Table 5), it does not make much sense initially. For instance, the carnivore level eats more than the herbivore-detritivore level produces (11.9 versus 9.8 respectively). There are several factors in the study which could account for this apparent violation of the first law of thermodynamics.

One source of error was introduced by the investigators' bias. The first sample contained a significant number of podurids (Order: Collembola). They are normally inhabitants of the litter and soil compartments of the prairie. The waterlogged condition of the soil in the spring apparently causes an upward migration of these organisms. Since they did not occur significantly in later samples it was decided to concentrate on the grazing food chain and omit them from the analysis. Their inclusion would not have made a significant difference in the outcome of the study, but this decision inadvertantly led to the assumption that there is not interchange of energy between the arthropods of the live herbaceous layer and those of the litter and soil layers of the system. Over 90% of the carnivory was accomplished by spiders (Araneida and Phalangida) and ants (Formicidae). It is certain that spiders and ants also fed in the litter layer from populations of organisms not considered in the study.

Another contributing factor was the inclusion of all carnivores in the same trophic level. It is certain that some of these carnivores consumed other carnivores.

The length of the sample interval probably caused more of an underestimation of herbivore-detritivore groups than it did carnivore groups. The carnivores tend to have an annual life cycle and tend to be active in a longer period of the growing season than a good many herbivores. Many leafhoppers have annual life cycles but there activity is compressed temporally. It is my opinion that weekly collections would be required (and perhaps more often) to accurately estimate the energetics of populations that turn over as rapidly as leafhoppers.

Since there are several factors that affect arthropod activity and distribution patterns (eg. temperature, wind, relative humidity), it is also advisable to determine collection efficiency at each sample time.

In a comparable study (Menhinick, 1967) on a lespedeza stand, the estimate of carnivore ingestion was more than the lower levels produced. His explanation was essentially the same as the one offered in this study but he concluded that the carnivore ingestion from litter and soil subsystems was at least partially compensated for (on an amount of time spent in different layer basis) by their collection from the herb layer. This could also partially explain the low density and biomass values encountered in this study during the hot dry period of the summer (Table 2).

The herbivore-detritivore ingestion as a percentage of plant net production for this study and those of Menhinick (1967) and Van Hook (1971) are 2.21, 0.89 and 10.56 respectively. Menhinick's (1967) estimate is probably low for two reasons. He based his ingestion estimate on the proportion Assimilation/Ingestion = .385. This is thought to be a little low. As-

TABLE 5

ANNUAL NET PRODUCTION OF THE PREVIOUS TROPHIC LEVEL [NP(n-1)], INGESTION (I), RESPIRATION (R), PRODUCTION (P) AND ASSIMILATION (A) DETERMINED IN THIS STUDY AND COMPARED WITH TWO OTHER STUDIES ON HERBACEOUS ECOSYSTEMS[a]

	NP(n-1)	I	A	R	P	%I[b]	
Herbivores	2032.0[c]	44.9	22.4	12.6	9.8	2.21	This Study
Carnivores	9.8	11.9	10.7	6.8	3.9		
Herbivores	2553.0	22.8	7.2	5.9	1.3	0.89	Menhinick 1967
Carnivores	1.3	1.6	.9	.8	.1		
Herbivores	1274.0	134.8	69.5	37.5	32.0	10.56	Van Hook 1971
Carnivores	32.0	6.8	6.1	3.8	2.3		

[a] Values are expressed as KCal/m^2/Yr. The herbivore category includes detritivores.

[b] The percentage net primary production consumed by the arthropod communities is denoted by %I.

[c] Kucera and Koelling (1965) estimated the above ground net plant production of the study area to be 508.0 gdw/m^2. A calorific value of 4000 cal/gdw was assumed based upon data by Golley (1961).

similation was also underestimated due to the method he used to estimate production. The production estimate was based upon the maximum biomass of each population that occurred during the season. This does not allow for prematurational mortality. The value obtained in this study (2.21) is also thought to be low. It is felt that the value probably does not exceed five.

CONCLUSIONS

The ingestion of herbivorous and detritivorous arthropods in a tall grass prairie was estimated to be 2.21% of the annual above ground primary production. This estimate is thought to be low mainly due to a sample interval that was too long and the omission of some developmental phases of species with complex life cycles.

While traditional compartments of the organic fraction of a tall grass prairie (ie. litter, roots, standing dead, green vegetation) exist as entities in our minds, they are intricately linked in the total picture of tall grass prairie energetics.

The most important herbivore-detritivore orders of insects based upon ingestion estimates found in the study area were Orthoptera and Homoptera. They accounted for over 60% of the ingestion of their trophic level.

The most important carnivorous arthropods were spiders (Araneida), harvestmen (Phalangida), and ants (Formicidae). They accounted for over 90% of the estimated carnivory.

ABSTRACT

The arthropod community was sampled periodically throughout the 1970 growing season. Collection consisted of vacuuming the arthropods out of a hand-thrown trap. Arthropods were sorted as to trophic level and size. Respiration for the various groups was calculated based upon weight-oxygen consumption rate relationships from the literature. The rates were corrected for field temperatures during the study. Other parameters of energetics (net production and ingestion) were calculated based upon their ratio to respiration as reported in the literature. The ingestion of herbivorous and detritivorous arthropods in a tall grass prairie was estimated to be approximately 2% of the annual above ground net primary production. This estimate is thought to be low mainly due to a sample interval that was too long and the omission of some developmental phases of species with complex life cycles. It is doubtful that the ingestion value exceeds 5 per cent. The most important herbivore-detritivore orders of insects (based upon ingestion estimates) found in the study area were Orthoptera and Homoptera. The most important carnivorous arthropods were spiders (Araneida) and ants (Hymenoptera: Formicidae). While traditional compartments of the organic fraction of a tall grass prairie (e.g. litter, roots, standing dead, green vegetation) exist as entities in our minds, they are intricately linked in the total picture of tall grass prairie energetics.

KEY WORDS

Arthropod energetics, prairie, food chain, bioenergetics.

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PRAIRIE ANT MOUND ECOLOGY: INTERRELATIONSHIPS OF MICROCLIMATE, SOILS AND VEGETATION

M. K. Wali and P. B. Kannowski

Ants, where abundant, form an extremely important consumer component of the ecosystem, and this is particularly true of the Great Plains in the United States. A few species, such as harvesting ants, are primary consumers, but the majority are primarily secondary consumers. An abundance of arthropods in the soil and herbaceous vegetation provide a rich food source that is well exploited by ants.

They are also important by making channels and burrows in the soil. Hopp and Slater (1948) stated that ants could be as effective as earthworms in creating conditions for improved plant growth. Shaler (quoted by Thorpe, 1949) believed that ants produce a far greater effect on soils than do earthworms, while Shrikhande and Pathak (1948) reported that ants increased the organic matter content of the soils (one and a half times) second only to the earthworms. However, Thorpe (1949) reported some harmful effects on vegetation because of ant activity.

Ecological data on the functional relations of ants are rather scanty. The group has been completely ignored in a recent comprehensive review on the ecological role of arthropods by Raw (1967). Interest, therefore, in the study of ants as functional components of the ecosystem is relatively recent. The role of individual ant species in community energetics has been studied by Golley and Gentry (1964) and Gentry and Stiritz (1972). The nest abundance of ants in grasslands has been studied in Japan by Yasuno (1963, 1964), in central Italy by Baroni-Urbani (1969), and at Oakville Prairie in North Dakota by Kannowski (1963). The relation of ant distribution to old-field vegetation in southern Michigan has been studied by Talbot (1953, 1961). Her work, together with the recent work of Czerwinski, et al. (1969, 1971), Petal, et al. (1970), and Rogers and Lavigne (1974) dealing with the influence of ants on soil chemical, physical and microbiological properties, are of particular significance to the present study.

Starting in the summer of 1970 and continuing through 1971, 1972, and 1973, we investigated the effect of ant activity in relation to (1) mound building, (2) physical properties and (3) chemical characteristics, including trace elements, in soils, and (4) the effect on vegetation growth and abundance.

THE STUDY AREA

The study was conducted at Oakville Prairie located 19 km west of Grand Forks in northeastern North Dakota (Fig. 1). Approximately 259 ha of this 323.75 ha field station of the University of North Dakota Biology Department are typical upland prairie (all virgin); the remaining 64.75 ha are lowland prairie (about 44.5 ha virgin). The part of lowland prairie that is not virgin was cultivated once about 1935 but has not been disturbed since that date. Oakville Prairie has been disturbed by farm tractors travelling over the ground, by equipment that laid the telephone cable in the ground, by a bulldozer that opened a side of the small hill in the center of the lowland and created a firebreak in the upland, and by the installation of the small building in the lowland. It is also disturbed by human activity in carrying out research studies.

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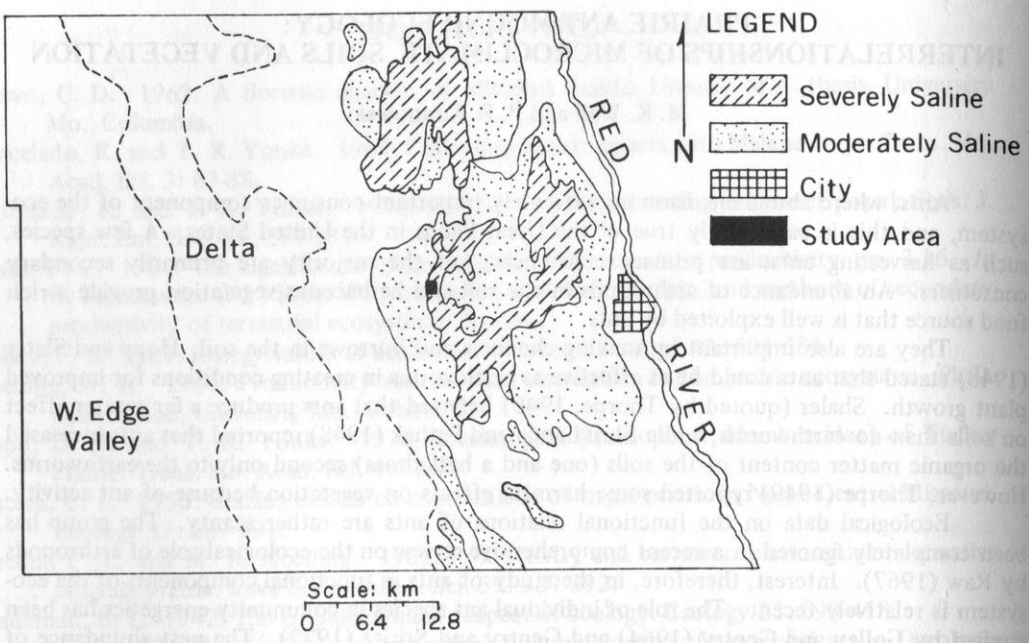

Fig. 1. Map of Grand Forks County, North Dakota showing saline areas and the study site (modified from L. C. Benz et al. 1961).

North Dakota is characterized by a continental climate. Below freezing temperatures are common during more than six months of the year (Fig. 2, data presented as in Walter and Leith, 1960). Records obtained over a 69-year period at the University of North Dakota Meterological Station in Grand Forks (U.S. Dept. Commerce, 1967) show the following averages: mean annual temperature, 4.4 C; mean temperature for July, the warmest month, 27.5 C; mean air temperature for the coldest month, January, -21.0 C. On the average there are 188 days with a minimum temperature at, or below, 0 C. The mean annual precipitation is a little above 52 cm, 75 percent of which falls between April 1 and September 30. Snowfall averages about 86.5 cm and falls mainly between the beginning of November and the end of February. The mean growing season (frost-free days) in the eastern part of the state, averaging 131 days, is the longest for the state. The winds, at an average of 16 km/hour, are mainly northwesterly.

Microclimatic observations at Oakville Prairie have included study of the temperature regimes of upland and lowland soils and of lowland prairie ant mounds (Kannowski, unpublished). The regimes for upland soil, lowland soil and a *Lasius umbratus* mound show some interesting differences (Figs. 3, 4 and 5). Comparison of the data from the two soil locations indicates a greater range of temperature in the lowland prairie. This can be accounted for on the basis of the lesser vegetative coverage in the lowland, thereby resulting in higher surface zone temperatures in the summer months and lower surface zone temperatures in the winter months, and of the higher water table in the lowland which hinders frost penetration. On the average, frosts penetrate to 120 cm depth in upland soils but only to 60 cm depth in lowland soils.

The ant mound serves to pick up more heat in the summer and lose more in the winter than the adjacent lowland soil. Comparison of subsurface temperatures beneath the mound, where some nest galleries are located, with those of the adjacent lowland soils shows little difference especially with increasing depth. Where ant activity occurs, slight modification of the temperature in and beneath the mound is evident.

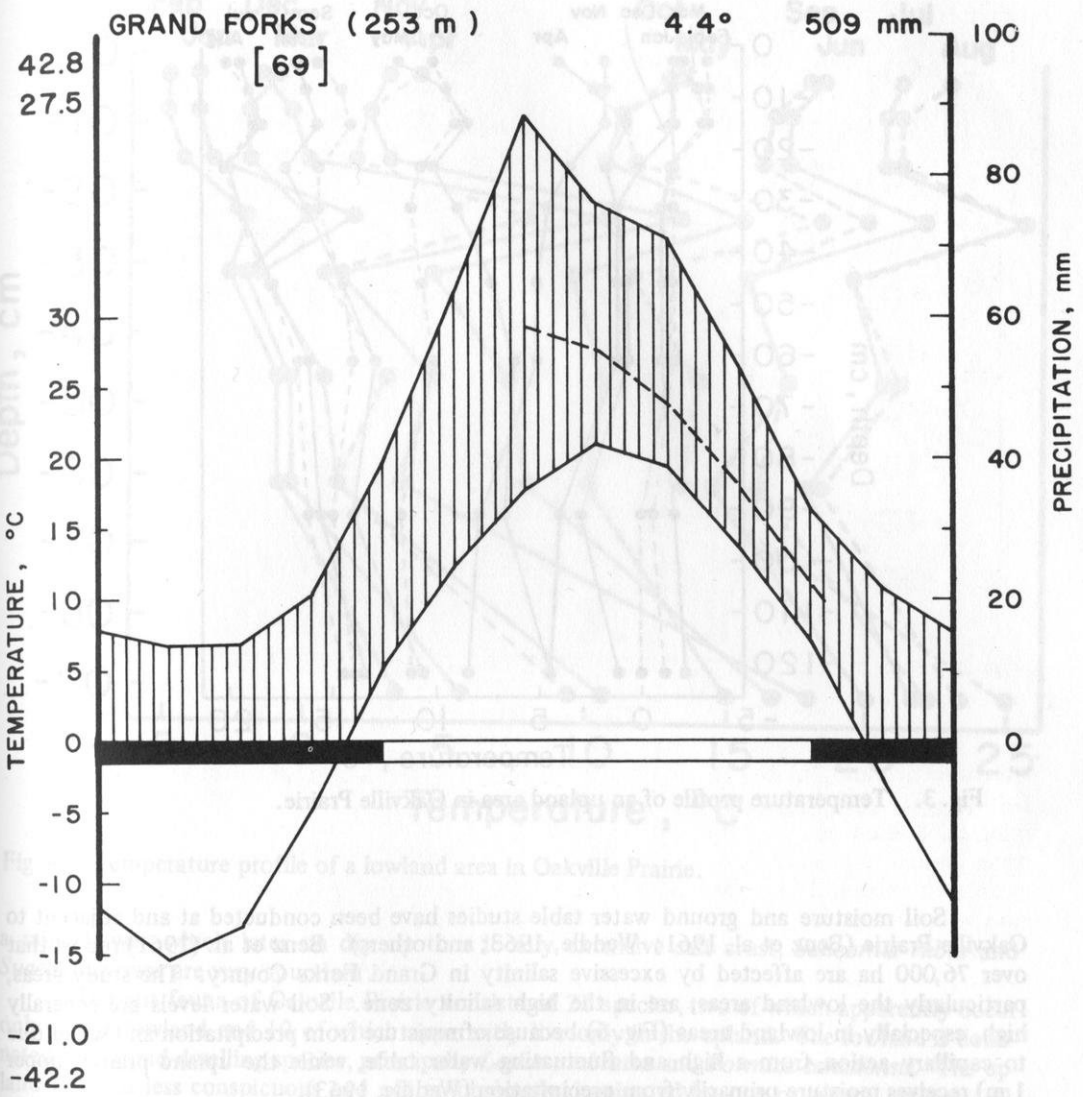

Fig. 2. Climatic diagram for Grand Forks, North Dakota. Across the top are the station, elevation, mean annual temperature, and precipitation. Below the station in brackets is the number of years for which the data have recorded. Vertically down on the left axis are absolute maximum, mean maximum of the warmest month, mean minimum of the coldest month and absolute minimum temperatures. Dashed line shows moisture stress period and solid horizontal line indicates months below 0° . (Data presentation follows Walter, H. and H. Leith, 1960. Klimadiagramm-Weltatlas. Gustav Fischer Verlag. Jena).

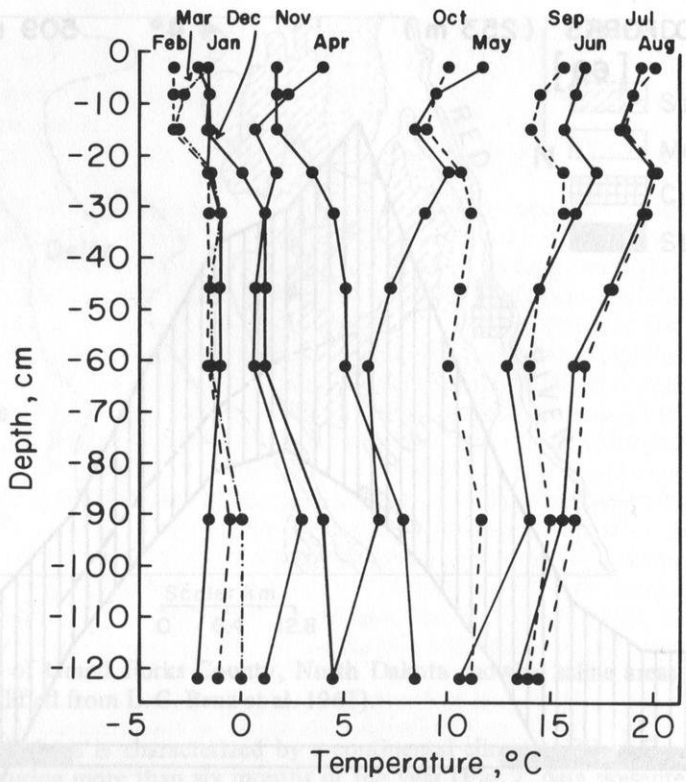

Fig. 3. Temperature profile of an upland area in Oakville Prairie.

Soil moisture and ground water table studies have been conducted at and adjacent to Oakville Prairie (Benz et al. 1961; Weddle, 1963; and others). Benz et al. (1961) report that over 76,000 ha are affected by excessive salinity in Grand Forks County. The study areas, particularly the lowland areas, are in the high salinity zone. Soil water levels are generally high, especially in lowland areas (Fig. 6) because of moisture from precipitation and water due to capillary action from a high and fluctuating water table, while the upland prairie (upper 1 m) receives moisture primarily from precipitation (Weddle, 1963).

The subsurface strata of Dakota sandstone and Pierre shale of Cretaceous age and limestone and sandstone of the Ordovician are overlain by silts and clay about 33 to 66 m in thickness. The typical soils at Oakville have developed under prairie vegetation from lacustrine and alluvial deposits in the Glacial Lake Agassiz. The dark black chernozems (now Mollisols) predominate with locally very extensive patches that are alkaline and saline. Soils at Oakville, particularly the lowlands, are constantly under the influence of a fluctuating water table; therefore, soils of the Typic Calciaquoll subgroup are common.

The vegetation of the upland is dominated by *Andropogon gerardi, A. scoparius* and *Poa pratensis*, with locally extensive patches of *Rosa arkansana* and *Symphoricarpos occidentalis. Helianthus maximiliani, Aster ericoides* and *Sonchus arvensis* are admixed in a large number of communities. The lowland communities abound in *Distichlis stricta, Hordeum jubatum, Muhlenbergia richardsonis* and *Spartina pectinata*. Where local pools are formed after

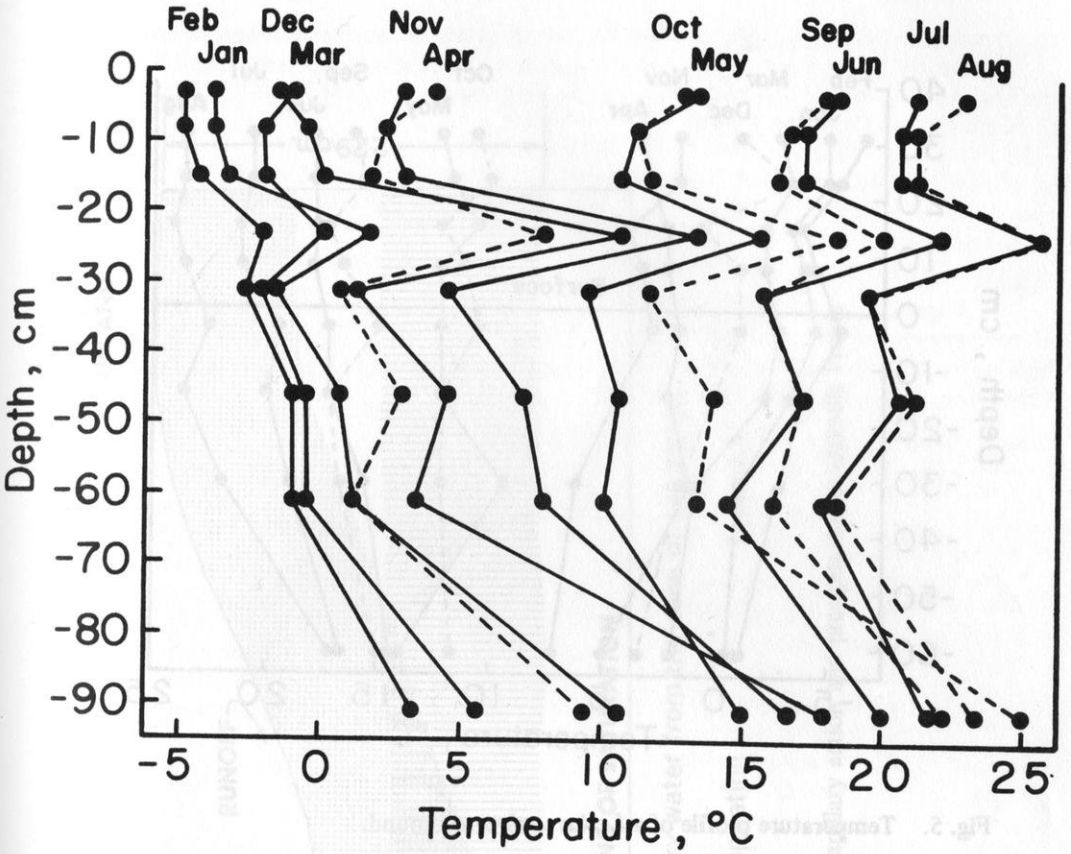

Fig. 4. Temperature profile of a lowland area in Oakville Prairie.

a rain shower which later on dry up to a locally extensive salt crust, *Salicornia rubra* and *Suaeda depressa* are very abundant.

The ant fauna of Oakville Prairie consists of 21 species, two of which apparently occur only in the lowland and 10 of which apparently live only in the upland. The lowland is dominated by mound-dwelling species, principally *Lasius umbratus* and *Formica canadensis*. The upland fauna is less conspicuous and not so obviously dominated by one or several species. Although the most characteristic upland species is *Formica obscuripes*, the areas studied were dominated by three species of *Lasius*.

METHODS OF STUDY

Field data were collected in the summers of 1970, 1971, 1972 and 1973 in both the upland and lowland prairie. A total of 75 ant mounds were studied. Of these, 25 were located on the upland prairie and 50 on the lowland which bears the largest number of mounds. Samples were also obtained from 14 sites adjacent to the mounds for the comparison of physical and chemical properties. The mound diameter and height were measured from which the volume of the mounds was calculated as follows:

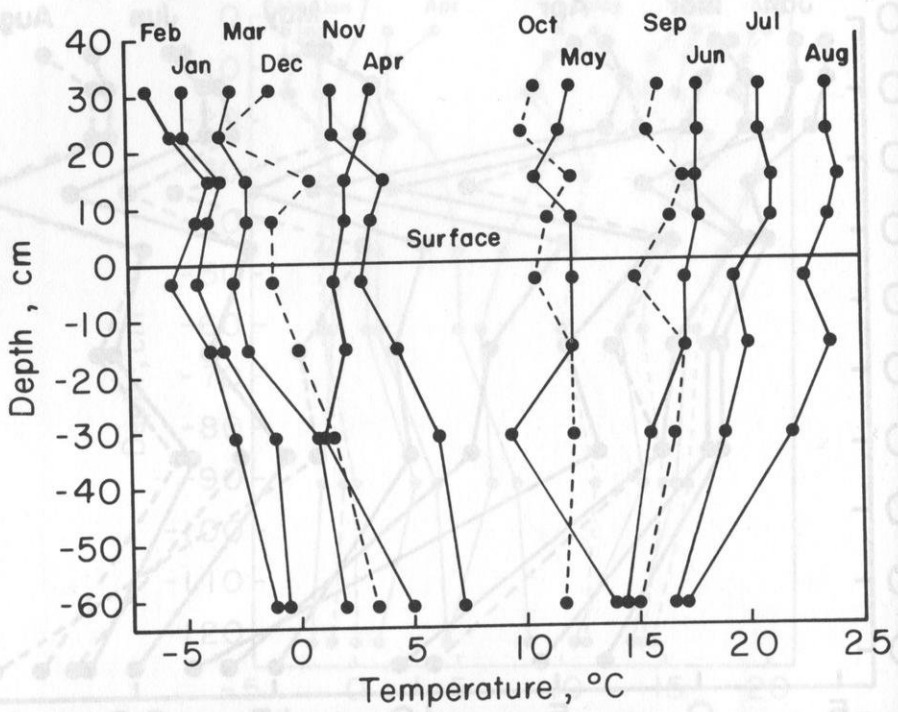

Fig. 5. Temperature profile of a *Lasius umbratus* mound.

$$V = \pi \frac{r^2 \times h}{3}$$

Where V is the volume of the mound
r is the radius of the mound
and h is the height of the mound

The vegetation of each mound was studied by 75 0.5 x 0.5 m quadrats in which the coverage and counts of each individual plant species were determined.

From each mound, several 7.5 cm soil cores were obtained for the determination of bulk density. Soil samples were also collected for physical and chemical analyses. Water retention properties of the soils were determined at 1/3 and 15 bars by the pressure plate apparatus (Richards, 1954).

Chemical properties investigated included pH, electrical conductivity, major cations and trace elements. Calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), lithium (Li), manganese (Mn) and strontium (Sr) were determined by extracting the soil with 1N ammonium acetate, pH 7±0.2. Determinations made with this method hereafter will be referred to as "replaceable" cations (Wali and Krajina, 1973). Trace elements, copper (Cu), iron (Fe), Mn, nickel (Ni), lead (Pb) and zinc (Zn) were extracted with 0.02 M disodium-EDTA (ethylenediaminetatraacetic acid). All determinations were made using a Perkin-Elmer atomic absorption

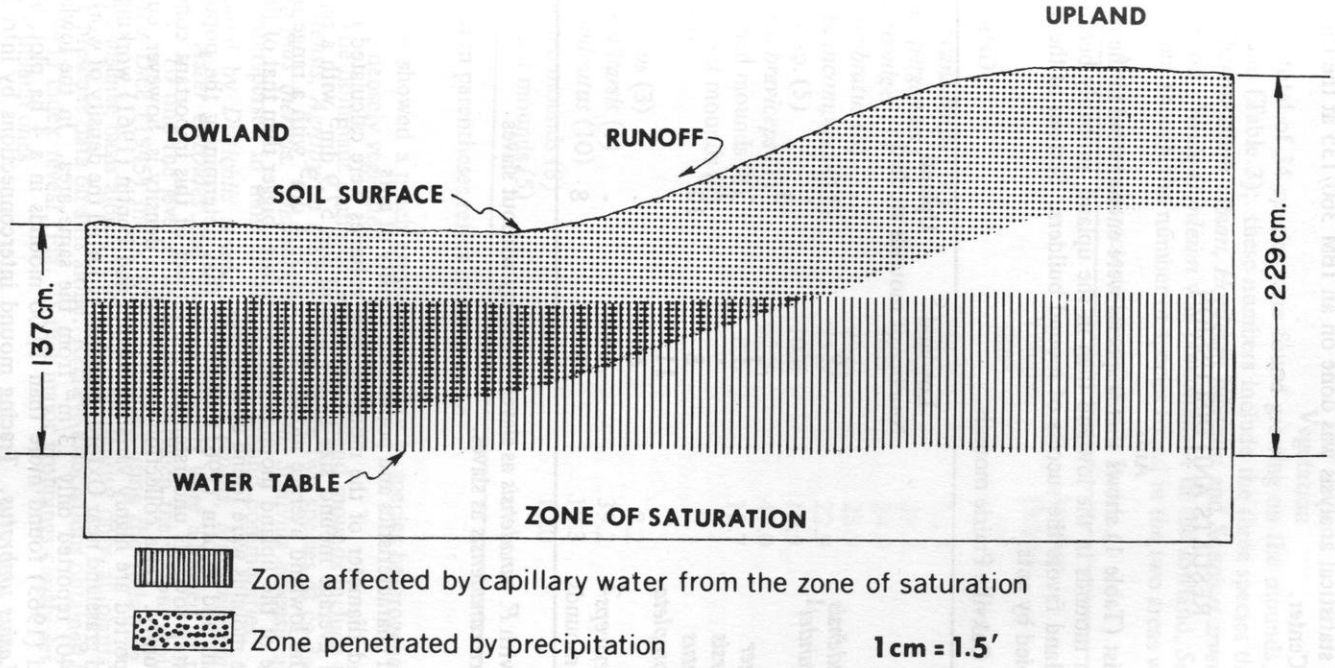

Fig. 6. Zones affected by water due to capillary action and precipitation in Oakville Prairie (from R. K. Weddle, 1963).

spectrophotometer Model 403 at wave-lengths as given in the Perkin-Elmer Manual (1973).

Association-analysis of the ant mounds was done by simple matching and the use of the Dice (1945) index. All statistical analysis was done on an IBM 360/135 at the University of North Dakota Computer Center.

RESULTS AND DISCUSSION

Ants

A species presence list (Table 1) shows that 9 species were encountered in the mounds. More species were found in mounds in the lowland than in the upland, probably because the high water table in the lowland favors the success of mound builders. Sixteen of the mounds (21%) were no longer occupied by ants.

Table 1: Presence of ants in Oakville Prairie mounds.

	Lowland	Upland
	Number of mounds studied	
Formica canadensis	16	-
Formica pergandei[1]	3	-
Lasius flavus	-	3
Lasius neoniger	1	-
Lasius pallitarsis	-	1
Lasius umbratus	8	10
Myrmica incompleta	11	-
Myrmica sp.	5	-
Polyergus breviceps[2]	1	-
Uninhabited mounds	8	8

[1]2 colonies with *F. canadensis* as slaves, 1 colony without slaves
[2]with *Formica canadensis* as slaves.

Mound characteristics and population density of ants

From the height and diameter of the mounds, their volumes were calculated in cubic decimeters (Table 2). The average mound size in the upland was 57.9 dm^3 with a range of 17.8-119.2 dm^3 while on the lowland average mound size was 35.4 dm^3 with a range of 8.5-66.6 dm^3. The average size of the upland mounds was, therefore, bigger than that of the lowland mounds. Several of the mounds were found abandoned.

Appropriately, Odum and Pontin (1961) suggested that determining the population density of ants is the first step towards understanding the impact of this important consumer group in a grassland community. Data collection on population density is, however, cumbersome, and the numbers reported are highly variable. Odum and Pontin (1961) working with *Lasius flavus* in an ungrazed grassland near Oxford, England, reported the density of workers at 486/m^2, while Pickles (1940) reported only 13/m^2 from the same area. In the lowland at Oakville Prairie, Kannowski (1963) found more than 1,000 mounds in a 4 ha plot, 624 of which were inhabited by *Lasius umbratus*. Tracing mound interconnections by introducing P^{32} in food supply (Kannowski, 1959), he found an average 3.8 mounds per colony of *Lasius umbratus* at Oakville. Later studies (Kannowski, unpublished) showed an average of nearly 50

colonies per ha and a mean per mound population of 13,828 individuals (eggs, larvae, pupae, and adults), based upon actual counts of 6 mounds, giving a density of about 265/m^2.

Vegetation

A total of 34 species were found growing on the mounds, 20 on the upland and 17 on the lowland (Table 3); these numbers include the three species that were common in both the areas, *Chenopodium album, Hordeum jubatum* and *Sonchus arvensis;* all three are colonizers on bare soil. While *Hordeum* was predominant in the lowland, *Sonchus* dominated in the upland. Even though the number of species found in the two areas was almost the same, the lowland areas showed a much greater variability in species heterogeneity. Upland mounds, however, were densely vegetated.

Table 2: Ant mound characteristics at Oakville Prairie.

	Volume dm^3	Average Height cm	Bulk Density gm/cm^3	Total Porosity %
LOWLAND				
Formica canadensis (16)[1]	34.7	30.5	0.68	74.2
Formica pergandei (3)	28.0	29.2	0.74	72.2
Lasius neoniger (1)	46.4	24.0	0.64	75.0
Lasius umbratus (8)	66.6	28.9	0.67	74.7
Myrmica incompleta (11)	25.8	22.9	0.74	72.0
Myrmica sp. (5)	10.6	10.9	0.75	71.8
Polyergus braviceps (1)	62.3	47.0	0.67	74.7
Abandoned mounds (8)	8.6	12.7	0.68	74.5
Soil without mounds (9)	-	-	1.15	56.6
UPLAND				
Lasius flavus (3)	17.8	7.2	0.77	70.9
Lasius pallitarsis (1)	119.2	39.2	0.82	69.0
Lasius umbratus (10)	57.6	18.3	0.81	69.6
Abandoned mounds (8)	46.9	12.0	0.79	70.1
Soil without mounds (5)	-	-	1.21	54.3

[1]Number in parentheses refers to sample size.

The dominant communities of the upland mounds include (in order of predominance), *Poa pratensis, Agropyron trachycaulum,* these two species as co-dominants, *Spartina pectinata* and *Bromus inermis. Helianthus maximiliani, Sonchus arvensis* and *Solidago altissima* were found interspersed in most of the upland mound communities. The lowland mounds were dominated by *Distichlis stricta, Agropyron repens, Muhlenbergia richardsonis* and *Spartina gracilis. Aster ericoides* and *Sonchus arvensis* were admixed in many of the lowland communities. To find the level of association between the various mounds, an association-analysis using the Dice (1945) index was performed using the following matrixes: all plants on a presence-absence basis alone, plants on high density only, all plants and ants on presence basis, and the presence data on ants alone. Relative associations obtained by simple matching and the Dice (1945) index reveal (Fig. 7) that major groupings clearly set apart the lowland mounds from the upland ones.

Table 3: Relative frequency (RF) and relative density (RD) of plant species on lowland and upland mounds at Oakville Prairie.

Ants	Abandoned Mounds (8)		*Formica canadensis* (16)		*Formica pergandei* (3)		*Lasius neoniger* (1)		*Myrmica incompleta* (11)		*Myrmica* sp. (5)		*Polyergus breviceps* (1)		*Lasius umbratus* (10) (8)		*Lasius pallitarsis* (1)		*Lasius flavus* (3)		Abandoned Mounds (8)	
Plants	RF	RD	RF	RD	RF	RD	RF	RD	RF	RD	RF	RD	RF	RD	RF	RD	RF	RD	RF	RD	RF	RD
Agropyron repens	18.9	14.3	9.4	8.8	10.6	8.3	10.0	8.0	8.9	17.4	13.1	17.0	-	-	15.4	13.2						
Ambrosia artemisifolia	6.3	4.4	4.1	1.3	-	-	10.0	8.0	5.9	3.1	4.3	4.0	-	-	13.6	10.9						
Asclepias ovalifolia	-	-	-	-	-	-	10.0	4.0	-	-	4.3	1.0	-	-	5.7	1.5						
Aster ericoides	12.6	7.5	4.1	2.6	-	-	10.0	8.0	4.5	1.3	8.7	3.0	14.3	5.0	7.7	3.6						
Atriplex patula var. *hastata*	-	-	7.9	3.6	10.6	3.3	-	-	8.9	5.1	4.3	2.0	14.3	15.0	-	-						
Distichlis stricta	21.9	40.7	16.0	21.5	15.8	36.9	10.0	20.0	18.4	32.3	21.8	40.0	14.3	30.0	15.4	43.1						
Grindelia squarrosa	3.0	1.2	4.1	1.3	10.6	5.0	10.0	4.0	7.4	5.4	4.3	6.0	-	-	5.7	2.9						
Kochia scoparius	-	-	2.6	1.6	-	-	-	-	-	-	-	-	-	-	-	-						
Muhlenbergia asperifolia	6.3	5.0	2.6	2.3	-	-	10.0	4.0	5.9	4.1	4.3	2.0	-	-	9.7	4.9						
Muhlenbergia richardsonis	9.3	4.4	6.6	3.3	5.2	1.7	-	-	8.9	6.8	8.7	5.0	14.3	15.0	3.8	1.9						
Poa arida	-	-	5.3	4.8	15.8	15.0	-	-	8.9	5.4	4.3	5.0	-	-	-	-						
Salicornia rubra	3.0	.1	1.3	.1	-	-	-	-	1.5	.9	-	-	-	-	-	-						
Spartina gracilis	9.3	6.3	6.6	25.7	-	-	10.0	12.0	1.5	.9	-	-	-	-	1.8	1.3						
Suaeda depressa	3.0	12.4	13.5	11.4	15.8	16.7	-	-	4.5	2.3	4.3	2.0	14.3	15.0	7.7	2.2						
															-	-						
Chenopodium album[1]	-	-	1.3	.2	-	-	10.0	8.0	-	-	-	-	-	-	1.5	.2						
															5.7	4.3						
Hordeum jubatum[1]	6.3	3.8	9.4	7.2	10.6	11.7	-	-	8.9	9.7	13.1	11.0	14.3	15.0	1.5	.2	-	-	4.5	.5	-	-
															7.7	10.8						
Sonchus arvensis[1]	-	-	5.3	4.2	5.2	1.7	10.0	24.0	5.9	5.1	4.3	2.0	14.3	5.0	13.6	3.8	-	-	13.7	4.0	12.5	2.2
Agropyron trachycaulum															7.6	29.0	25.0	3.5	9.2	30.0	2.5	.3
Poa pratensis															9.1	30.0	25.0	88.1	17.9	55.5	20.0	86.6
Achillea lanulosa															1.5	.2	-	-	-	-	-	-
Bromus inermis															3.0	4.6	-	-	-	-	-	-
Cirsium vulgare															-	-	-	-	-	-	2.5	.1
Galium boreale															10.6	2.3	-	-	13.7	1.3	5.0	.3
Glycyrrhiza lepidota															-	-	-	-	-	-	2.5	.1
Helianthus maximilliane															15.2	2.4	25.0	7.5	13.7	5.8	20.0	5.5
Koeleria cristata															3.0	.4	-	-	4.5	.6	-	-
Melilotus alba															4.5	.5	-	-	4.5	1.1	5.0	.1
Rosa arkansana															3.0	.2	-	-	4.5	.1	-	-
Ratibida columnifera															6.1	2.4	-	-	4.5	.3	5.0	.3
Solidago altissima															12.1	2.3	25.0	.9	9.2	1.0	5.0	1.9
Spartina pectinata															3.0	21.4	-	-	-	-	2.5	.2
Tragopogon dubius															4.5	.3	-	-	-	-	15.0	2.2
Zizia aptera															-	-	-	-	-	-	2.5	.2

[1] Upper numbers refer to lowland mounds, lower numbers refer to upland mounds.

Soil characteristics

The entire Oakville Prairie constitutes a saline environment. The lowlands are under the influence of a fluctuating water table for the larger portion of the growing season while the upland mounds are under such an influence only for a short period of time. Thus, water rises by capillary fringe in the lowlands and these soils may reach a wilting percentage only for a very short period of time. The upland mounds on the other hand, are very well drained but a denser cover of vegetation not only buffers the temperature changes but also cuts the water loss due to evaporation. Thus, the upland mounds show a range of 28.5-45.6% water by weight at one-third bar (field capacity) and 17.9-33.9 at 15 bar level (approximately the permanent wilting percentage). This, of course, is intimately tied with properties of the particle size and organic matter content of soils. The bulk density and percent total porosity values (Table 2) for the upland and lowland mounds do not show any significant differences, the averages for the two areas being 0.77 gm/cm^3 and 70.8%, and 0.71 gm/cm^3 and 73.9%, respectively. However, both bulk density and porosity are significantly higher in soils without mounds both in the upland and the lowland showing higher values of bulk density up to 1.6 gm/cm^3 and a lower porosity of 38%. Similar findings have been reported by Rogers and Lavigne (1974) from Colorado.

Chemical characteristics of the soils (Tables 4 and 5) revealed some significant differences between the mounds and the non-mound areas on the one hand and between the upland and lowland mounds. Soil reaction (pH) was generally lower in the mound areas than in the other areas of the prairie. This trend towards circumneutrality of soils has also been reported by Czerwinski et al. (1969, 1971) and Petal et al. (1970) in Poland where they found an increasing trend in soil pH in otherwise predominating acid conditions.

Electrical conductivity, an indicator of soluble salt concentration, was generally significantly higher in soils without mounds. While the upland mounds show a range of 1.1-1.7 Mmhos/cm, the soils showed four times that value. In the lowlands, electrical conductivity was generally much higher than the uplands. Whereas soils in lowland showed as high a value as 85 Mmhos/cm, the mounds seldom exceeded 15 Mmhos/cm. Replaceable cations Ca, Mg and K were higher, but Na lower, in the lowland mounds than neighboring soils. A similar trend is evident from the upland mounds. Generally higher levels of replaceable cations, particularly K, have been reported from ant mounds by Czezwinski et al. (1969, 1971), Petal et al. (1970), Gentry and Stirtiz (1972), and Rogers and Lavigne (1974). Sodium levels were very high in the lowland areas compared with the uplands. Replaceable Mn was higher in the upland mounds, while the lowland mound and soils did not show any appreciable differences. Li values were similar in all the samples. However, Sr was significantly higher in the lowland mounds than any other areas sampled. Most of the Sr in soils, as reported elsewhere (Wali and Krajina, 1973; Wali et al. 1973; Wikum and Wali, 1974), seems to be held on the exchange complex.

Chelated and/or complexed Cu, Fe, Mn and Zn showed a high concentration in both the upland as well as the lowland mounds as compared to their neighboring soils. It is interesting to note that lowest Fe concentrations were in the lowland soils. The predominance of water logged conditions and a fluctuating water table seem to be the only plausible factors explaining the suppression of available Fe levels. Because of a rise in curvature, this problem is alleviated in the mounds. Pb values were generally higher in the lowland areas, being the highest in lowland soils without mounds. Cu and Ni were higher in lowland mounds than control soils, while no appreciable differences were noted for the upland areas.

In conclusion, it appears that the presence of ants seems to moderate the soil conditions resulting in greater soil fertility. This is a direct result of increasing soil porosity by pedoturbation, and a change in chemical constituents because of storage of insect parts, plant components, excretory material of the ants and the leaching out of excessive salts. Thus pH and soluble salt concentration increases in areas that are predominantly acid (Czerwinski et al.

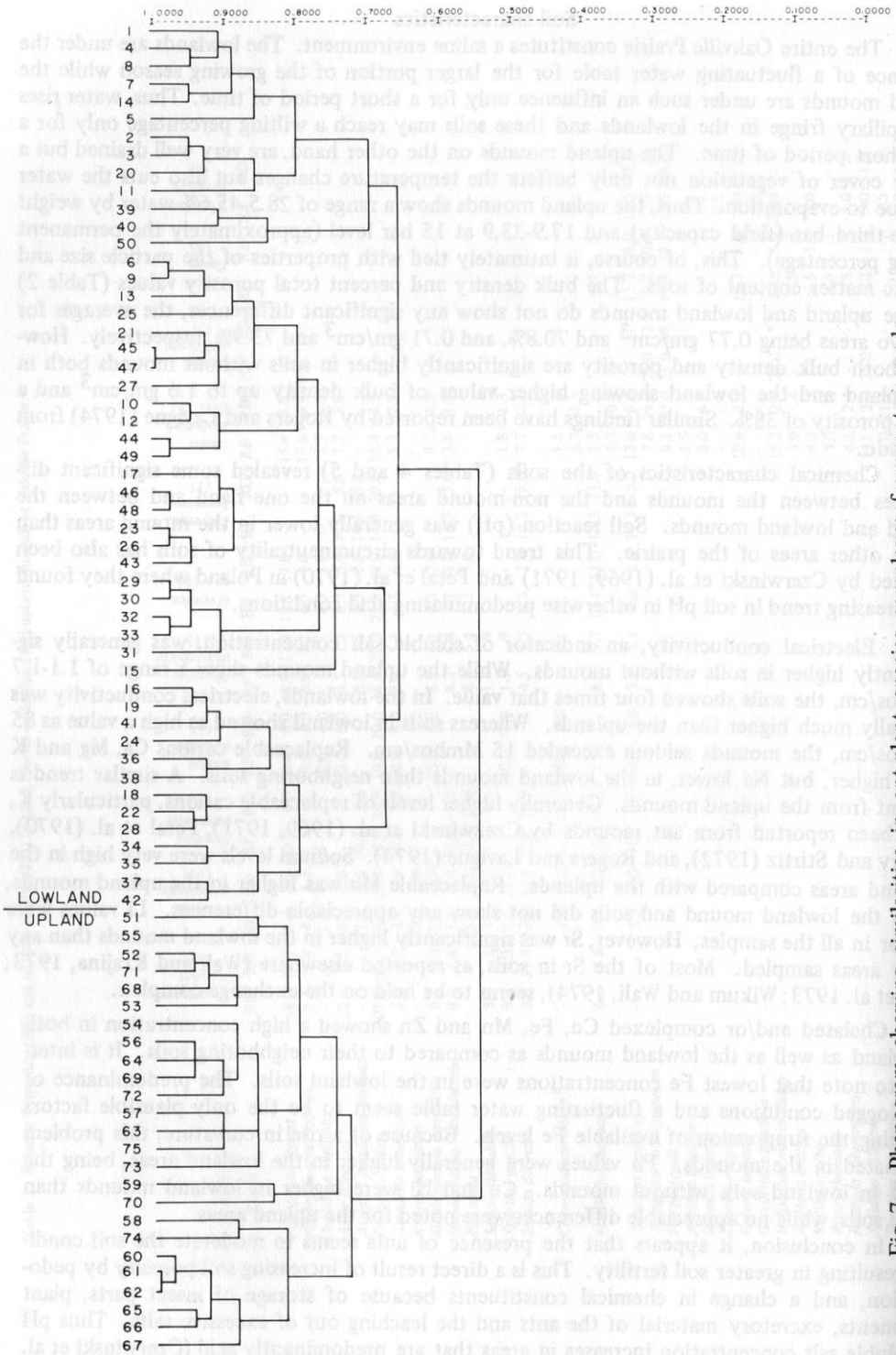

Fig. 7. Phenogram showing similarities in ant-plant species complexes from ant mounds studied as constructed by simple matching. (see F. J. Rohlf et al. 1972. NT-SYS, SUNY, Stony Brook, N.Y.)

Table 4: Soil chemical characteristics of the ant mounds.

	pH	EC	Ca	Mg	K	Na	Mn	Sr	Li
		mmhos/cm		me/100 g				ppm	
LOWLAND									
Formica canadensis (16)[1]	7.59	13.11	32.5	13.9	2.7	29.9	3.0	104.1	2.3
Formica pergandei (3)	7.61	14.42	32.0	14.7	2.6	33.0	2.7	123.8	2.2
Lasius neoniger (1)	7.47	7.58	37.3	12.9	2.0	9.2	1.6	62.5	1.7
Lasius umbratus (8)	7.46	10.52	28.8	13.4	2.5	22.2	1.7	85.3	2.1
Myrmica incompleta (11)	7.54	11.60	26.3	13.8	2.4	27.8	2.0	97.4	2.0
Myrmica sp. (5)	7.60	11.05	33.6	14.3	1.9	24.0	1.4	107.3	2.1
Polyergus breviceps (1)	7.48	15.34	28.9	15.0	2.4	38.3	2.4	125.5	2.2
Abandoned mounds (8)	7.64	8.62	26.0	12.5	1.9	18.9	2.2	86.4	1.9
Soil without mounds (9)	7.8	18.6	12.1	12.0	1.5	23.1	2.05	44.3	2.1
UPLAND									
Lasius flavus (3)	7.7	1.57	21.38	6.83	1.27	0.94	8.3	22.9	1.5
Lasius pallitarsis (1)	7.8	1.07	22.83	7.37	0.91	0.86	10.9	23.1	0.9
Lasius umbratus (10)	7.8	1.25	23.40	7.70	0.93	0.86	7.8	23.8	1.1
Abandoned mounds (8)	7.7	1.66	24.93	7.51	1.04	0.87	8.3	24.9	1.4
Soil without mounds (5)	8.0	4.8	25.8	8.5	.29	10.16	2.1	22.4	1.2

[1]Number in parentheses refers to sample size.

Table 5: Trace element concentration in the ant mounds.

	Cu	Ni	Fe	Mn	Pb	Zn
			ppm			
LOWLAND						
Formica canadensis (16)[1]	4.4	4.4	29.5	216.5	8.6	6.0
Formica pergandei (3)	4.3	4.2	19.2	186.6	5.9	6.0
Lasius neoniger (1)	2.8	3.0	12.1	76.3	9.1	4.1
Lasius umbratus (8)	2.4	3.0	10.2	103.2	8.2	4.4
Myrmica incompleta (11)	4.4	4.4	22.5	187.2	7.5	5.3
Myrmica sp. (5)	3.5	3.8	18.9	142.6	7.9	4.8
Polyergus breviceps (1)	3.3	4.2	17.2	195.8	8.1	5.2
Abandoned mounds (8)	4.7	4.3	37.3	204.5	7.2	5.5
Soil without mounds (9)	1.6	1.2	7.8	68.6	10.1	2.1
UPLAND						
Lasius flavus (3)	3.2	4.7	26.3	144.1	4.8	6.0
Lasius pallitarsis (1)	4.05	4.5	31.0	136.7	7.0	7.9
Lasius umbratus (10)	3.7	4.4	29.2	130.3	5.2	6.0
Abandoned mounds (8)	4.4	4.2	33.7	130.2	5.3	6.4
Soil without mounds (5)	3.3	4.4	29.4	41.4	4.9	2.2

[1]Number in parenthesis refers to sample size.

1969, 1971 and Petal et al. 1970) while it tends to decrease in predominantly alkaline and saline areas as shown in the present study. This increase in soil fertility greatly enhances plant growth.

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ABSTRACT

An investigation of 75 ant mounds and 14 adjacent sites at the Oakville Prairie in eastern North Dakota reveals an increase in soil fertility due to ant activity. Essential replaceable cations and chelated and/or complexed trace element levels are higher in the ant mounds. Because of enhanced soil drainage, better soil aeration and chemical enrichment by the storage of insect components, ant excreta and plant material, the plant growth conditions are greatly improved by mound building.

KEY WORDS

Ant mounds, Oakville Prairie, replaceable cations, trace elements, North Dakota, lowland prairie, upland prairie.

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GRASSLAND USE PATTERNS AND PRAIRIE BIRD POPULATIONS IN MISSOURI

Robert M. Skinner

INTRODUCTION

Little information exists concerning the effect of various methods of management of grassland on the total avian community. The objective of this study was to determine what type or types of grassland management produce optimum cover for prairie bird diversity and density and to suggest feasible means of obtaining such cover on both private and public lands.

THE STUDY AREAS

This study was conducted on 290 separate fields varying in size from 4.0 to 202.3 ha (10 to 500 acres) in 11 counties in northern and western Missouri. The topography of the fields ranged from flat to very hilly and the soils from shallow and rocky to deep and loamy.

The percentage of land in grass in the study areas varied from almost all to nearly none. Most of the fields were composed of introduced grasses, but some were native grasses. Most of the native grass fields were on virgin sod, but a few had been seeded.

Northern and western Missouri was originally tall grass prairie or park lands, with only scattered areas of forest along streams (Steyermark, 1963).

METHODS AND MATERIALS

Feeding and Loafing Cover

Seven methods of grassland management were rated as to the feeding and loafing cover they provided for seven species of obligate grassland birds. The seven management methods were: idle, hayed, combined for seed and grazed at four intensities. The seven species of obligate prairie birds studied were: upland sandpiper (*Bartramia longicauda*), horned lark (*Eremophila alpestris*), short-billed marsh wren (*Cistothorus platensis*), eastern meadowlark (*Sturnella magna*), bobolink (*Dolichonyx oryzivorus*), Henslow's sparrow (*Passerherbulus henslowii*), and grasshopper sparrow (*Ammodramus savannarum*). The 290 fields were visited from mid-June through August 1973.

Average grazing height was determined by estimating the acreage of the field to be covered and then measuring the effective height of the grass at a minimum of five points per ha (two points per acre) selected by randomly tossing a stick. Each field was recorded in one of four average grazing height categories: 0-10.2, 10.2-20.3, 20.3-30.4, and over 30.4 cm (0-4, 4-8, 8-12, and over 12 inches).

The principal grass species in each field were identified and the percentage of forbs was estimated. All fields were thoroughly walked and all birds seen or heard were recorded.

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Observations in the seven grassland management types were standardized on the basis of time. Twenty hours were spent in each management category except seed-combined fields; only ten hours were spent in combined fields due to scarcity of this form of management.

Nesting Cover

Five idle fields totaling 44.5 ha (110 acres) and two grazed fields totaling 20.2 ha (50 acres) with an average grazing height of 22.9 cm (9 inches) were searched for nests of birds. The fields were searched with a crew completely and thoroughly in measured 1.52-meter (5-foot) swaths. Each searcher carried a 1.52-meter (5-foot) pole for parting the grass and for marking off swaths to be searched.

RESULTS

Feeding and Loafing Cover

Comparison of bird diversity and density in seven grassland management types revealed that idle grassland, in which no disturbance such as mowing or grazing was allowed, had the fewest species (3) and individuals (Table 1, Fig. 1). Only short-billed marsh wrens and Henslow's sparrows were abundant in idle grasslands.

Hayfields and seed-combined fields had more species (5) and more individuals than did idle grasslands. The combined fields with 45.7-cm (18-inch) cover provided better habitat for Henslow's sparrows than did cut hayfields. However, the shorter grass of the hayfields provided better cover than did the combined fields for upland sandpipers, eastern meadowlarks, and grasshopper sparrows.

Grazed fields had, in all height categories, more individuals and as many or more species (5-7) than did hayfields, combined fields, or idle fields. Grazed fields in the 10.2-20.3 and 20.3-30.4 cm (4-8 and 8-12 inch) height categories (Figs. 1 and 2) had about twice the number of individuals as did fields with grass heights between 0 and 10.2 cm (0 and 4 inches) or greater than 30.4 cm (12 inches). All seven species of birds were present in the 20.3-30.4 cm (8-12 inch) height category. In grass as short as 0-10.2 cm (0-4 inches), neither short-billed marsh wrens nor Henslow's sparrows were found. Short-billed marsh wrens were not found in the 10.2-20.3 cm (4-8 inch) category. In grazed fields more than 30.4 cm (12 inches) in height, horned larks were absent.

Three patterns of bird abundance in relation to grass height were found. Horned lark populations were found to be inversely related to grass height. Short-billed marsh wren and Henslow's sparrow populations were directly related to grass height. Upland sandpiper, eastern meadowlark, bobolink, and grasshopper sparrow populations were most dense when grass heights were between 10.2 and 30.4 cm (4 and 12 inches).

Pure and mixed stands of grasses were compared as to their use for feeding and loafing. Pure stands were those that contained only a single species of grass; mixed stands contained two or more species of grass or a grass plus a legume. Pure and mixed stands were studied on grazed fields with average heights of 10.2-30.4 cm (4-12 inches). Little difference could be found between pure and mixed stands of grasses as measured by their use as feeding and loafing cover.

Data from pure stands of grasses were not sufficient to permit comparison of different species' use for feeding and loafing. However, I noted little difference between species of grasses and density of bird populations as long as the height, density, and structure of the vegetation was similar. Cody (1968) also found that height and structure of grassland was of particular importance in selection of habitat by birds.

A distinct relationship between the amount of forbs present in a field and bird density was found in grazed grassland (Table 2). When forbs increased from zero to a point where

Table 1. Number of birds found from mid-June to August 1973 feeding or loafing in various cover types.

	Idle	45.7 cm (18") combined	5.1 cm (2") hay regrowth	Grazed (centimeters) 0-10.2 (0-4")	10.2-20.3 (4-8")	20.3-30.4 (8-12")	30.4 (12")
Upland Sandpiper	0	2	225	310	587	520	135
Horned Lark	0	0	0	71	20	14	0
Short-billed Marsh Wren	17	0	0	0	0	5	23
Eastern Meadowlark	64	110	451	612	1032	1104	309
Bobolink	0	6	36	16	87	121	52
Henslow's Sparrow	617	308	0	0	136	419	689
Grasshopper Sparrow	0	0	197	393	868	645	55
Hours searched	20	10	20	20	20	20	20
Total sightings	698	426	909	1402	2730	2828	1263

there existed a light scattering across the field, the number of birds increased. However, when forbs predominated, bird numbers declined drastically.

Dickcissels (*Spiza americana*) and, to a lesser extent, red-winged blackbirds (*Agelaius phoeniceus*) were particularly associated with forbs. A light scattering of forbs greatly enhanced their numbers. Dickcissels and red-winged blackbirds also declined in fields where forbs predominated, but both were abundant in idle fields and grazed fields when forbs were scattered. These species used forbs for nest sites and song perches.

Nesting Cover

A nest search of 44.5 ha (110 acres) in five fields of idle grassland revealed 69 nests of three species (eastern meadowlarks, dickcissels, and red-winged blackbirds) or 1.6 nests per ha (0.63 nests per acre). Two grazed fields with an average height of 22.9 cm (9 inches) totalling 20.2 ha (50 acres), were searched and 150 nests of seven species were found, or 7.4 nests per ha (3.0 nests per acre). The species found in the grazed fields were upland sandpipers, eastern meadowlarks, bobolinks, grasshopper sparrows, red-winged blackbirds, dickcissels, and bobwhites (*Colinus virginianus*).

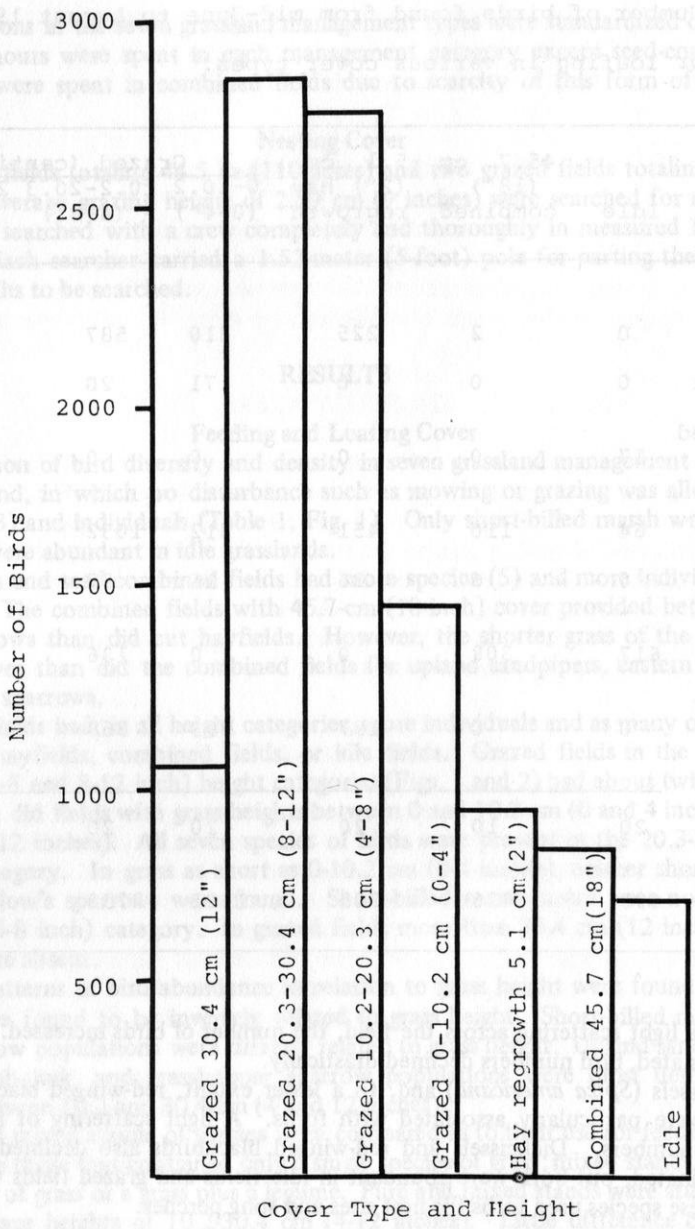

Fig. 1. Number of birds found from mid-June to August 1973 feeding and loafing in various cover types (20 hours of observation in each type).

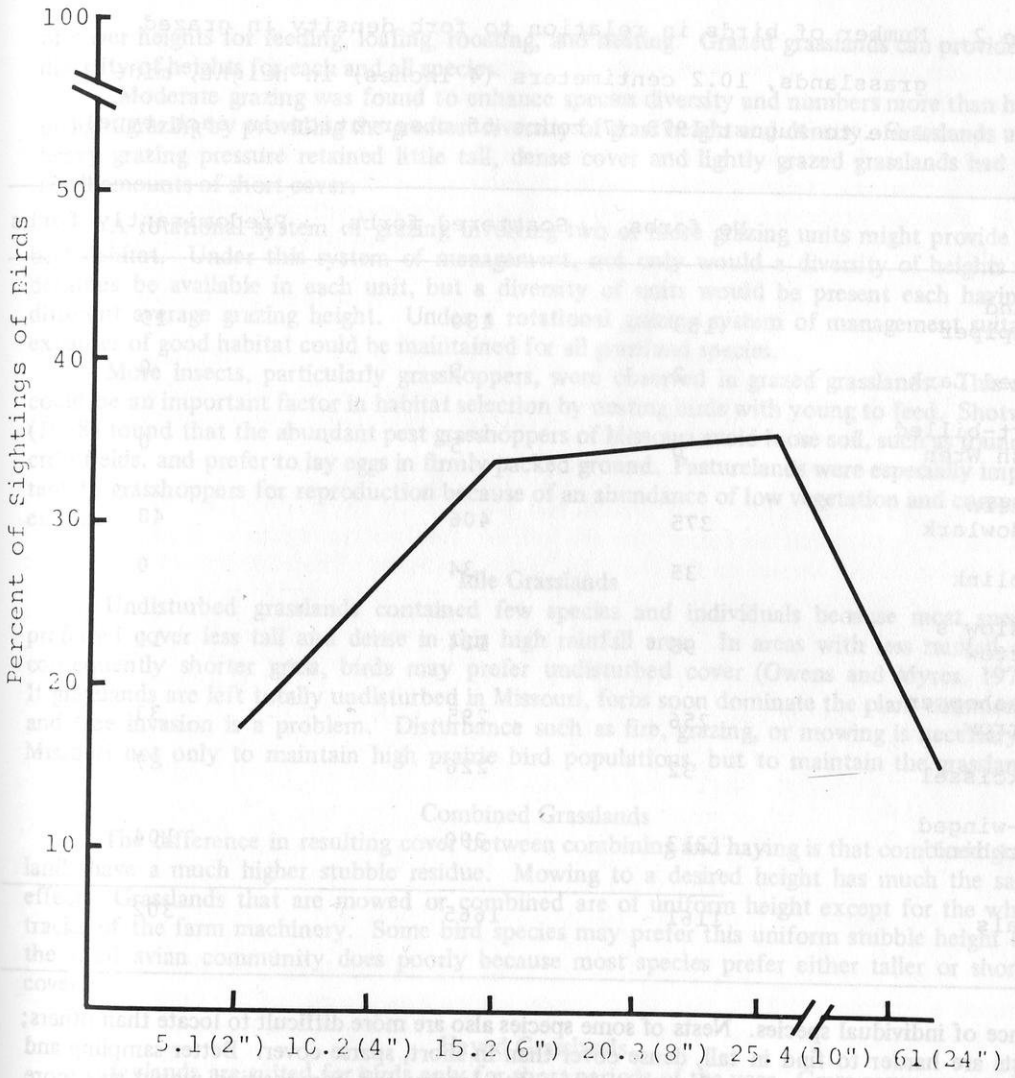

Fig. 2. The relationship between height of grass in grazed fields and the abundance of seven species of prairie birds.

DISCUSSION AND CONCLUSIONS

Bias in Methods and Results

The methods used and results obtained in this study were biased in several respects and care should be taken not to extrapolate more from the results than is justified. The cover type that birds favored in this study may not be the best possible, but only the best available. Some grassland birds are easier to locate than others. Therefore, figures only indicate change in occurrence of individual species from one cover type to another and do not indicate the abun-

Table 2. Number of birds in relation to forb density in grazed grasslands, 10.2 centimeters (4 inches) in height, mid-June to August 1973 (7 hours of observation in each type).

	No forbs	Scattered forbs	Predominantly forbs
Upland Sandpiper	153	180	19
Horned Lark	2	5	0
Short-billed Marsh Wren	0	5	0
Eastern Meadowlark	375	406	48
Bobolink	35	34	0
Henslow's Sparrow	95	124	11
Grasshopper Sparrow	256	295	33
Dickcissel	32	226	87
Red-winged Blackbird	213	390	104
Totals	1161	1665	302

dance of individual species. Nests of some species also are more difficult to locate than others; nests are harder to find in tall, dense cover than in short, sparse cover. Better sampling and more accurate measurement of vegetation height, density and composition would give more precise information regarding bird species diversity and abundance. Finally, it is important to understand that quality grassland wildlife habitat in Missouri may be quite different from quality habitat in other areas with different climates, plants, and animals.

Grazed Grasslands

The greatest number of species and individuals in this study were found under a grazing system of management which maintained an average height of 20.3-30.4 cm (8-12 inches). Grazed grasslands maintained high bird species diversity and numbers because of the maximum edge effect created by uneven or selective grazing producing great diversity in grass height and density.

Leopold (1933) wrote that game is a phenomenon of edges. The abundance of wildlife is directly related to the abundance of edge or the interspersion of cover types. Grazed grasslands with their complexity of height and density combinations provide habitat for a diversity of species requiring different grass cover heights. Individual species also require an interspersion

of cover heights for feeding, loafing, roosting, and nesting. Grazed grasslands can provide this diversity of heights for each and all species.

Moderate grazing was found to enhance species diversity and numbers more than heavy or light grazing by providing the greatest diversity of grass height and density. Grasslands under heavy grazing pressure retained little tall, dense cover and lightly grazed grasslands had only small amounts of short cover.

A rotational system of grazing involving two or more grazing units might provide the best habitat. Under this system of management, not only would a diversity of heights and densities be available in each unit, but a diversity of units would be present each having a different average grazing height. Under a rotational grazing system of management suitable expanses of good habitat could be maintained for all grassland species.

More insects, particularly grasshoppers, were observed in grazed grasslands. This also could be an important factor in habitat selection by nesting birds with young to feed. Shotwell (1958) found that the abundant pest grasshoppers of Missouri avoid loose soil, such as found in crop fields, and prefer to lay eggs in firmly packed ground. Pasturelands were especially important to grasshoppers for reproduction because of an abundance of low vegetation and compacted soil.

Idle Grasslands

Undisturbed grasslands contained few species and individuals because most species preferred cover less tall and dense in this high rainfall area. In areas with less rainfall and consequently shorter grass, birds may prefer undisturbed cover (Owens and Myres, 1973). If grasslands are left totally undisturbed in Missouri, forbs soon dominate the plant community and tree invasion is a problem. Disturbance such as fire, grazing, or mowing is necessary in Missouri not only to maintain high prairie bird populations, but to maintain the grasslands.

Combined Grasslands

The difference in resulting cover between combining and haying is that combined grasslands have a much higher stubble residue. Mowing to a desired height has much the same effect. Grasslands that are mowed or combined are of uniform height except for the wheel tracks of the farm machinery. Some bird species may prefer this uniform stubble height but the total avian community does poorly because most species prefer either taller or shorter cover.

Hayed Grasslands

Haylands are suited for birds only for short periods of the year. Grass cover managed in this manner is too short during the fall, winter, and early spring. As the growing season progresses, growth quickly surpasses the requirements of most species. At some point during the summer all growth is quickly and completely removed. Some cover is available during the fall, winter, and early spring months if hayfields are cut early enough in the season to allow regrowth.

Fire in Relation to Cover Management

No study was made of fire as a management tool, due to lack of a sufficient number of study areas. Other researchers have shown that fire alone is a successful management tool (Kirsch and Kruse, 1973) or in combination with other management practices (Westemeier, 1973).

Plant Species Composition

Although little difference was found between pure and mixed stands of grasses in relation to bird populations differences probably do exist. A mixed grass community produces uneven cover, due to the difference in heights and densities of different species. Also, some grasses are more palatable to livestock than others and are therefore selectively grazed. This difference creates a patchwork of closely and lightly grazed cover, which is favorable to birds.

Few birds occurred in grasslands where forbs predominated. The forbs present in such situations were generally of the tall, robust type. Such tall forbs, if too abundant, may raise the effective height of a grassland beyond the habitat preferences of most species. A few tall forbs were found desirable for song perches and for nest sites of dickcissels and red-winged blackbirds.

In conclusion, the greatest diversity and density of prairie birds in Missouri was maintained under a grazing system of management. Optimum conditions existed when the average grazing height of the grass was about 20.3-30.4 cm (8-12 inches) with a light scattering of forbs.

Habitat Restoration and Management

In pristine times, the great prairies and plains of the North American continent were maintained by two principal forces: fire and buffalo. Elk, deer, pronghorns and other forms of wildlife also had an impact on the character of the grasslands. The wildlife and the grasslands evolved with, adapted to, and benefitted from fire and grazing (Anderson et al., 1970). All the grasslands of what is now the state of Missouri were in the tall grass prairie region (Weaver, 1954; Kucera, 1961). This richest of all grasslands in luxuriant growth was dominated by native warm season grasses. As the prairies of Missouri were destroyed, they were replaced principally by cropland and by pasture land composed of introduced cool season grasses. Cool season grasses grow in the spring and in fall and are dormant during the hot summer months. Warm season grasses put on most of their growth during the summer when cool season grasses are inactive (Rountree et al., 1971).

Cool season grasses can be grazed closer to the ground without reducing their vigor, both in the summer and the winter, than warm season grasses. Therefore, it is difficult to economically maintain ideal wildlife habitat on private lands utilizing only cool season grasses. Warm season grasses, for maximum forage production, should never be grazed below 10 inches (Rountree et al., 1971) during the growing season in the tall grass prairie region where the natural height of these grasses is 6 feet or more. During the winter months, little or no stubble removal is recommended because warm season grasses grow during the dry summer on water stored from winter snow and spring rains. Stubble removal also opens stands of warm season grasses to weed invasion during the spring months when these grasses are still dormant (Anderson et al., 1970).

An occasional fire is recommended in warm season grass management in late spring just before green up. Fire, at this time, reduces invasion by and competition from undesirable cool season grasses and forbs. Fire also better distributes grazing pressure and makes the grass more palatable and nutritious (Weaver, 1954; Anderson et al., 1970).

Cattle gain weight on green, growing grass. For maximum gains and therefore profits it is desirable to maintain grazing animals on producing pasture during the entire growing season. Today in Missouri, most cattlemen rely solely on cool season grasses during the growing season for beef production. Cattle gain in the spring and fall, but usually only maintain themselves or lose weight during the summer (Rountree et al., 1974). For maximum beef production, I believe that 1/3 or more of Missouri's 4,047,000 hectares (10 million acres) of grassland should be converted to warm season grasses for summer pasture. This means that under proper grazing management the potential exists for creating several million hectares of prime grassland habitat productive of wildlife.

The native warm season grasses currently considered for pasture and range plantings are big bluestem (*Andropogon gerardi*), Indiangrass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*); major components of Missouri's original tall grass prairie. These grasses can be planted in pure stands or in mixtures. Forage production can be expected to equal or exceed that of cool season grasses (Rountree, 1973). If native grasses are reestablished and managed correctly for long-term sustained production by proper grazing and fire, then we will obtain again, through management of a natural plant community by natural means, a maximum quantity and quality of all things desirable -- birds, beef, and beauty.

ACKNOWLEDGEMENTS

I wish to thank Dr. William H. Elder, Rucker Professor of Fisheries and Wildlife, University of Missouri, Mr. Donald Christisen, Biologist of the Missouri Department of Conservation and Mr. Bill Crawford, Superintendent of Wildlife Research, Missouri Department of Conservation, for their advice and assistance during this study.

ABSTRACT

Methods of grassland management were evaluated for capability of providing cover for grassland birds. The evaluation included 290 separate grasslands in northern and western Missouri.

Grazed grasslands in all height categories had more individual birds and as many or more species than other grasslands. About twice the number of individual birds were present in cover of 10.2-30.4 cm (4-12 inches) than in lesser or greater heights of grazed grassland. Little difference was found between pure and mixed stands of grasses relative to feeding and loafing cover.

A relationship between the amount of forbs and bird density was noted on grazed grasslands. Birds tended to increase as forbs increased, but when forbs became dominant, the number of birds declined drastically.

Nest searches revealed 7.4 nests per hectare (3.0 nests per acre), representing seven species in grazed grassland and 1.6 nests per hectare (0.63 nests per acre) of three species in idle grassland.

KEY WORDS

Grassland management, cover height, grassland birds, Missouri.

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VIEWING THE INVISIBLE PRAIRIE

Francis E. Clark

Men of letters have variously and effectively described the visible prairie. Their phraseology ranges from Kipling's "it makes you weep for sheer loneliness" to Bryant's "these are the gardens of the desert" and Fletcher's "smooth dry carpet of velvet embroidered with brown patterns." The lay writer such as myself cannot hope to match their eloquence. Accordingly, I shall almost entirely ignore the visible prairie while discussing its unseen counterpart. Hopefully, that portion is sufficiently obscure that the lay public will not know whether I am speaking fact or fiction.

Actually, there are two invisible prairies. Firstly, there is the belowground macroscopic component, consisting of the roots and rhizomes of grasses and forbs and shrubs together with a miscellany of soil-dwelling insects and worms and small mammals. These are normally obscured from view simply because of the opacity of the soil. Such attention as I will give to this component will be primarily to bring its total biomass into perspective with the aboveground biomass of the visible prairie. The invisible prairie about which I shall speak in more detail is the microscopic prairie, consisting of all those myriads of organisms too small to be seen with the unaided eye, and therefore invisible whether they dwell above or belowground.

Presumably the lay public already knows all about microorganisms. It has repeatedly been told that countless millions of microbes can be placed on the head of a pin. Just why they should be so placed I do not know. Rather than to speak of microbes on pins, I want to talk about them in the soil, and about their importance in the total ecosystem. After all, it is the microbial component that makes the visible prairie flourish, that makes the prairies appear as the gardens of the desert rather than as lunar landscapes.

The plant biomass in grassland

To what extent do microbes contribute to the structure of grassland, that is, to the total biomass to be found on or in grassland soil? In answering this question let us look first at the biomass of the photosynthetic or primary producer component of grassland. Sims and Singh (1971) have given plant biomass data for grazed and ungrazed North American Grasslands at nine locations in almost that many different states. The average aboveground biomass, inclusive of live, standing dead and litter, was 275 g/m^2; and the average belowground, 1625 g/m^2. Percentagewise this means that roughly 15 percent of the total standing crop occurs aboveground, and 85 percent, belowground. Elsewhere in their paper, Sims and Singh (1971) allocate 40 percent of the roughly 600 g/m^2 annual net productivity in grassland to aboveground, and 60 percent, to belowground plant parts. The discrepancy in the above and belowground percentages for standing crop and annual productivity, as shown in Fig. 1, occurs because the belowground plant parts have a slower turnover and decay time than do the aboveground parts.

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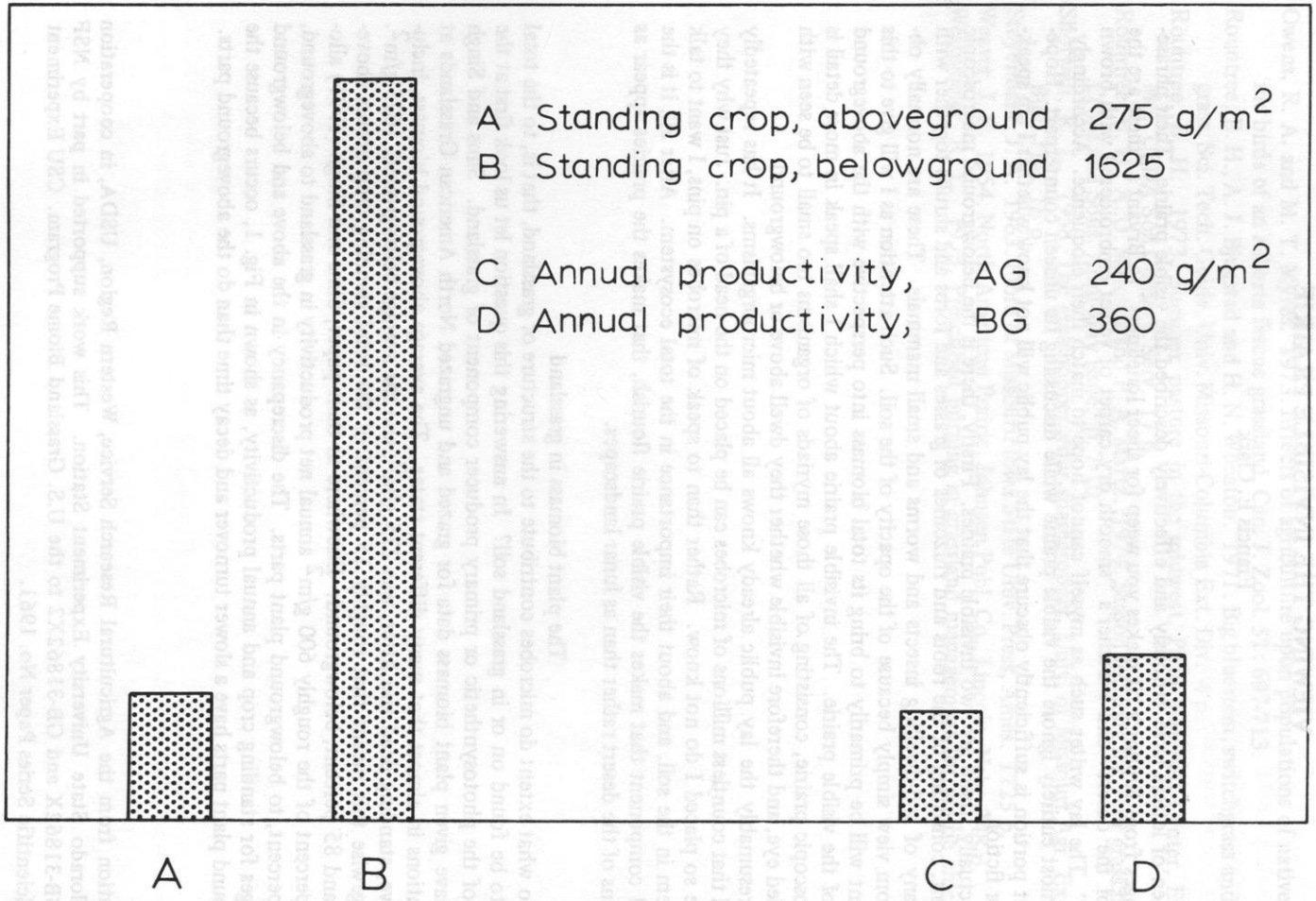

Fig. 1. Standing crop and annual productivity above and belowground in grassland.

Biomass of consumers and decomposers

Next, let us turn to the biomass of the diverse populations, macroscopic and microscopic, that feed on the standing crop. When mammalogists, ornithologists, herpetologists or entomologists are told that in the total secondary productivity structure of the prairie, the biomass of the microscopic members exceeds that of all the large mammals, rabbits, mice, toads, snakes, gophers, birds, grasshoppers, spiders, and other invertebrates too numerous to mention, their reaction almost invariably is one of disbelief. Again let us look at some numbers.

Insofar as a large mammal component is concerned, I have calculated that the dry weight biomass of the standing crop of cows on a western grassland subjected to a moderate stocking rate is of the order of 4 g/m^2. This calculation is in good agreement with values of 1 to 5 g/m^2 given by animal ecologists for other large mammals in other ecosystems (Petrusewicz, 1967). Small mammals, birds and reptiles taken collectively seldom contribute as much as 1 g/m^2. What about the invertebrates? Blocker (1973) has recently reported the biomass of all the aboveground arthropods in a tallgrass prairie as approximately 0.1 g/m^2.

The several above values, even when summed with other similarly small values for other component groups not separately mentioned, yield a biomass total far short of the 200 g/m^2 given by Clark and Paul (1970) for the microbial biomass in a Saskatchewan grassland. Their calculation may be somewhat high, but even if reduced to 100 g/m^2, the value still remains far larger than the sum of such values as are commonly given for mammals, birds, and arthropods. Fig. 2 depicts the relative biomass of primary producers, several groups of consumers, and microorganisms.

Energy flow in grassland

Is it reasonable to believe that the microbial biomass in grassland is ten to twenty times the total herbivore biomass? The skeptic will possibly contend that in a grazed pasture the cow consumes just about all the vegetation that is produced. He will further contend that if the annual net productivity is channeled mostly through the cow, then, obviously it would be impossible to nourish a far larger microbial biomass on that same grassland.

Let me try to answer the skeptic. Citation has already been made that 60 percent of the annual net productivity is channeled to belowground plant parts. That portion is unavailable to grazing animals. Of the 40 percent that does remain aboveground, it has been estimated that not more than 30 percent is ingested by large herbivores. This means that the cow probably ingests about 12 percent (i.e., 0.30 x 0.40) of the net productivity. Of the material ingested, approximately one-half passes through the alimentary tract and emerges from the cow as feces. That the dung of large herbivores is indeed energy-rich was well recognized by pioneer settlers on the prairie, who used buffalo chips to alleviate a part of the energy shortage with which they had to contend. After deducting the fecal loss, even the remaining six percent cannot be ascribed solely to the cow, inasmuch as the large animal must share a portion of the ingested energy with the microorganisms in the rumen and in the intestines. In brief, only a minor portion of the net productivity in grassland is channeled to consumers, and the portion remaining is entirely adequate to maintain a large standing crop of microorganisms.

It is also interesting to compare the biomass and energy flow relationships of plant roots with those of soil microorganisms. As noted earlier, Sims and Singh (1971) estimated a plant biomass belowground of 1625 g/m^2, and Clark and Paul (1970), a microbial biomass of 200 g/m^2. Both of these standing crop estimates need to be revised downward insofar as functional or active biomass is concerned. Let us assume the reductions are proportional and that the functional root biomass is eight times the functional microbial biomass. Several recent studies have partitioned the total soil respiration into plant root and microbial respiration. Estimates of root respiration have been obtained by comparing fallow and vegetated plots (J. Pigg and D. C. Coleman, personal communication, 1974), by ^{14}C radiotracer technique (Warembourg

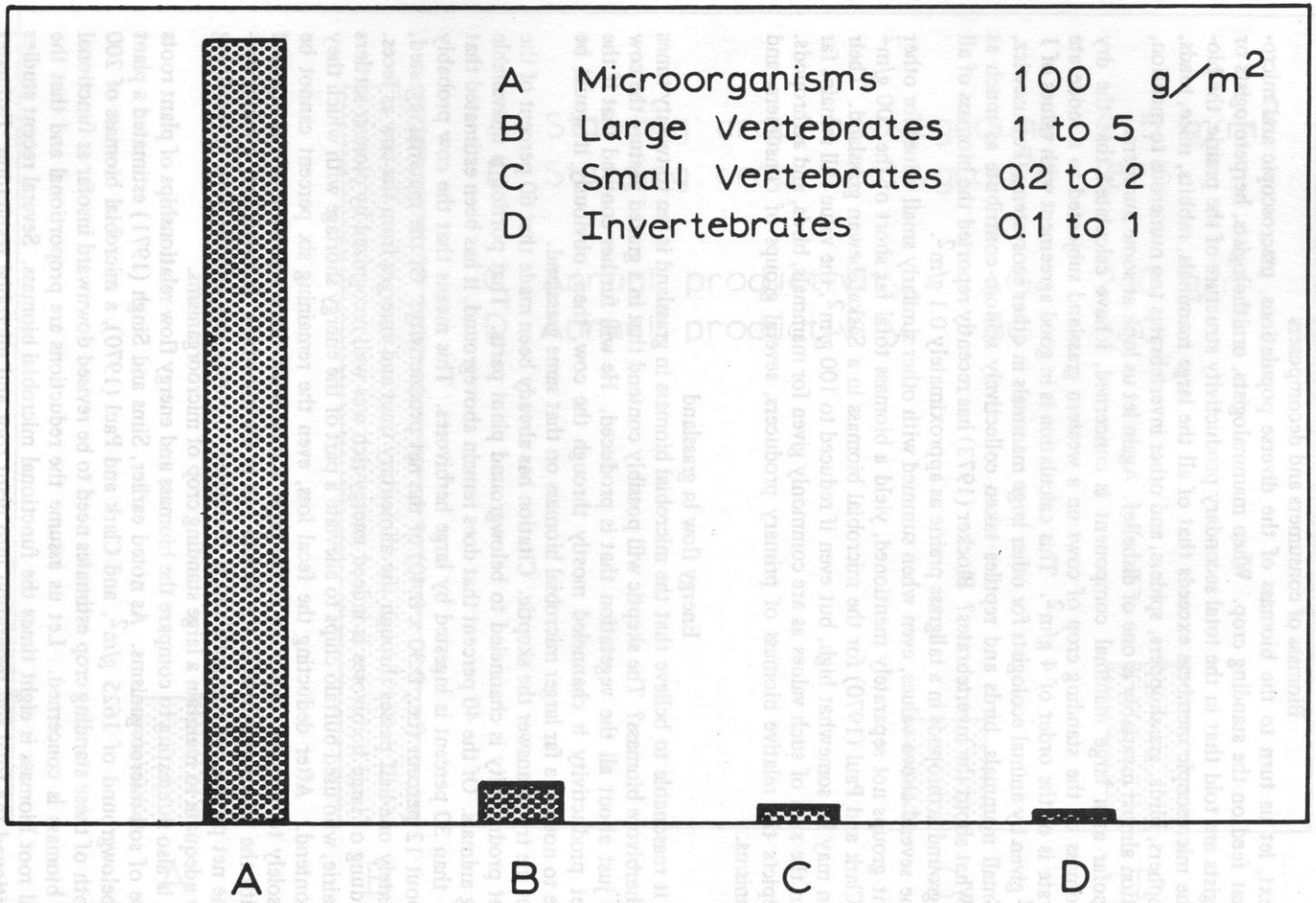

Fig. 2. Comparison of microbial biomass with that of certain consumer groups in grassland.

and Paul, 1974), and by CO_2 entrapments following the collection of soil cores and the hand sorting of roots therefrom (Clark and Coleman, 1972). In each instance, the root respiration was found to account for only about 20 percent of the total soil respiration. If one-eighth as much biomass produces four times as much carbon dioxide, then per unit weight of biomass the microorganisms are capable of respiring at a rate 32 times that of plant roots.

Role of microorganisms in the ecosystem

Microorganisms exert many and diverse influences on the total ecosystem. I shall discuss three topics which have been of particular interest to me in recent years. These are (1) the microbial tie-up and release of nutrients; (2) microbe-plant relationships beneficial to the living plant; and (3) microbes and the amelioration of environmental pollutions.

Emphasis has already been given to the fact that microorganisms are dominant components of the ecosystem both in respect to biomass and energy flow. As living organisms, microbes require the same nutrients as do the higher plants. Because they permeate the soil even more thoroughly than do plant roots and because they have a high surface/volume ratio, they are extremely efficient competitors for nutrients that are in short supply. Jansson (1968) has pointed out that the heterotrophic microflora in the soil successfully and principally fills its requirement for mineral nitrogen regardless of the needs of higher plants or autotrophic nitrifiers. On the basis of several years of fertilizer trails on grassland, Power (1974) has concluded that microbial cells and other organics immobilize slightly more of the applied nitrogen than do the plants themselves.

Microbes are also proficient in immobilizing phosphorus. Stewart, Hahn, and Cole (1973) have partitioned the total phosphorus of a native grassland into plant, microbial, and soil components as shown in Fig. 3. More phosphorus is immobilized in the soil organisms than in all the aboveground and belowground plant material. Much of the phosphorus contained in microbes is that which has been released during decomposition of plant tissues. The microorganisms are short-lived, and after death the phosphorus in their bodies again becomes available for either plant or microbial uptake. The continued productivity of an ecosystem is highly dependent on the recycling of nutrients by soil microorganisms.

A great deal of attention has been given to the mineralization processes in soil and to the cycling of mineral nutrients. Notwithstanding such intensive study, simulation models of nitrogen and phosphorus cycles still find it necessary to employ approximations concerning the mineral nutrient flow from litter. Knowledge is much more precise concerning the amount of applied fertilizer recoverable in the plant and of the effects of fertilizer on yield, crop quality, maturity, and susceptibility to disease. The greatest gap in knowledge is what happens belowground and in the invisible prairie. Ironically, insofar as fibrous-rooted plants are concerned, there is no really good way to differentiate between live and dead roots. Obviously alive and obviously dead roots can readily be distinguished, but when the entire gramineous root system is examined, most of the root material does not fall readily into either of the two obvious categories. Vital staining procedures have been widely used, but they are time-consuming and in part subjective. Radiotracer techniques appear somewhat more promising. Singh and Coleman (1974), using ^{14}C, found that in shortgrass prairie 62 percent of the total root biomass to a depth of 60 cm was functional. This value was largely determined by the great concentration of functional roots in the top 20 cm of the soil profile. Below 20 cm, roughly two-thirds of the total root biomass consisted of nonfunctional tissue. The 62 percent activity value of Singh and Coleman (1974) was relatively constant during the growing season. Distribution of photoassimilates to roots and shoots was not similarly constant. Of the total photoassimilate recovered in plants three days after pulse labelings in May, July, and September, 69, 79, and 85 percent, respectively, were recovered in roots and crowns.

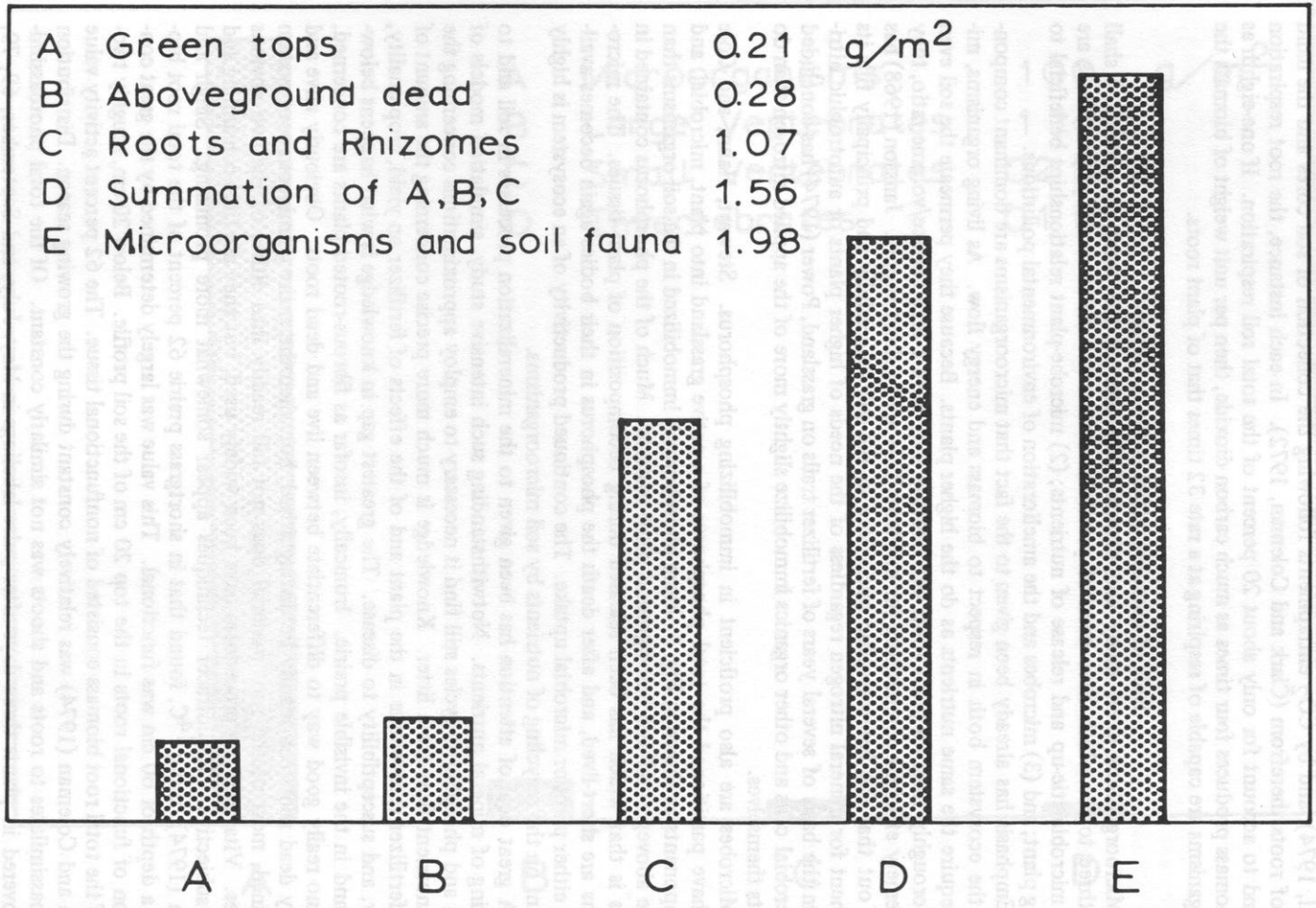

Fig. 3. Distribution of phosphorus in plant materials and microorganisms in Matador grassland (from data of Stewart, Halm, and Cole, 1973).

Such short-term partitioning does not represent seasonal productivity above and belowground. Warembourg and Paul (1974), also using ^{14}C labeling of native grassland, estimated seasonal shoot production at 130 g C/m^2, and root production, at about 100 g C/m^2. Working with ^{15}N on the same shortgrass prairie as did Singh and Coleman, Clark (1974) estimated that only 36 percent of the total root mass was functional. These several citations are made to emphasize the problems and the discrepancies to be encountered in studying the belowground herbage dynamics of grassland.

Uptake and partitioning of ^{15}N in grassland

During the past several years, W. A. O'Deen, G. C. Warren and myself have been engaged in measuring the flow of nitrogen through a grassland system. Our experimental approach has involved the ^{15}nitrogen isotope and a compartmentalization of the plant materials obtained during destructive samplings of mini-plots in a natural grassland. Sample processing involved division of the standing crop of plant materials into six compartments. Names of these compartments and the percentage of the total plant carbon found in each during the growing season are shown in Fig. 4.

In order to follow the cycling of nitrogen through these six compartments, a first step was to determine the distribution of the total standing crop of plant nitrogen. A composite distributional histogram, based on seven destructive samplings during the growing season, is shown in Fig. 5. At first glance this histogram appears to largely duplicate that given for carbon (Fig. 4). Nevertheless there are differences. These are brought more sharply into focus by tabulation of the C/N ratios of the six categories of plant material. Reading in the same order as the compartmental names in Fig. 5, the C/N ratios are: 23.3, 25.5, 34.6, 38.5, 21.7, and 13.5. These ratios attest that in the decomposition of plant material, the nitrogen cycle does not closely duplicate the carbon cycle. In brief, carbon escapes from the substrate as carbon dioxide, while nitrogen tends to remain in the substrate, the soil, or in the bodies of the decomposer organisms.

A second step in the experimental work was to determine the partitioning among the plant materials of applied nitrogen, or more specifically, of a pulse of new and distinctively marked nitrogen into the system. The pattern of uptake of ^{15}N during the 14 days immediately following its application to soil is shown in Fig. 6.

Two hours after application the percentages of the applied nitrogen in each of the sampling compartments roughly duplicated the percentage distribution of the plant carbon. The percentages of the total carbon in green tops, crowns, and live roots were 1.9, 25.3, and 10.2, respectively; and for the recovered ^{15}N, 1.1, 21.2, and 11.8, respectively. Quite possibly the ^{15}N values at two hours represented only physical adsorption of the applied nitrogen; however, inasmuch as the distribution of microorganisms can be expected to parallel organic matter distribution, it is quite possible that some microbial immobilization of ^{15}N occurred almost immediately after its application. The data show no evidence of active uptake of ^{15}N by the plant within the first two hours after application.

During the course of the first 14 days following ^{15}N fertilization, there was firm evidence of active plant uptake of the applied nitrogen. The plant crowns were the principal recipients or accumulators of ^{15}N during the early part of this time span, and the green tops, during the latter part (Fig. 6).

The fate of a pulse of tagged nitrogen in grassland over a time span of three growing seasons is shown in Fig. 7. Quantities of ^{15}N plotted for each of the six sampling compartments are those measured in June of three successive years. There were significant decreases (0.01 level) in ^{15}N in the green tops between the first and second and between the second and third seasons (Fig. 7a). There was a significant increase in ^{15}N in aboveground litter between the first and second year, but no significant change between the second and third year (Fig.

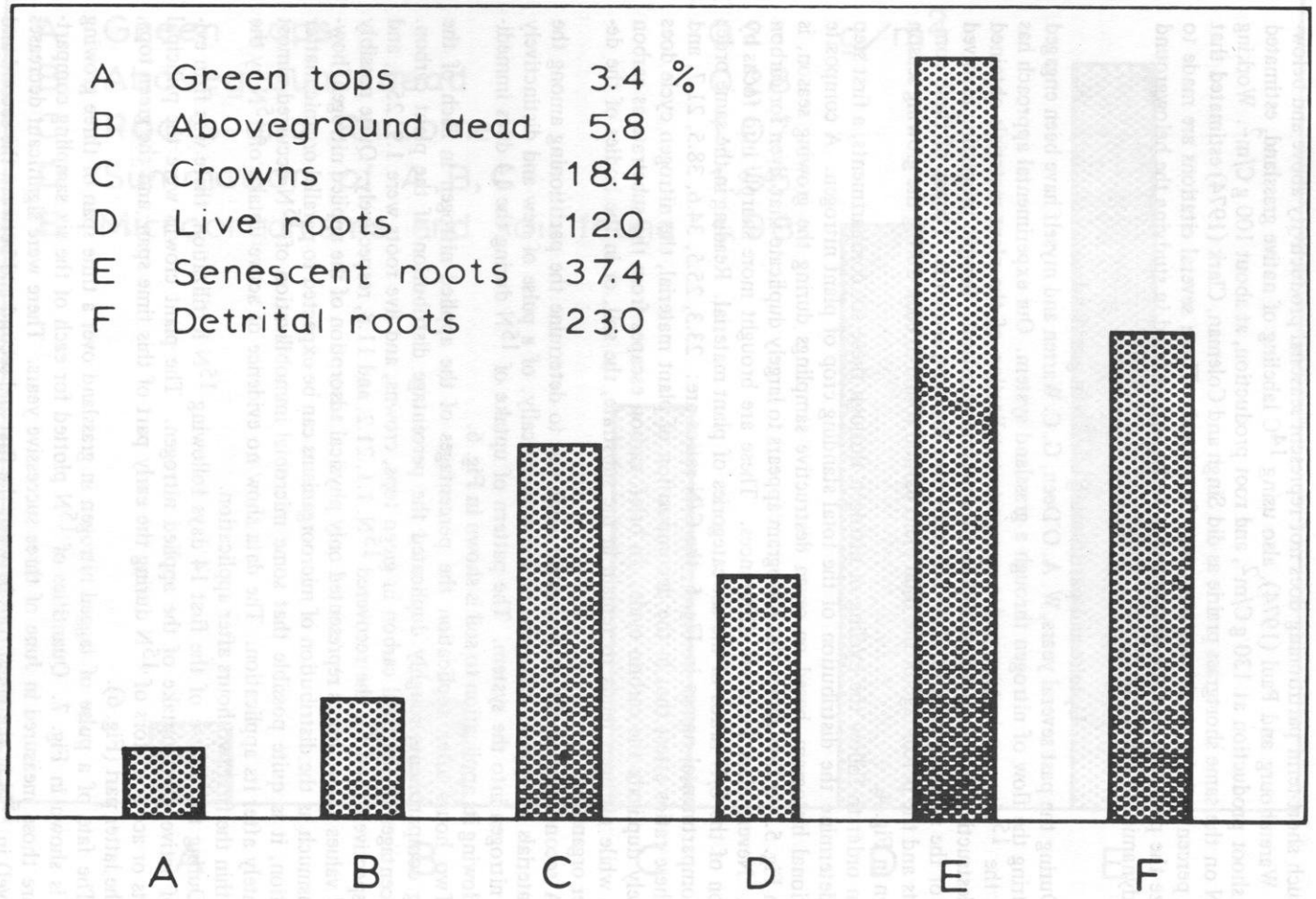

Fig. 4. Distribution of plant carbon in blue grama grassland.

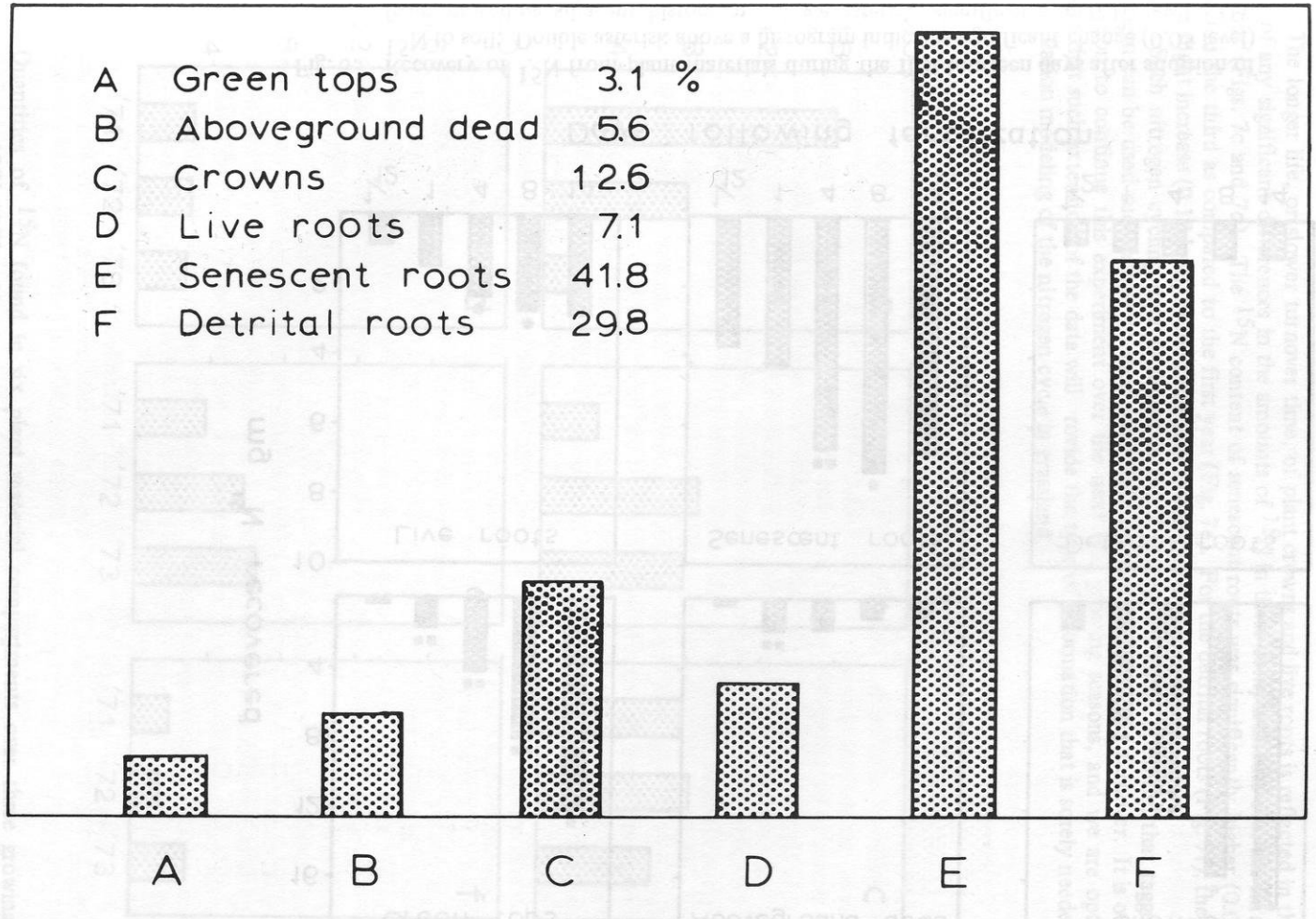

Fig. 5. Distribution of plant nitrogen in a blue grama grassland.

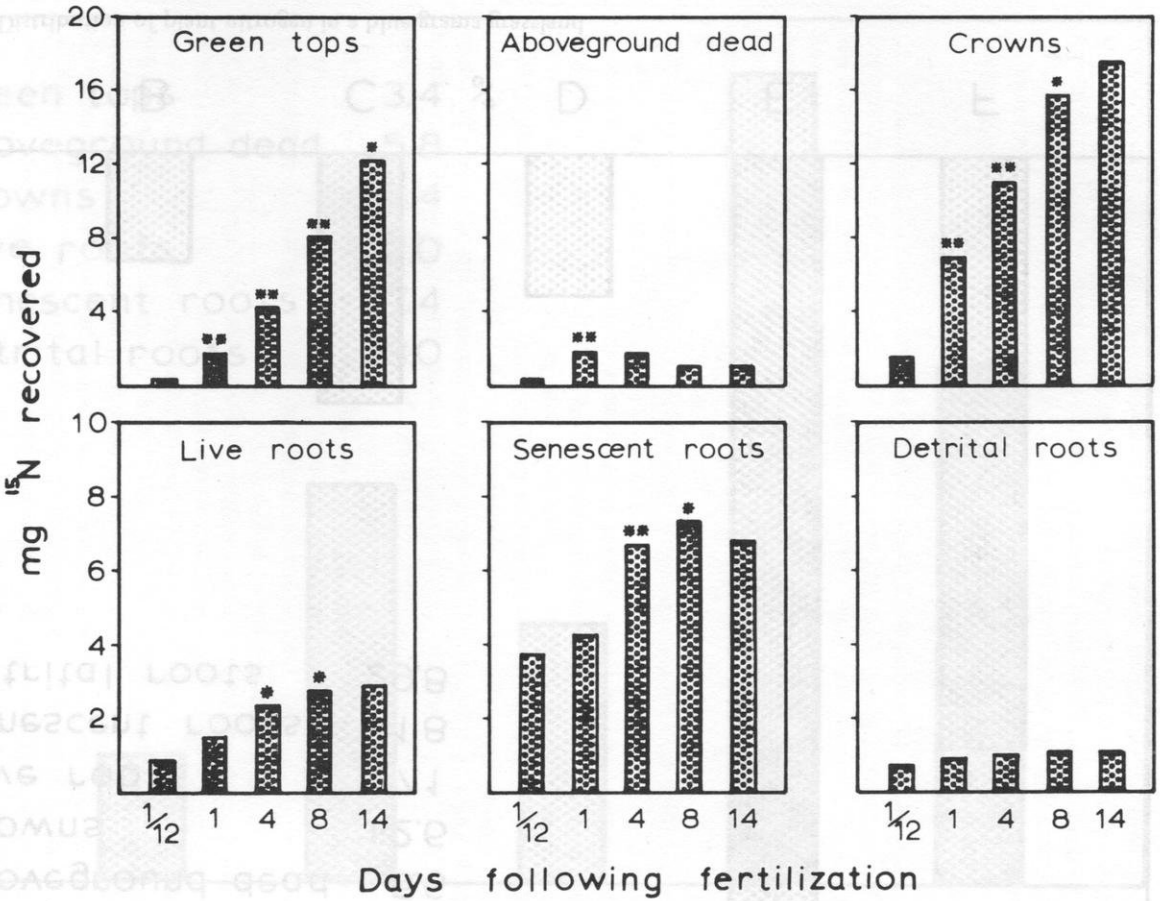

Fig. 6. Recovery of ^{15}N from plant materials during the first fourteen days after addition of ^{15}N to soil. Double asterisk above a histogram indicates significant change (0.05 level) from preceding adjacent histogram; single asterisk, significance at 0.10 level. Unpublished data of Clark, Warren, and O'Deen, 1974).

7b). The longer life, or slower turnover time, of plant crowns and live roots is reflected in the lack of any significant differences in the amounts of ^{15}N in these compartments over the three seasons (Figs. 7c and 7d). The ^{15}N content of senescent roots was significantly higher (0.05 level) in the third as compared to the first year (Fig. 7e). For the detrital roots (Fig. 7f), there was a slight increase (0.10 level) in the third year as compared to the first two years.

Such nitrogen cycling data as shown in Fig. 7 justify our initial optimism that tagged nitrogen can be used successfully to shed some light on root longevity and turnover. It is our intention to continue this experiment over the next two growing seasons, and we are optimistic that such extension of the data will provide the type of information that is sorely needed in simulation modeling of the nitrogen cycle in grassland.

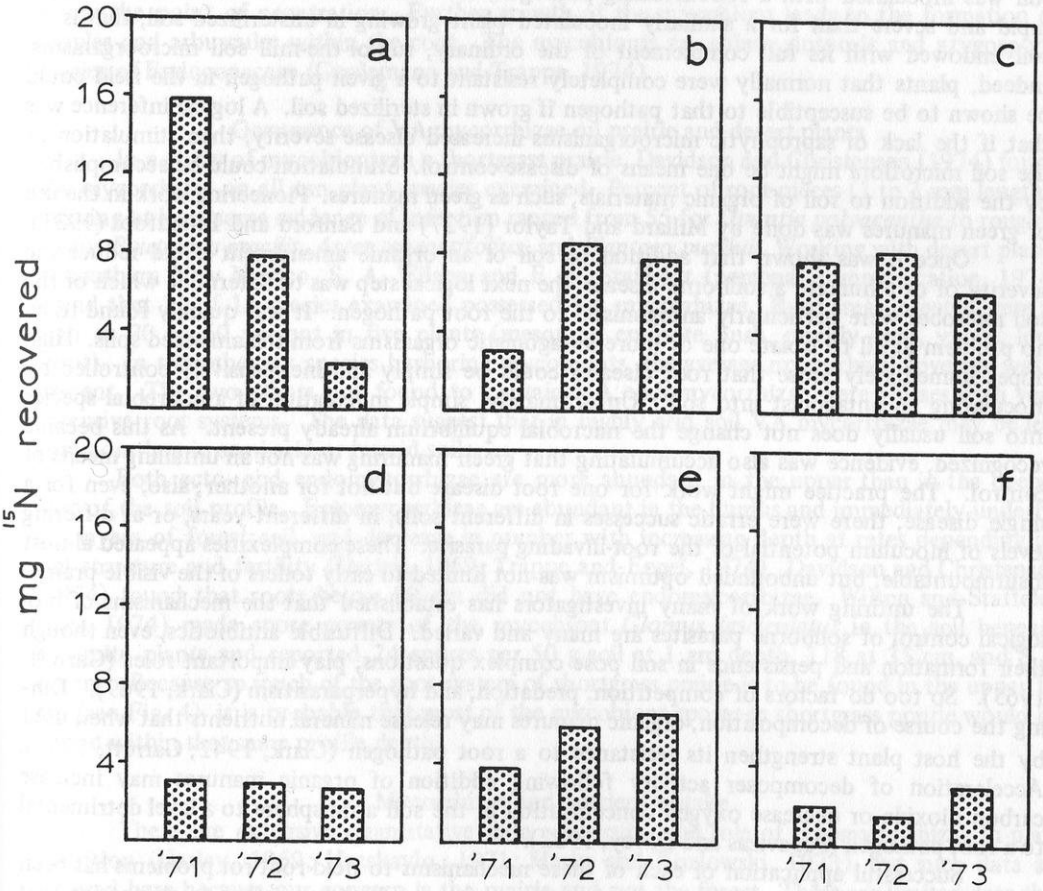

Fig. 7. Quantities of ^{15}N found in six plant material compartments over three growing seasons, 1971-1973. Numbers of ordinates show mg ^{15}N recovered per miniplot. For identities of compartments a through f, see Fig. 4 or 5. Unpublished data of Clark, Warren, and O'Deen.

Microbe-plant relationships beneficial to the living plant

Soil microorganisms promote plant welfare in many different ways. Among these are their fixation of molecular nitrogen, their solubilizing or chelating effects on mineral nutrients, their extension of root capability in the adsorption and storage of mineral nutrients, their suppression or control of soil-borne plant pathogens, their synthesis of accessory growth substances, and their influences on soil physical properties and on the water intake and water storage properties of soils. From this formidable array of topics, I shall discuss only two, namely, the role of soil microorganisms in protecting plants from soilborne diseases, and the phenomenon of mycorrhiza. A mycorrhiza is a fungus-root association or symbiosis that extends or takes over, to a greater or lesser degree, the nutrient uptake and water transport functions of plant roots.

First let us consider the microbial control of soilborne root diseases. During the first third of this century, it became evident that if a host plant growing in a previously sterilized soil was inoculated with a root-invading pathogen, the onset and course of disease was more rapid and severe than for a similarly inoculated plant growing in unsterilized soil, that is, in soil endowed with its full complement of the ordinary, run-of-the-mill soil microorganisms. Indeed, plants that normally were completely resistant to a given pathogen in the field could be shown to be susceptible to that pathogen if grown in sterilized soil. A logical inference was that if the lack of saprophytic microorganisms increased disease severity, then stimulation of the soil microflora might be one means of disease control. Stimulation could be accomplished by the addition to soil of organic materials, such as green manures. Pioneering work in the use of green manures was done by Millard and Taylor (1927) and Sanford and Broadfoot (1931).

Once it was shown that addition to soil of an organic amendment could reduce the severity of or eliminate a soilborne disease, the next logical step was to determine which of the soil microbes were particularly antogonistic to the root pathogen. It was quickly found to be no problem at all to isolate one or more antagonistic organisms from the amended soils. High hopes immediately arose that root diseases could be simply and inexpensively controlled by inoculating an antagonist into soil. Unfortunately, simple inoculation of a microbial species into soil usually does not change the microbial equilibrium already present. As this became recognized, evidence was also accumulating that green manuring was not an unfailing means of control. The practice might work for one root disease but not for another; also, even for a single disease, there were erratic successes in different soils, in different years, or at differing levels of inoculum potential of the root-invading parasite. These complexities appeared almost insurmountable, but unbounded optimism was not limited to early toilers of the visible prairie.

The untiring work of many investigators has established that the mechanisms of biological control of soilborne parasites are many and varied. Diffusible antibiotics, even though their formation and persistence in soil pose complex questions, play important roles (Garrett, 1965). So too do factors of competition, predation, and hyperparasitism (Clark, 1969). During the course of decomposition, organic manures may release mineral nutrients that when used by the host plant strengthen its resistance to a root pathogen (Clark, 1942; Garrett, 1965). Acceleration of decomposer activity following addition of organic manures may increase carbon dioxide or decrease oxygen concentration in the soil atmosphere to a level detrimental to a root pathogen (Papavizas and Davey, 1962).

Successful application of each of these mechanisms to field root rot problems has been achieved. It is not my intention to review those successes here but rather to emphasize that there is still a long way to go. Nearly a decade ago Boswell (1965) stated that there is probably no more difficult, urgent, and profitable area of research in agricultural biology than that of soil ecological phenomena in relation to plant disease. Hopefully, the microbiologists will continue to augment their knowledge of the tangled webs of interdependence of living things.

Mycorrhizae

Fossil roots obtained from the Carboniferous Period of the Palezoic and found to contain mycelial strands and vesicles (Osborn, 1909) testify that fungal-root associations have existed for several hundred million years. Mycorrhizae are now known to occur in the vast majority of all terrestrial plants. Trappe and Fogel (1974) state that most woody plants require mycorrhizae to survive, and most herbaceous plants need them to thrive.

In general, woody plants form ectomycorrhizae, characterized by a mantle of fungal tissue around the host rootlet. The fungal-feeder root associations possess a distinctive macroscopic appearance; typically they are short and stubby and multi-branched. There is a tremendous literature on ectomycorrhizae. Among monographic treatments during the past five years are those of Harley (1969), Hacskaylo (1971), and Marks and Kozlowski (1973).

The grasses and forbs of the prairie typically are endowed with vesicular-arbuscular (VA) endomycorrhizae. Mycobiont mycelium on the root surface remains sparse and infection is not macroscopically evident. Mycelial strands penetrate the root and form hyphal coils below the point of penetration. Further growth of the mycobiont leads to the formation of vesicles and arbuscules within the root. The mycobionts are chlamydosporic and azygosporic species of Endogonaceae (Gerdemann and Trappe, 1974).

Occurrence of VA mycorrhizae on prairie and desert plants

In a study of mycobionts in a shortgrass prairie, Davidson and Christensen (1974) found VA mycorrhizae on all ten plant species examined. Percent of root pieces (1 to 2 mm lengths) showing at least some evidence of infection ranged from 55 for *Opuntia polyacantha* to roughly 90 for *Bouteloua gracilis, Aster tenacetifolius,* and *Plantago purshii*. Working with desert plants in southern New Mexico, S. A. Wilson and E. E. Staffeldt (personal communication, 1974) found that 11 of 13 species examined possessed VA mycorrhizae. Root areas infected were as high as 30 to 60 percent in five plants (mesquite, creosote bush, prickly pear, yucca, loco weed). In the other six species harboring mycobionts, the average mycorrhizal coverage was 5 percent. The two plants not found to contain VA endomycorrhizae were grasses with very extensive root systems. The data suggest that in highly arid soil VA mycorrhizae may be less common than in semi-arid or humid soils.

Both ecto- and endomycorrhizae are more abundant in the upper than in the deeper part of the soil profile. Ectomycorrhizae are abundant in the humus and immediately underlying layers of forest soil, and decrease in number with increasing depth at rates depending on soil structure and fertility (Harley, 1969; Trappe and Fogel, 1974). Davidson and Christensen (1974) found that roots below 50 cm did not have endomycorrhizae. Wilson and Staffeldt (p.c., 1974) made spore counts of the mycobiont *Glomus fasciculatus* in the soil beneath mesquite plants and reported 24 spores per 50 g soil at 1 cm depth, 118 at 35 cm, and 8 at 60 cm. Because so much of the root system of shortgrass prairie is to be found in the upper 10 cm (see Fig. 4), it is probable that most of the mycobiont spores in shortgrass prairie would be found within that same profile depth.

Mycorrhizae and nutrient uptake

There are extensive quantitative data concerning the role of ectomycorrhizae in plant nutrition (Harley, 1969; Hacskaylo, 1971; Marks and Kozlowski, 1973), but such data are ignored here because our concern is the prairie and not the forest. There are limited data that formation of endomycorrhizae by vascular plants with Endogonaceae results in increased nutrient uptake and water transport by the host plants (Gerdemann, 1970; Safir, Boyer and Gerdemann, 1971; Mosse, 1972). Ho and Trappe (1973) reported translocation of ^{14}C from *Festuca* plants to their endomycorrhizal fungi. Davidson and Christensen (1974) compiled no data on plant nutrition but stated that Endogonaceae hyphae were sufficiently abundant on blue grama to play an important role in nutrient transfer. Wilson and Staffeldt (p.c., 1974)

expressed the opinion that plants with only about 5 percent mycobiont infection of their roots probably reaped no nutritional benefit from the symbiosis, whereas plants with 30 percent or more mycorrhizal involvement of their roots probably were benefited. These citations are given to emphasize how sparse is our information on the role of endomycorrhizae on grasses and forbs. This portion of our knowledge of the invisible prairie is still largely unexplored.

Microbes and the amelioration of environmental pollution

Microbes have been disposing of plant litter and animal carrion since long before the evolution of man. Alexander (1967) has stated that few instances can be found in nature of major accumulations of organic material where microorganisms can grow freely and where oxygen is plentiful. Prehistoric man used microorganisms to convert ordinary foods and foodstuffs into specialty foods and specialty beverages. Modern man has continued such usages and has added many others, such as using microbes to produce industrial alcohols and solvents, to process fibers, and to obtain antibiotics.

Microorganisms are also used to ameliorate certain problems in environmental Perhaps the classic example of a long-continued and deliberate use of microbes to provide a more esthetic environment is the municipal sewage treatment process. Phenomenal tonnages of raw sewage are subjected to microbial decomposition annually. Bacteria continue to be the primary agent of disposal for the effluent from the flush toilet and the kitchen sink.

Environmental legislation is now forcing mankind to rely more fully on microbial incineration of the end product of the sewage plant, namely, sewage sludge. This product is a mixture of the diverse inorganic inputs into sewage and of the recalcitrant parts or constituents of organic matter. Although some products of organic chemistry are fully recalcitrant to microbial degradation, for the most part the term recalcitrant is more relative than absolute. Comment has been made above that approximately half the dietary intake of the cow is recalcitrant to the digestive processes and emerges as feces. This emergence occurs not because the expelled material is totally undigestible or completely recalcitrant. It is indigestible in the length of time that the cow can normally afford to clog up its energy pipeline. The same holds true for the sewage treatment plant, wherein the so-called recalcitrant materials must periodically be removed or flushed from the digestion tanks. Prior to legislation to reduce air pollution, the sludge could be dried and then burned. This is no longer permissible. Accordingly, the spreading of sewage sludge on agricultural lands in order that the microbes can have a sufficiently long interval in which to more nearly complete organic matter decomposition is now becoming a necessity.

A closely related problem is the handling of more than a billion tons of manure from cattle feedlots each year. Current restrictions on air, water, and land pollution have caused some feedlot operators to devise systems of collecting, aerating, and exposing manure in order to hasten its breakdown by bacteria and in some instances, to obtain a product that can be packaged and sold as fertilizer. Other feedlot operators envision manure as even more valuable as a source of energy or feed for livestock. Packing plant paunch manure from grainfed cattle can be dried and blended with bloodmeal to produce a protein feed supplement superior to cottonseed meal (Matsushima, 1974). It has been estimated that at a cost of about $35 a ton, dried poultry manure can be turned into a protein feed supplement worth about $100 a ton, and also that re-cycled cow manure may soon supply up to 20 percent of the nation's livestock feed (Winter, 1974).

In short, whereas man has heretofore been largely concerned with using microbes on highly esthetic substrates to make such products as yogurt and cognac and silage and light-textured bread, he is now becoming increasingly interested in exposing such unesthetic substrates as sewage sludge and animal manure to microbial attack in managed environments. He hopes to make such substrates less objectionable to the general public and to exploit some of the feed and fertilizer values still remaining in them.

To the extent that manure is re-cycled and energy material diverted from microbial utilization to herbivore utilization, the role of microorganisms in the carbon cycle is being diminished. Percentagewise this reduction is quite insignificant; the decomposers remain as easily the major sink for the photosynthates of the primary producers. Re-cycling of manure and diversion of energy from the microbe to the cow may, however, further complicate a problem in semantics. Should the cow that is being fed re-cycled manure be called a consumer or a decomposer? Can the ecologist really differentiate between consumers and decomposers? At least one thing is certain. Microbes will continue to be the dominant decomposers and there is small probability that they will become endangered species. The invisible prairie is also the invincible prairie.

I opened this discussion with a quotation from Rudyard Kipling describing the invisible prairie. I would like to close with plagiarism of the 16th century English poet Robert Southwell (1561-1595) and with appreciation to Trappe and Fogel (1974) for bringing Southwell's original lines to my attention.

He that high growth on the visible prairie did bestow,
Gave also the invisible microbes leave to grow.

ABSTRACT

Attention is given to the invisible components of the prairie and to the functions performed by them which cause the prairies to be the gardens of the desert. Simple histograms are used to give a perspective of the primary and secondary productivity structure of grassland. Relationships of certain carbon and nutrient flows and biomass structure are discussed. Illustrative details on flow rates are offered from ongoing work monitoring the cycling of ^{15}nitrogen in a shortgrass prairie. The role of microorganisms in the control of soilborne plant pathogens, in mycorrhizal formations, and in certain waste disposal problems is discussed.

KEY WORDS

Microorganisms, ^{15}nitrogen, carbon, litter, biomass, decomposition, mycorrhizae, biological control, manure, sewage.

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DECOMPOSITION OF NATURAL AND SIMULATED LITTER IN OAKVILLE PRAIRIE

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INTRODUCTION

Determination of primary production and turnover in natural communities remains one of the fundamental endeavors of ecology. This information is basic to an understanding of the effects of environmental variables upon communities and their component species, and of energy dynamics at the ecosystem level. Grassland vegetation, due to its herbaceous composition and importance to agriculture, is ideal for studies of primary production and turnover in natural communities, and considerable attention has been devoted to grassland and prairie communities recently.

A long-term study of productivity of upland and lowland prairie communities has been initiated in Oakville Prairie, a native prairie in the Red River Valley of eastern North Dakota. Hadley and Buccos (1967) described community composition, habitats and primary production for six upland and lowland community types in this prairie during the 1965 growing season. Hadley (1970) compared primary production in those community types during 1965 and 1966 and associated major differences between the two growing seasons with amounts of early season rainfall. This paper is a part of the long-term study, and reports preliminary findings on litter decomposition in two of the community types examined in the earlier papers. Litter turnover is important in the maintenance of community productivity and nutrient availability.

The present paper will concentrate on turnover of above ground litter in an upland and a lowland community. Specific objectives include: examination of microenvironmental differences between the two community sites; analysis of decomposition differences in simulated litter samples between the two communities, between bag positions within communities, and between different years; and comparison of the turnover data for the simulated litter samples with natural litter data reported for the two communities by Hadley and Buccos (1967) and Hadley (1970).

COMMUNITY SITES IN OAKVILLE PRAIRIE

The upland and lowland prairie community sites were chosen to be representative of the *Poa-Andropogon-Stipa* and the *Distichlis-Hordeum* community types described by Hadley and Buccos (1967). The upland community consists of a floristically rich stand dominated by species of *Poa, Andropogon* (mostly *A. scoparius* Michx.) and *Stipa*. It occurs on an upland ridge with good internal soil drainage and soil salinity of less than 3mmhos/cm^2 ("unaffected or salt free"). The lowland community is a floristically poor stand dominated by *Distichlis stricta* (Torr.) Rydb. and *Hordeum jubatum* L. It occurs in a lowland site with restricted soil drainage, considerable bare ground and soil salinity of 17-23mmhos/cm^2.

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METHODS

Microenvironmental monitoring stations were maintained at both the upland and lowland sites during the 1971 and 1972 growing seasons. A Foxboro recording thermograph with humidity sensing element at 48-62 cm was placed in a ventilated shelter at each site. Temperature leads were situated at 60 cm (air), the soil surface, and -15 cm (soil). Temperature and relative humidity data were gathered from 15 July to 15 September 1971, and from 20 May to 1 September 1972. Hourly temperature and relative humidity values were averaged on a weekly basis, and weekly averages were compared between the two sites within years and between the two years within sites utilizing Student's "t" tests.

Standing herbage at both community sites was harvested by clipping during August in both the 1971 and 1972 growing seasons. Green herbage was separated from litter and oven dried at 80 C for 24 hours. In addition, green herbage of *Andropogon scoparius* was separated from clippings taken from the upland community and was similarly oven dried. Representative samples (10 g) were removed from the oven dried "pure *Andropon*" and "mixed species" herbage, and weighed to the nearest 0.1 g before being placed in nylon mesh bags. The mesh bags (20 by 9 cm with a pore size of 1.4 mm) were placed in pairs near the original collection sites, with one bag of each pair suspended 15 cm above the ground level and the other at the soil surface. These pairs of bags were placed at approximately one-meter intervals, and forty upland pairs and forty lowland pairs containing herbage collected in August 1971 were returned to the community of origin during early September 1971. An additional thirty pairs containing lowland herbage collected in August 1972 were placed in the lowland community in late September of that year.

In addition, packets of oven dried herbage from the upland community were placed in direct contact with the soil surface at the upland site in 1971. These "covered" samples were not placed in mesh bags but instead were merely covered by nylon mesh held in place by long nails driven into the ground.

Litter bags have been collected at six-month intervals since their placement in the field. At each collection date, five pairs of bags from each community were selected at random. Unfortunately, fire in 1973 destroyed all remaining bags in the upland community. Therefore, no pure species or mixed species litter samples were available in the upland site after the first year.

After collection, the litter bag and covered litter samples were oven dried and weighed to the nearest 0.1 g. Subsequently, the samples were ground in a Wiley Mill and caloric determinations were made on duplicate subsamples utilizing a Parr Oxygen Bomb Calorimeter. Additional subsamples were run whenever the duplicates differed by 50 cal/g. Caloric values were collected for ash residue, and are expressed as cal/g oven dry ash-free weight of herbage. In order to estimate the total caloric contents of litter sample, the caloric value per gram of sample was multiplied by the weight of the sample. These values will hereafter be referred to as total caloric content of a sample.

RESULTS AND DISCUSSION

Microclimatic data for the upland and lowland prairie communities during the 1971 and 1972 growing seasons are presented in Tables 1-2. As might be expected air temperatures at the two community sites were similar to those recorded at the nearby Larimore and Grand Forks weather stations (Environmental Data Service, 1972, 1973). Maximum deviations of mean air temperatures in each community from the averages for the Larimore and Grand Forks weather stations never exceeded 4.0 C for any of the 7-day periods and usually were less than 1.5 C.

Mean soil temperatures were generally significantly higher at the lowland than the up-

Table 1. Weekly means of temperature and relative humidity from upland and lowland sites at Oakville Prairie, 1971

7-day period beginning	Temperature +60 cm	Temperature surface	Temperature -15 cm	Relative humidity (%)
July 11				
Upland	17.8	14.6	13.9	65.7
Lowland	19.6	19.6***	18.2***	60.2***
July 18				
Upland	19.0	17.4	15.0	63.4
Lowland	17.6	19.8*	18.0***	67.0
July 25				
Upland	14.8	14.5	13.5	78.7
Lowland	12.8	15.6*	15.7***	68.0*
August 1				
Upland	16.1	15.5	12.9	74.7
Lowland	14.0	16.7	15.7***	64.2***
August 8				
Upland	19.9	17.3	15.2	78.9
Lowland	19.6	20.3***	18.6***	61.7***
August 15				
Upland	21.6	17.3	16.5	76.8
Lowland	----	----	----	----
August 22				
Upland	17.8	16.7	15.0	77.6
Lowland	16.8	18.3*	17.3***	70.3*
August 29				
Upland	20.2	17.5	15.4	84.8
Lowland	18.1	19.2	17.3*	78.1*
September 5				
Upland	16.3	14.6	14.1	79.2
Lowland	14.4***	16.4*	15.9*	71.8
September 12				
Upland	12.4	11.3	11.8	75.8
Lowland	10.3	12.4	12.9	69.2
September 19				
Upland	9.3	8.7	9.7	75.6
Lowland	7.8	10.2*	10.8**	68.1**

Temperatures are °C. * denotes $p \leq 0.05$, ** denotes $p \leq 0.01$, *** denotes $p \leq 0.005$

land community site during both growing seasons, and mean surface temperatures tended to be significantly higher in the lowland site during 1971. No significant differences were noted in surface temperature during 1972. Similarly, differences in mean air temperatures generally were not significant, although the deviations between the two sites did range up to 2.3 C.

Relative humidity generally was higher in the upland than in the lowland community site. These higher relative humidity percentages reflected the denser growth cover and taller plant stature in the upland community.

Soil moisture and precipitation were not examined in the present study. However, the soils of the lowland site were wetter than those of the upland site during periods of the growing season due to poorer internal drainage characteristics and saline artesian conditions in the lowland community.

Table 2. Weekly means of temperature and relative humidity from upland and lowland sites at Oakville Prairie, 1972

7-day period beginning	Temperature +60 cm	Temperature surface	Temperature -15 cm	Relative humidity (%)
May 28				
Upland	18.5	15.7	13.0**	59.8
Lowland	19.2	16.7	15.2	65.9
June 4				
Upland	20.2	17.8	14.8***	66.1
Lowland	20.2	18.5	17.0	66.1
June 11				
Upland	17.2	19.4	14.2**	74.3
Lowland	18.5	17.2	15.1	71.4
June 18				
Upland	14.0	18.2	13.1***	75.1***
Lowland	16.3	16.0	14.9	57.1
June 25				
Upland	21.0	23.7	15.2***	67.3
Lowland	22.3	19.9	17.8	66.8
July 2				
Upland	16.8	20.6	14.4	75.1
Lowland	19.0	18.9	17.0	67.9
July 9				
Upland	20.1	20.2	16.0***	80.1
Lowland	21.8	21.0	18.4	72.2
July 16				
Upland	18.7	18.4	15.5***	81.9
Lowland	19.8	19.0	17.7	76.7
July 23				
Upland	19.4	19.4	15.7***	76.6
Lowland	20.2	20.3	17.7	77.7
July 30				
Upland	17.3	20.6	16.1***	76.3***
Lowland	17.9	19.8	17.9	69.2
August 6				
Upland	17.4	17.8	15.0**	83.2***
Lowland	18.8	18.1	16.3	68.2
August 13				
Upland	24.8	25.4	18.8***	84.1***
Lowland	26.4	24.3	20.7	65.2
August 20				
Upland	19.3	20.9	16.8*	77.8**
Lowland	21.5	20.4	17.8	69.9
August 27				
Upland	21.9	21.4	16.3***	75.1***
Lowland	24.3	21.4	18.9	57.4

Temperatures are °C. * denotes $p \leq 0.05$, ** denotes $p \leq 0.01$, *** denotes $p \leq 0.005$

Thus, major temperature and moisture differences existed between the two community sites and between years within the sites. Temperature and moisture content of litter samples are two critical environmental factors regulating microbial activity in litter (Old, 1969; Witkamp, 1966). Witkamp (1966) reported that in simulated forest litter samples respiration was correlated with bacterial population density and that respiratory rate was positively correlated with weight loss of the litter samples. Old (1969) observed that litter contact with the soil surface remained wet for longer periods of time than litter samples suspended 12 cm above the ground. Presumably, microbial activity proceeded for longer periods of time in those ground samples.

In light of the differences in temperature and soil moisture between the upland and lowland community sites, differences in decomposition rate between the sites and between ground litter bags and bags suspended at 15 cm were anticipated. The anticipated difference in decomposition losses between the two communities was realized during the first year (Fig. 1). Lowland samples on the soil surface and suspended 15 cm above the ground lost 28.0 and 31.1% of their initial weights, whereas corresponding losses at the two levels in the upland community were only 9.9 and 16.0%, respectively. These differences were significant between community types, and were not significant between bag position within community types. Older samples in the lowland community also failed to yield significant differences in weight loss associated with bag position. This is in marked contrast to the findings of Old (1969) that weight losses were slower in suspended bags in the Illinois prairie.

Weight losses in the present study were most rapid during the first six months (over winter) in the simulated litter samples and then declined markedly. Conversely, Old (1969) noted that weight losses mostly occurred from March to November and that weights remained relatively constant throughout the winter. However, Kucera, Dahlman and Koelling (1967) found that only 57-65% of the total weight loss occurred during the growing season.

After 30 months weight losses in the lowland simulated litter samples averaged 50.6 and 49.3% at the ground and 15 cm levels, respectively. These losses were slightly slower than those in the Illinois and Missouri prairies. In the former prairie, Old (1969) found that decomposition losses after two years averaged 64% in the bags on the soil surface and only 44% in bags suspended at 12 cm. In the latter prairie, Koelling and Kucera (1965) reported a loss of 60% during a two-year period and Kucera et al. (1967) noted that the loss had reached 91% after four years. Although losses in litter older than three years have not yet been examined in the present study, an estimate of 91% within 4.5 years will probably prove reliable. Such a turnover time would be in accord with the natural litter turnover times reported by Whitman and Wali (1975) for eastern North Dakota grasslands in another paper in these Proceedings of the IV Midwest Prairie Conference.

Weight losses in the 18 and 24 month samples of litter placed in the field in 1972 did not differ markedly from those predicted for those times by the samples placed in the field in 1971 (Fig. 1). Thus, in the simulated litter samples litter of the two different years appeared to decompose at approximately the same rates. Examination of additional sampling times for the 1972 litter will allow a more detailed comparison of decomposition in the 1971 and 1972 simulated litter samples.

Caloric contents per gram of tissue in the simulated litter samples are presented in Table 3. Caloric values were similar to those reported in other studies of tall grass prairie litter (Hadley and Kieckhefer, 1963; Kucera et al. 1967). Values for both upland and lowland litter samples increased as the litter aged. These increases, although not significant statistically, were consistent and would suggest that the more slowly decomposable materials had higher caloric contents than more readily decomposable plant materials. Kucera et al. (1967) have reported similar increases in caloric content on an ash-free basis in older litter samples.

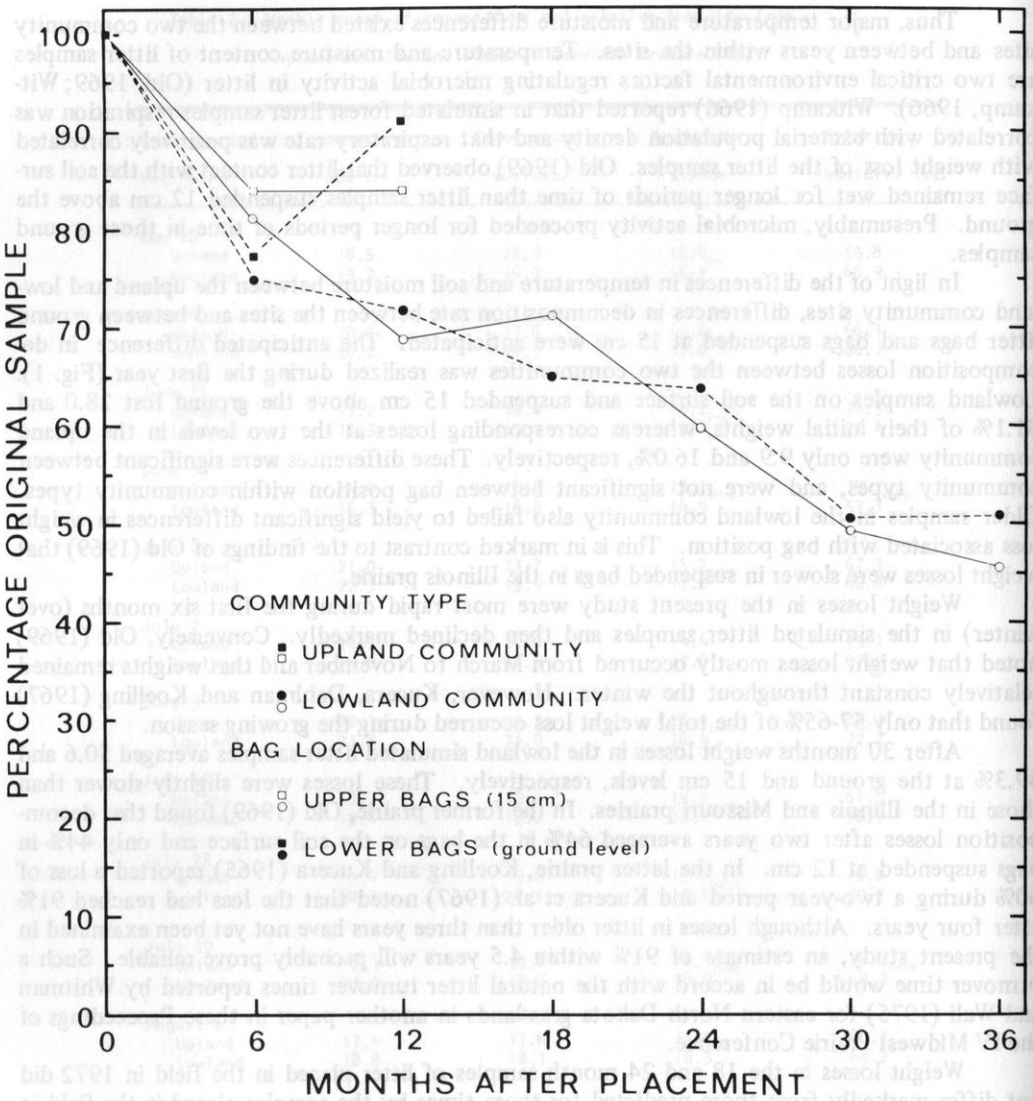

Fig. 1. Changes in biomass (g/sample) of simulated mixed species litter placed in the upland and lowland communities in Oakville Prairie. Litter bags were placed in the field in early September 1971 (6, 12, 30 and 36 month samples) or late August 1972 (18 and 24 month samples).

Table 3. Changes in caloric content (cal/g ash-free ovendry weight) of simulated pure and mixed species litter in upland and lowland prairie communities in Oakville Prairie

Community type and bag placement	Months after placement			
	0	12	18	30
Upland mixed species				
Upper bag	4645	4713	----	----
Lower bag	4645	4685	----	----
Lowland mixed species				
Upper bag	4541	4719	4783	4796
Lower bag	4541	4677	4775	4737
Upland pure Andropogon				
Upper bag	4631	4610	----	----
Lower bag	4631	4704	----	----
Upland mixed species (covered)	4625	4650	----	----
Upland pure Andropogon (covered)	4631	4677	----	----

Upper bags (+15 cm) and lower bags (ground level) were placed in September 1971 (0, 12, and 30 month samples) or late August 1972 (18 month samples)

Table 4. Changes in total caloric content (cal/sample) of simulated pure and mixed species litter in upland and lowland communities in Oakville Prairie

Community type and bag placement	Months after placement			
	0	12	18	30
Upland mixed species				
Upper bag	46713	39579	-----	-----
Lower bag	46713	42281	-----	-----
Lowland mixed species				
Upper bag	45692	32837	33881	23924
Lower bag	45692	33943	31055	24332
Upland pure Andropogon				
Upper bag	46773	38245	-----	-----
Lower bag	46773	39595	-----	-----
Upland mixed species (covered)	46500	41141	-----	-----
Upland pure Andropogon (covered)	46770	40174	-----	-----

Upper bags (+15 cm) and lower bags (ground level) were placed in September 1971 (0, 12, and 30 month samples) or late August 1972 (18 month samples)

Caloric content are expressed as total calories in litter samples in Table 4. The changes in total caloric values with time paralleled the weight loss curves.

The estimate of 2.5 years for 50% decomposition of simulated litter samples in the present study was markedly slower than that obtained from the natural litter data for these same communities during the 1965 growing season (Hadley and Buccos, 1967). Their data for standing litter in the spring and fall of that year would suggest that litter decomposition was in the range of 300-320 $g/m^{-2}/year^{-1}$ for both upland and lowland communities and that litter turnover times were only approximately 1.5 years. However, natural litter data for the 1966 growing season (Hadley, unpubl.) would suggest turnover times of approximately 3.0 years.

The variation between estimates was partially attributable to the year-to-year variation in primary herbage production. Hadley (1970) found that primary herbage production values varied by 30-47% in upland and 20-26% in lowland communities in Oakville Prairie between the 1965 and 1966 growing seasons. These differences appeared to be correlated with early season rainfall. A cause for the slower turnover estimate in the simulated litter sample may have been the exclusion of larger herbivores from the simulated litter samples by the mesh bags. Whatever the causes, the estimates of litter turnover from the simulated samples and the 1966 natural litter data appeared to be in good agreement with the estimates from natural litter data for grasslands elsewhere in eastern North Dakota (Whitman and Wali, 1975).

ACKNOWLEDGEMENTS

The authors gratefully acknowledge the Biology Department, University of North Dakota for providing use of the laboratory facilities at Oakville Prairie.

ABSTRACT

Decomposition of native plant material was studied in upland and lowland communities in an eastern North Dakota prairie. Simulated upland litter samples at the soil surface and suspended 15 cm above the ground in the upland community lost 9.9 and 16.0% of their initial weights within the first year. Comparable losses for the lowland samples at the two levels in the lowland community were 28.0 and 31.1%. After 2.5 years, the losses in the lowland samples had reached 49.3 and 50.6% at the two levels, respectively. Caloric contents of the simulated litter samples in both communities increased slightly during the 2.5 years. The simulated litter data yielded estimates of litter turnover which were considerably slower than those indicated by the natural litter data previously reported for these same communities. The simulated litter and natural litter data would indicate that decomposition rates varied both with year and community type and did not vary markedly with bag position.

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SOIL TEMPERATURE AND PLANT GROWTH IN THE NORTHERN GREAT PLAINS

W. O. Willis and J. F. Power

Soil temperature has a major influence on plant growth, and discussions of such invariably turn to "cause and effect." This review article presents a few examples of interrelated factors that have a bearing on soil temperature vs. plant growth in the northern Great Plains. For those interested in pursuing the subject, two recent reviews (Cooper, 1973; Willis and Amemiya, 1973) are a recommended starting point.

It is well known that water viscosity and surface tension are inversely related to temperature, and relative hydraulic conductivity increases as temperature increases. A plant needs water to grow and, if temperature affects rate of water flow in the soil, then soil-temperature: soil-water:plant growth relations must be considered. In a similar fashion, as other biological factors are added the system becomes additively complex.

The soil-temperature regime during the growing season can be conditioned by antecedent soil water effects and snow cover during the preceding fall and winter. For example, Figure 1 shows depth of frost overwinter for soil that was wet or dry in the fall before freezing (Willis et al., 1961). A dry soil freezes quicker and deeper than a wet soil, and thaws quicker in the spring. This behavior reflects the higher thermal conductivity and heat capacity of wet soil as compared to dry soil (Willis and Raney, 1971). Crawford and Legget (1957) showed frost depth was reduced about 1 foot for each foot of undisturbed snow cover and, in some instances, as much as 2 feet reduction in frost penetration for each foot of snow. Potter (1956) obtained similar results at Fargo, North Dakota. Observations of snowpacks created by tree windbreaks or snow fences at Mandan, North Dakota have indicated that if a snowdrift is more than about 4 feet deep, the soil under the snowdrift is not likely to be frozen.

Figure 2 shows overwinter frost depth in an area with a fairly high water table (Willis et al., 1964). The water table begins to rise in April even though frost remains in the upper profile. This indicates the frost mass has changed sufficiently to allow some permeation of liquid flow. Generally, as the profile cools or warms, the water table drops or rises in response to the known fact that a cold soil holds more water than a warm soil (Potter, 1956; Willis et al., 1961; Benz et al., 1968). Figure 2 also shows that frost remains in the profile for a significant time after the surface has thawed. Thus, for this or similarly wet soils, if planting is done about May 1, plant roots must grow into soil colder than the surface (Wilkinson, 1967).

Another factor affecting depth and longevity of snowpack is the type and amount of vegetative cover. Figure 3 shows the duration of snowmelt with different heights of standing wheat stubble (Willis et al., 1969). Snowpack runoff is faster and greater with increased stubble height. Conceivably, vegetative cover could be manipulated as a management practice for soil water conversation and for soil temperature regulation.

All plants do not respond the same to a given soil temperature regime, so knowledge of magnitude and variation in soil temperature is necessary. Figure 4 represents the annual temperature curve from averaged measurement at the 1-, 2-, and 3-foot depths (Willis and Amemiya, 1973). Figure 5 shows soil temperature measurements to a depth of more than 20 m at 2-month intervals. Below the 10-m depth, temperature is virtually constant. Figure 6 gives a

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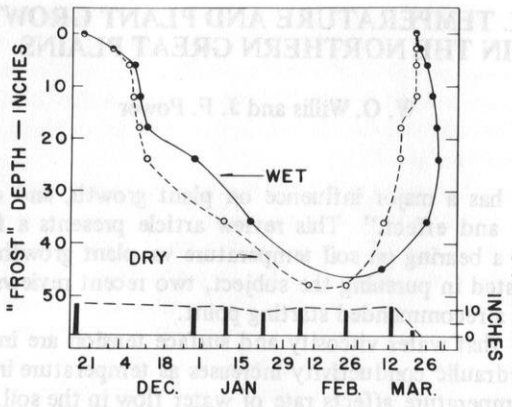

Fig. 1. Depth of freezing temperature (32 F isotherm) as a function of time for a wet or dry soil (from Willis et al. 1961).

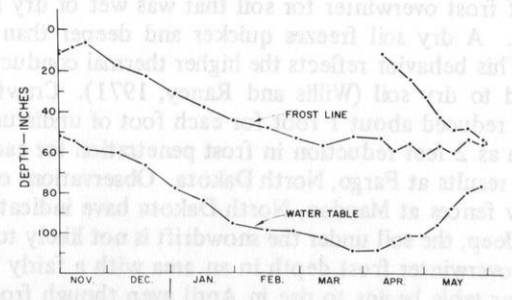

Fig. 2. Measured depths of water table and frost over a winter period (from Willis et al. 1964).

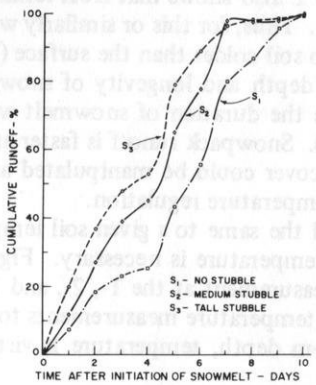

Fig. 3. Percent cumulative snowpack runoff with time and 3 stubble heights for 6 spring thaw periods (1961-1967) (from Willis et al. 1969).

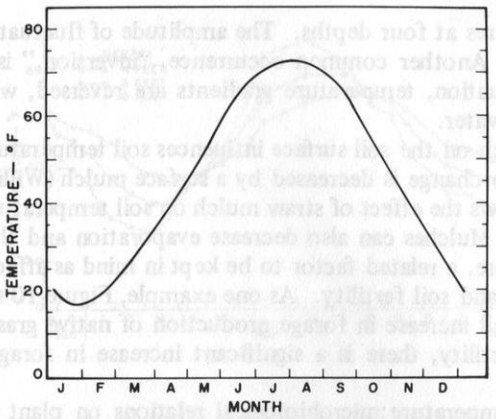

Fig. 4. Composite average of soil temperature at the 1-, 2-, and 3-foot depths, measured at weekly intervals over a number of years (from Willis and Amemiya, 1973).

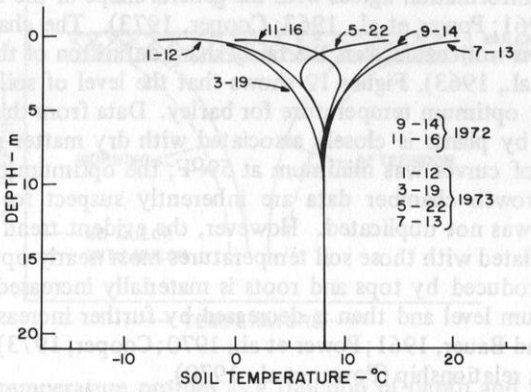

Fig. 5. Soil temperature as a function of depth measured at bimonthly intervals (unpublished data, Northern Great Plains Research Center, Mandan, North Dakota).

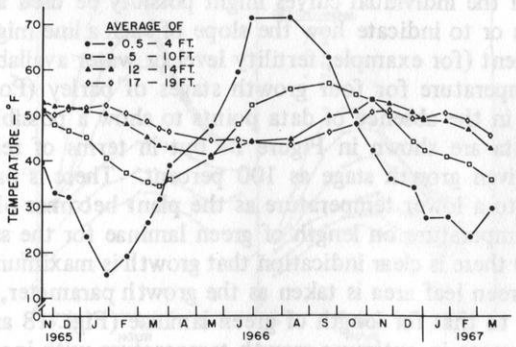

Fig. 6. Average soil temperature at four depths as a function of time (unpublished data, Northern Great Plains Research Center, Mandan, North Dakota).

comparison of temperatures at four depths. The amplitude of fluctuation is more pronounced for the shallow depths. Another common occurrence, "inversion," is more clearly shown in Figure 7. In such a situation, temperature gradients are reversed, which in turn influences liquid and vapor flow of water.

Any kind of mulch on the soil surface influences soil temperatures. Figure 8 shows the amplitude of temperature change is decreased by a surface mulch (Willis and Raney, 1971). In more detail, Figure 9 shows the effect of straw mulch on soil temperature at different depths in the soil during one day. Mulches can also decrease evaporation and thereby increase available water to plants. Therefore, a related factor to be kept in mind as affecting plant growth is the interaction of soil water and soil fertility. As one example, Figure 10 shows that with low fertility, there is only a small increase in forage production of native grass as available soil water increases; with higher fertility, there is a significant increase in forage as available water increases (Smika, 1965).

Effects of soil temperature:microbiological relations on plant growth will not be discussed, although they can be important.

Figure 11 shows the growth rate of maize seedlings as a function of temperature (Lehenbauer, 1914). Other information agrees with the general shape of the curve (Willis et al., 1957; Radke and Bauer, 1961; Power et al., 1963; Cooper, 1973). The change in slope before and after the "optimum" is noticeable, as is the fairly sharp definition of the optimum peak. From other data (Power et al., 1963), Figure 12 shows that the level of soil phosphorus can extend the range of generally optimum temperature for barley. Data from this same work (Figure 13) show that water use by plants is closely associated with dry matter production and that the slope of this family of curves was minimum at 59°F, the optimum temperature indicated in Figure 12. These growth chamber data are inherently suspect for extension to the field, because field climate was not duplicated. However, the evident trend is that maximum water use efficiency is associated with those soil temperatures most nearly optimum for plant growth.

Dry matter produced by tops and roots is materially increased by increasing soil temperature to an optimum level and then is decreased by further increase in temperature (Willis et al., 1957; Radke and Bauer, 1961; Power et al., 1970; Cooper, 1973). Figure 14 is presented as one example of this relationship (Power et al., 1970).

Up to this point, the data presented have been factual but very brief to highlight particular major effects. It is of interest, now, to speculate on one behavioral response of plants to soil temperature; Figure 15 shows, hypothetically, some factor of plant growth (say growth rate) as a function of (soil) temperature for different ages of a plant. This concept has been previously considered (Willis et al., 1957; Willis and Amemiya, 1973). The dotted line passing through the maxima of the individual curves might possibly be used as an index number for a particular plant species or to indicate how the slope of such a line might change in response to a given cultural treatment (for example, fertility level or water availability). Figure 16 shows dry weight versus temperature for four growth stages of barley (Power et al., 1967). The dotted lines are added in the absence of data points to show a possible position of maximum growth. The same data are shown in Figure 17 but in terms of relative growth, using the highest weight for a given growth stage as 100 percent. There is partial indication that the maximum has shifted to a lower temperature as the plant becomes older. Figures 18 and 19 show the effects of temperature on length of green laminae for the same plants as in Figures 16 and 17; in this case there is clear indication that growth is maximum at a lower temperature as the plant ages. If green leaf area is taken as the growth parameter, the growth:temperature relation is very similar to that for length of green laminae (Figs. 18 and 19). For sugarbeets, Figure 20 shows a decrease in optimum-growth temperature with increased age when relative weight was the measured growth function (Radke and Bauer, 1961). A similar response has been shown for corn (Willis et al., 1957; Walker, 1969). Thus, there is factual support for the

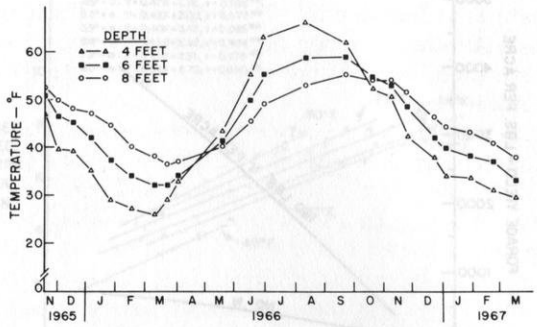

Fig. 7. Soil temperature at the 4-, 6-, and 8-foot depths as a function of time (unpublished data, Northern Great Plains Research Center, Mandan, North Dakota).

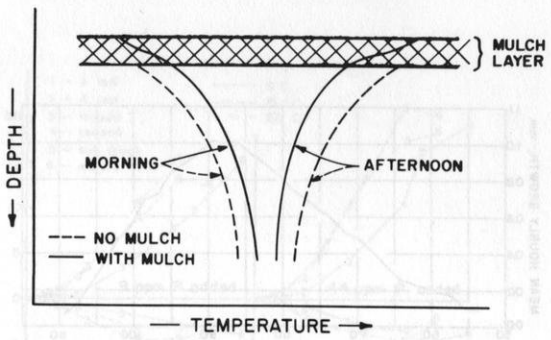

Fig. 8. Expected soil temperature profiles as a function of depth and time in a soil with and without mulch cover (from Willis and Raney, 1971).

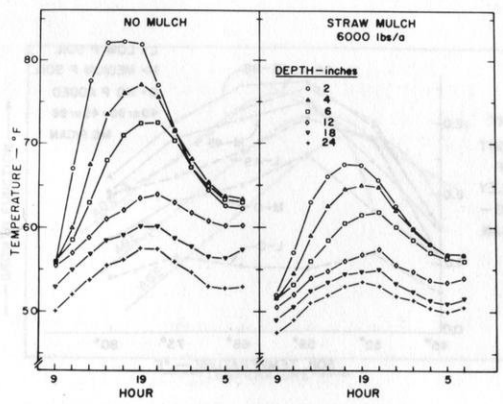

Fig. 9. Soil temperature at indicated depths, with and without mulch taken at 2-hour intervals during a 24-hour period in May (from Willis and Amemiya, 1973).

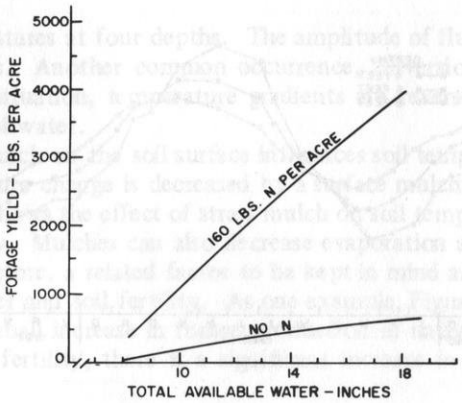

Fig. 10. Effect of available water on native grass forage production with 0 and 160 pounds nitrogen fertilizer applied annually (from Smika et al. 1965).

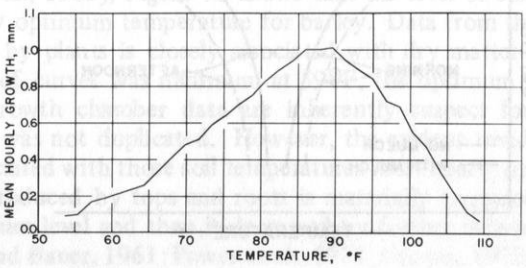

Fig. 11. Growth rate of maize seedling shoots at different temperatures (data from Lehenbauer, 1914).

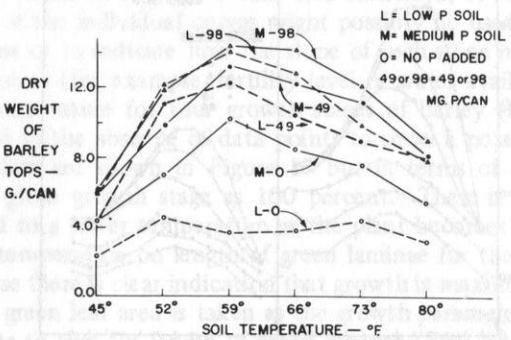

Fig. 12. Effect of soil temperature on dry matter production of barley tops (from Power et al. 1963).

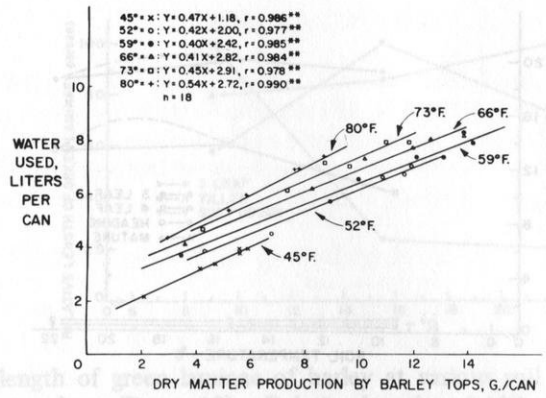

Fig. 13. Relationship of barley water use to dry matter production at indicated soil temperatures (from Power et al. 1963).

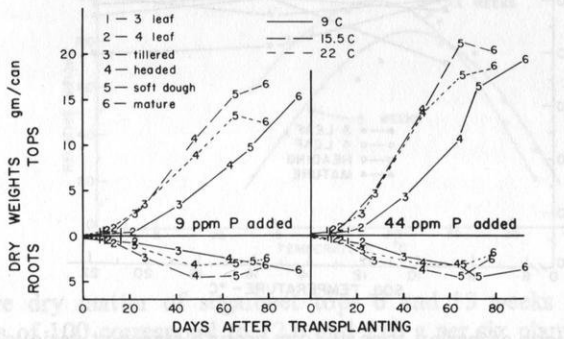

Fig. 14. Dry weight of barley tops and roots as affected by soil temperature, P supply and time (from Power et al. 1970).

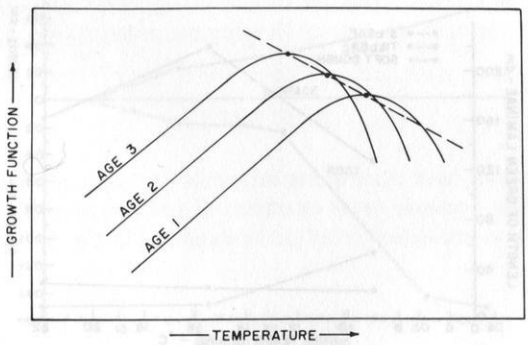

Fig. 15. Hypothetical diagram of change in growth as a function of soil temperature for increasing age of plant (age 3 is oldest). The dashed line passes through the apex of each curve (from Willis and Amemiya, 1973).

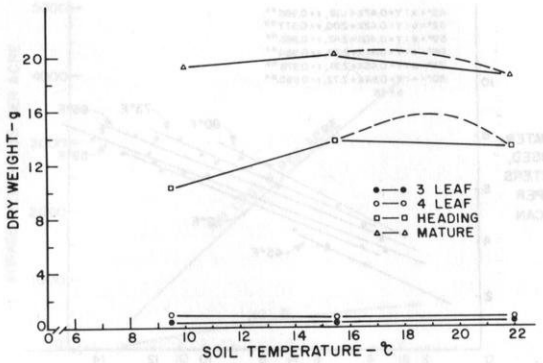

Fig. 16. Dry weight (tops) of barley produced at four growth stages at various soil temperatures (data from Power et al. 1967). Dashed lines are projections.

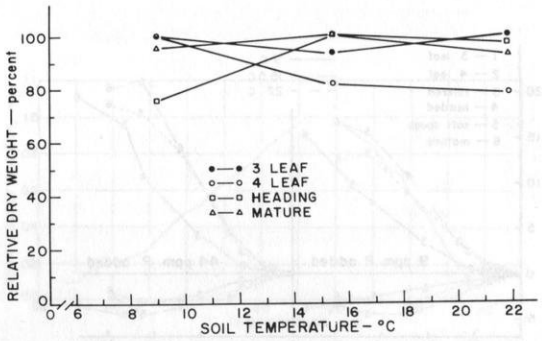

Fig. 17. Relative dry weight of barley tops at four growth stages at various soil temperatures (data from Figure 16). Relative weights of 100 correspond to the highest weight for individual growth stages.

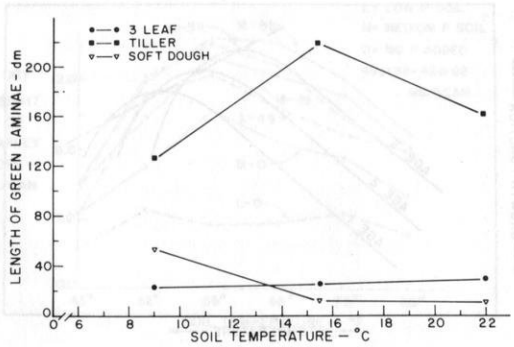

Fig. 18. Length of green laminae of barley at various soil temperatures and growth stages (data from Power et al. 1967).

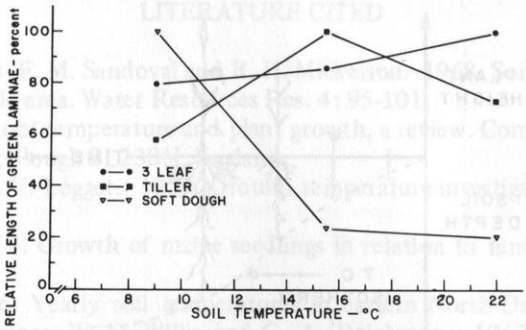

Fig. 19. Relative length of green laminae of barley at various soil temperatures and growth stages (dates from Figure 18). Relative lengths of 100 correspond to the greatest length for individual growth stages.

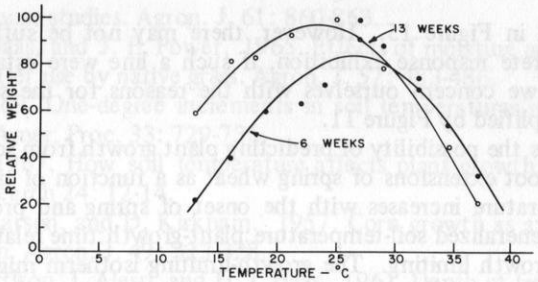

Fig. 20. Relative dry matter of sugarbeet tops 6 and 13 weeks after emergence. Relative weights of 100 correspond to 12.0 and 210 g per six plants for 6 and 13 weeks after emergence, respectively (from Radke and Bauer, 1961).

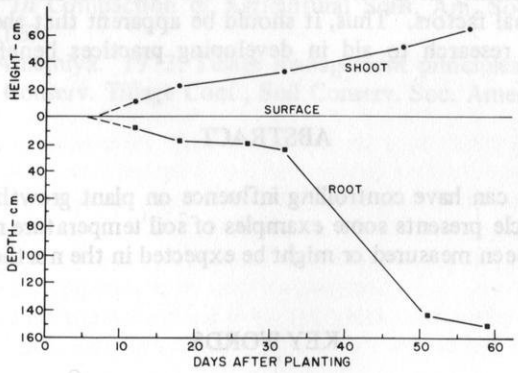

Fig. 21. Extension of spring wheat shoots and roots with time (unpublished data, Northern Great Plains Research Center, Mandan, North Dakota).

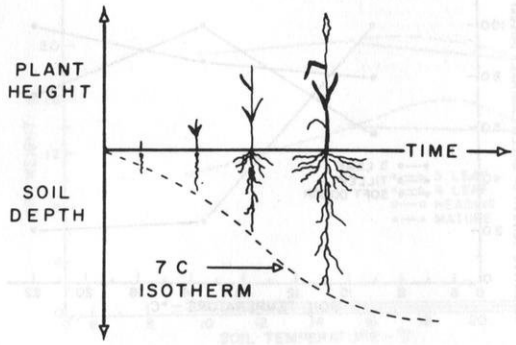

Fig. 22. Hypothetical diagram of plant growth as a function of time and a growth-limiting isotherm.

speculation illustrated in Figure 15. However, there may not be sufficient sensitivity in an "index" line for discrete response exhibition, if such a line were established. Perhaps it is more important that we concern ourselves with the reasons for the shape of the growth response curves as exemplified by Figure 11.

A final point is the possibility of predicting plant growth from soil temperature. Figure 21 shows shoot and root extensions of spring wheat as a function of time after planting. We know that soil temperature increases with the onset of spring and progression into summer. Figure 22 portrays a generalized soil-temperature:plant-growth:time relation; the 7C isotherm is inserted as possibly growth limiting. The growth-limiting isotherm might be established for a particular species and might be mechanically predictable. Also, soil water and nutrient uptake relative to soil temperature is reasonably known in some cases. If average active rhizosphere temperatures could be identified, then plant behavior could be predicted more easily and accurately. Pursuit of such prediction seems to be a worthy research objective.

In conclusion, soil temperature has a dominant influence on plant growth, both directly and indirectly. Whether temperature has direct or indirect effect is a moot question, particularly because we are primarily interested in some yield function, and the plant acts as an integrator of many individual factors. Thus, it should be apparent that there is definite need for additional temperature research to aid in developing practices beneficial to plant growth.

ABSTRACT

Soil temperature can have controlling influence on plant growth in the northern Great Plains. This review article presents some examples of soil temperature regime and its effect on plant growth that have been measured or might be expected in the northern Plains.

KEY WORDS

Soil temperature, plant growth, northern Great Plains.

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INFLUENCE OF PLANTS ON NITROGEN TRANSFORMATION IN SOILS

J. O. Legg

Nitrogen is one of the most widely distributed elements required by plants but, paradoxically, it is the element that most often limits plant growth. This results from the relative inertness of elemental nitrogen in the atmosphere and of combined forms of nitrogen in minerals and organic matter. Since plants can use very little of these forms of nitrogen directly, they must depend largely on microorganisms to fix elemental nitrogen or decompose organic nitrogen into simpler forms. Although rocks and minerals contain large amounts of nitrogen, the fraction that actively enters the nitrogen cycle is so small that it will not be considered.

Most of the nitrogen in soils that is potentially available to plants is associated with organic matter. The accumulation of soil organic matter in natural ecosystems may require several thousand years to reach an equilibrium level. The level attained depends on such factors as climate, vegetation, topography, physical and chemical characteristics of the soil, and activities of the microflora and microfauna. Since the system is very dynamic, any changes in the environment may lead to a new equilibrium level of organic nitrogen. When steady-state conditions exist, the rate at which nitrogen is added to the soil equals the rate at which nitrogen is lost by such processes as leaching and denitrification.

Type of vegetation is especially important in the accumulation, retention, and conservation of soil nitrogen. Other things being equal, organic matter and nitrogen contents usually are higher in soils developed under grassland than in soils developed under forest-type vegetation. Grassland soils contain a mass of fibrous roots that usually extend throughout the soil to a depth of several feet. These roots not only serve as absorptive organs for water and plant nutrients, but also contribute considerable debris to the soil in the form of excretions, sloughed-off root tissue, and dead root hairs that are continually being produced during the regenerative process of root proliferation. This carbonaceous material is utilized by a wide variety of microorganisms that gradually transform part of the carbon and nitrogen into stable forms of organic matter. In forest soils, however, plant debris is added to the soil primarily as fallen leaves that accumulate on the surface. The organic layer that forms under these conditions remains at the surface and does not become distributed throughout the rooting zone. The main roots contribute little to the organic content of the soil, which remains light-colored and contains relatively low amounts of nitrogen.

Nitrogen transformations in soil after organic material is added are greatly influenced by the inorganic components of the soil. The kind and amount of clay minerals are especially important. For a given climatic zone, heavy clay soils normally contain more organic nitrogen than loamy soils. The type of clay mineral also affects the retention of organic nitrogen. Clay minerals with expanding lattices, such as montmorillonite, have greater surface area and absorptive capacity for organic molecules than clay minerals with nonexpanding lattices, such as kaolinite. Both the organic and inorganic constituents of soils influence the kind and amount of aggregation of soil particles into granules that are especially important in relation to root penetration and water movement. The formation of clay-organic and metal-organic complexes, as well as the formation of aggregates, is believed to be responsible for much of the resistance of soil organic nitrogen to decomposition by microorganisms.

Although a soil may require several thousand years under natural conditions to reach an equilibrium level of organic nitrogen content, a number of studies have shown dramatic de-

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creases in soil nitrogen content with cropping. The loss is most rapid during the first years of cultivation. Jenny (1941) showed that, under average practices in the North Central Region of the U.S., soil nitrogen declined about 40% in 60 years. Nearly 20% of the total nitrogen disappeared during the first 10 years of cultivation. Thus a new equilibrium is becoming established under cultivation, and the soil organic nitrogen is now approximately one-half of the original content in this region.

The nitrogen level of most soils cannot be maintained or increased unless a continuous grass sod is present. High applications of organic matter in the form of plant residues, manures, composts, or green manures usually do not completely prevent the decline in organic nitrogen during cropping. The accumulation of nitrogen and organic matter in grassland soils, therefore, cannot be explained simply by the amount of plant residues produced. Under grassland conditions there are two apparent mechanisms whereby nitrogen is conserved in an organic form: (a) The plant roots continually remove mineral nitrogen from the soil as it is formed, and since much of this nitrogen is transported to the tops, it is effectively removed from the soil-root system. (b) The roots contribute a large amount of carbonaceous material that serves as an energy source for soil microorganisms. This greatly increases microbial activity and results in immobilization of nitrogen and carbon in microbial tissues. Both of these mechanisms remove mineral nitrogen from the soil system, and this eventually creates a nitrogen stress. As the plant continues to grow under nitrogen stress, the percentage of nitrogen in the plant tissues decreases and the C/N ratio of the root material increases. To utilize an energy source with a high C/N ratio, microorganisms require additional nitrogen, and thus intensify the stress. Nitrogen that is mineralized from soil organic matter, therefore, is removed quickly either by the plants or microorganisms and is not subject to leaching from the system. Nitrogen added naturally or by the use of fertilizers is also immobilized in the same manner and leaching losses are kept to a minimum.

It can be seen, therefore, that the equilibrium for soil organic nitrogen may range from a very low level under continuous cultivation to a relatively high level under continuous grass sod. Intermediate equilibrium levels may be established by the use of rotations or other management practices. One of the most promising practices being developed for various parts of the country is the no-till or minimum tillage system. Variations in the different forms of minimum tillage systems will not be described; however, the success of most systems has depended largely on the development of herbicides that reduce competition from the sod or cover crop, as well as from weeds, during most of the growing season. In West Virginia, Bennett (1970) has successfully grown sod-planted corn after using only enough herbicide to stunt the grass. Late in the growing season, the grass recovers sufficiently to furnish grazing or a hay crop. This is possibly the ultimate system in which row crops may be grown with a minimum loss of organic matter and nitrogen. In fact, preliminary evidence indicates that with ample amounts of nitrogen and other nutrients supplied, within a year the organic and mineralizable nitrogen contents are measurably higher in such a system than in a conventional tillage system. In North Dakota, Power (1972) also obtained a quick buildup of organic nitrogen by applying relatively high rates of fertilizer to grassland soil. Several hundred pounds of nitrogen per acre were immobilized in grass roots and soil organic matter in 3 or 4 years, most of which was immobilized during the first year. Apparently, a buildup of carbonaceous material in the root zone over a period of years caused the high immobilization rate, and fertilization was necessary to prevent nitrogen stress from limiting plant growth. Further studies are required to determine the nitrogen transformations that take place under the above conditions when adequate nitrogen is supplied for near-maximum yields. Present studies in West Virginia and North Dakota, utilizing the stable isotopes of nitrogen, should provide some very useful information on these transformations.

Although it is generally acknowledged that plant roots greatly influence the microbial population of the soil, there is still lack of agreement as to the relative influence of the increased microflora on nitrogen transformations in soils. Possibly a major reason for this lack of agreement is the lack of quantitative data on the amount of roots produced during the growing season and on the relative proportion of the roots and root excretions that serves as an available carbon source for microorganisms. Such information is difficult to obtain, because roots in the soil environment are not easily observed or measured. Furthermore, root growth, dieback, and decomposition take place simultaneously, and the amount of roots remaining at the end of growth is not necessarily a good measure of the total amount produced.

The contribution of roots to the energy supply of microorganisms has probably been underestimated in the past. Recently, Samtsevich (1968) presented data showing the presence of transparent gel-like substances on the root tips of a number of plants. This substance forms a protective zone around the root caps, meristem, and elongation areas, and is abundantly filled with plant cells that continuously disengage from the root caps. The material is invisible if unstained, but is readily seen under the microscope if the roots are stained with methylene blue or gentian violet. Samtsevich estimated the volume of the gel-like material produced by wheat and maize, and concluded that, even if the material contained only 1% dry matter, during the vegetative period plant roots exude into the soil at least as much dry matter as is produced in high yields of the crops (7 metric tons/ha for winter wheat and 12.5 tons/ha for maize). He suggested that the amount of excretions is even greater for perennial plants. Tests for sugars, amino acids, proteins, and starch were negative for the substance obtained from maize, but the test for hemicellulose was positive. Although Samtsevich's estimates may be high, further work should increase our understanding of the plant effect on nitrogen transformations.

Early studies were concerned chiefly with the long-term effects of plants on organic nitrogen buildup or depletion. More recently, interest has centered on the influence of plants on nitrogen transformations during a given cropping season. A study by Goring and Clark (1949) provides a good example of the influence of plants on net mineralization of soil organic nitrogen during a 13-week growth period in the greenhouse. In a comparison of uncropped and cropped soils, they found little difference in net mineralization during the first 5 weeks; after 13 weeks, however, net mineralization in the cropped soil was only about 50% of that in the uncropped soil. The data were interpreted to indicate an increased immobilization of nitrogen by the rhizosphere microflora. Since the population of soil microorganisms is highest in the rhizosphere, owing to the supply of energy material sloughed off or excreted by roots, it is conceivable that the quantity and nitrogen content of this material, while undergoing decomposition, would considerably affect the use of mineral nitrogen by the plant.

In related studies in which the stable nitrogen isotope, ^{15}N, has been used as a tracer, a number of workers have found that plant uptake of soil nitrogen increases as the rate of ^{15}N-labelled fertilizer nitrogen increases. Legg and Allison (1960) attributed the observed differences to greater immobilization of soil nitrogen at lower fertilizer nitrogen levels than at higher nitrogen levels. It seems apparent that one of the main effects of increasing nitrogen additions is reduction of the C/N ratios of the plant material produced. This, in turn, decreases the need for additional nitrogen by microorganisms decomposing the root residues and excretions. As plant growth proceeds, the supply of mineral fertilizer nitrogen in the soil is depleted, and any additional nitrogen needed by rhizosphere microorganisms must be obtained largely from mineralized soil nitrogen.

An alternative explanation for the increase in soil nitrogen uptake with increases in fertilizer nitrogen applications depends on the observation that, in some soils, net mineralization of soil nitrogen is increased during incubations when ^{15}N-labelled fertilizer is present. This

is especially true when nitrogen is applied as ammonium, which is preferentially utilized by microorganisms in relation to nitrate. This is not really an alternative explanation, however, since it deals with the same microbiological reactions. Net mineralization is the difference between total mineralization and immobilization. When the soil contains sufficient available carbon, regardless of source, for appreciable immobilization to take place, net mineralization of soil nitrogen will increase when fertilizer nitrogen is present. Published data show that the increase in mineral soil nitrogen is balanced by immobilization of fertilizer nitrogen in organic forms. Plants introduced into the system accentuage the immobilization process by removing nitrogen from the soil and by supplying microorganisms with carbonaceous material.

The increased plant uptake of soil nitrogen induced by fertilizer applications is mainly of academic interest, when it is considered that the additional uptake is more than balanced by fertilizer nitrogen immobilization. Studies of this nature, however, improve our understanding of the nitrogen transformations taking place in the presence of growing plants. The immobilization process is important in nitrogen conservation, particularly in soils with low mineralization capacities. Legg and Stanford (1967) demonstrated that six soils, having low mineralization rates, immobilized more fertilizer nitrogen at the higher rates than was removed by plants from soil sources. Six other soils, having high mineralization rates, showed a net loss of nitrogen from the system, since the removal of mineralized soil nitrogen exceeded the amount of fertilizer nitrogen immobilized.

Much of the fertilizer nitrogen added to grassland soils is not recovered directly in the plant tops, but is immobilized in the soil. Frequently, the amount recovered in the first crop is less than 50%, so it is of practical importance as well as scientific interest to determine the fate of nitrogen added to the soil-plant system. Such studies are greatly facilitated by the use of ^{15}N as a tracer. Broadbent and Nakashima (1967) determined the availability of labelled nitrogen in plant uptake and mineralization studies. They calculated a quantity designated as "availability ratio" according to the equation:

$$\text{Availability ratio} = \frac{\dfrac{T_c}{U_c + T_c}}{\dfrac{T_s}{U_s + T_s}}$$

where T_c = tagged nitrogen in plant material (or in mineralized nitrogen from incubation),
U_c = untagged nitrogen in the corresponding material above,
T_s = tagged nitrogen in soil at beginning of vegetative or incubation period,
U_s = untagged nitrogen in soil at the same time.

If the labelled nitrogen in the soil has the same availability to plants or microorganisms as the soil nitrogen, the availability ratio will be unity. On the other hand, if it is more available than soil nitrogen, the ratio will be greater than unity. Broadbent and Nakashima found that in successive cuttings of sudangrass, availability ratios ranged from 11.9 in the second cutting to 1.2 in the seventh cutting of plants grown on Yolo soil. In incubation tests lasting up to 592 days, several ratios below 1.0 were obtained, but they usually were between 1 and 2 during the latter half of the experiment.

Recently, Legg et al. (1971) carried out a long-term greenhouse experiment in which ^{15}N-labelled $(NH_4)_2SO_4$ was incorporated into the soil organic matter by successive cropping

with oats. The plant material was returned to the soil, except for pots that were removed from the experiment at the end of each cropping period. Plant material and soil from each set of triplicate pots were analyzed for total and ^{15}N-labelled nitrogen. The results, calculated in terms of availability ratios, declined from an initial value of 10.4 to about 2 at the end of the experiment. Soil samples obtained after 2, 5, and 8 cropping periods were incubated at 35°C and leached with 0.01 M $CaCl_2$ (followed by *N* solution) biweekly for 40 weeks. The availability ratio, calculated for the mineralized nitrogen at each incubation period, gradually declined for the second-crop soil until it was about 2; thereafter it remained essentially constant. For the fifth- and eighth-crop soils, little change was noted in availability ratios which remained somewhat above 2 throughout incubation. The data suggest that inorganic nitrogen applied to soils may be converted to stable organic forms similar to indigenous organic nitrogen. It could be speculated that with a soil having a stable availability ratio of 2, one-half of the indigenous soil organic nitrogen is essentially inert, owing to physical or biochemical inaccessibility to microorganisms.

Stanford et al. (1970) subjected samples of the fifth-crop soil mentioned above to repeated extractions with boiling 0.01 *M* $CaCl_2$ (100 C), or autoclaving (121 C), or both, to study the behavior and properties of immobilized fertilizer nitrogen relative to soil organic nitrogen. They found the distribution of ^{15}N among chemical fractions of the hot-water extracts, acid hydrolysate, and acid-insoluble portion was similar to the distribution of indigenous soil nitrogen. Since appreciable equilibration between added ^{15}N and the more resistant forms of soil organic nitrogen appeared unlikely, it was postulated that the fertilizer nitrogen reacted to form new compounds, similar in composition to preexisting forms of soil nitrogen. This postulate was supported by the observation that the percentage removals of total and ^{15}N-labelled nitrogen by repeated extraction were almost identical.

Using the same soil but different fractionation and extraction procedures, Chichester (1970) found further support for the above hypothesis. He initially separated the soil components into separate size fractions by wet sieving and centrifugation without using chemical dispersants. The resulting silt-size separate was then subjected to repeated 15-minute ultrasonic vibration treatments, followed by centrifugation to separate the clay-size material that resulted from the physical dispersion. The separates were extracted with 0.5 *N* sodium pyrophosphate at 100 C, and the extracts were fractionated into distillable, acid-hydrolyzable, ninhydrin-reactive, and residual nitrogen components. The results obtained in this detailed study gave further evidence of the similarity in composition of the labelled and unlabelled fractions for the different treatments. It appears highly significant that biological, chemical, and physical methods lead to the same conclusion concerning the fate of immobilized fertilizer nitrogen in soil, and it is likely that findings of this nature will have considerable influence on our understanding of the basic mineralization-immobilization processes.

Other nitrogen transformations, such as nonsymbiotic nitrogen fixation and denitrification, are influenced by plants, but the amounts of nitrogen fixed or lost are not always easily measured. There is little evidence that significant quantities of nitrogen are fixed nonsymbiotically in the rhizosphere, although root exudates might be considered a favorable nutrient medium for the microorganisms involved. Nitrogen losses by denitrification in the presence of plants are generally considered to be low, since plants readily take up nitrate. In areas such as the Netherlands, however, where large amounts of fertilizer nitrogen are applied to permanent grassland, considerable loss of nitrogen has been detected. Woldendorp (1963) reported denitrification losses of 10 to 40% in pot experiments with sods and sown grass supplied with labelled nitrate-nitrogen. Losses were much smaller (3 to 9%) when the grass had been killed by clipping the tops several times. This stimulating effect of living root systems on denitrification was attributed to oxygen deficiency in the rhizosphere and to the excretion of organic compounds functioning as hydrogen donor in denitrification. Losses of nitrogen in greenhouse experiments

in which ^{15}N is used as a tracer often are 10 to 15% or more, but it is not clear whether this results from the creation of anaerobic areas by watering, or from reactions occurring in the rhizosphere as described by Woldendorp.

Summary and Conclusions

Numerous factors are involved in the buildup of soil organic nitrogen contents to equilibrium levels in natural ecosystems. Several thousand years may be required to attain equilibrium. Type of vegetation influences both the amount and distribution of organic nitrogen in the soils. Under a given set of environmental conditions, high organic nitrogen content is generally best maintained in grassland soils. The fibrous root system of grasses serves both as an efficient absorptive organ for mineralized nitrogen and as an energy source for microorganisms that immobilize mineral nitrogen into organic forms. Experiments with ^{15}N-labelled fertilizer that has become immobilized in the soil organic fraction indicate that the ^{15}N is incorporated relatively quickly into organic forms similar to a large fraction of the indigenous soil nitrogen. This suggests, of course, that the long time required for equilibrium levels of organic nitrogen to become established under natural conditions is the time necessary for nitrogen to accumulate through symbiotic and nonsymbiotic fixation, rainfall, and other means.

ABSTRACT

Soil nitrogen is a very important part of the nitrogen cycle, and the transformations taking place within the soil influence greatly the amounts of nitrogen retained in organic and inorganic forms. In natural ecosystems, the total amount of nitrogen accumulating in soils depends on the major factors of soil formation, and the nitrogen content may increase gradually over several thousand years. Type of vegetation is especially important in the accumulation, retention, and conservation of nitrogen. In grassland soils, the distribution of a fibrous root system throughout the rooting depth enhances immobilization of nitrogen in organic forms by moving excess mineral nitrogen into the plant and by contributing a continuous carbon source for soil microorganisms. In cultivated soils, the nitrogen content generally declines over a long period to an equilibrium level much lower than that in the natural state. At equilibrium the rate of loss through removal by plants, leaching, denitrification, and other means must be balanced chiefly by additions through biological fixation and fertilization. Studies with ^{15}N-labelled fertilizer indicate that ^{15}N is incorporated relatively quickly into organic forms similar to a large fraction of the indigenous soil nitrogen.

KEY WORDS

N accumulation, soil N, N mineralization, N immobilization, N isotopes, soil organic N, N availability, N fractionation, denitrification, root activity.

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RESPONSES OF *OPUNTIA POLYACANTHA* TO WATER AND NITROGEN PERTURBATIONS IN THE SHORTGRASS PRAIRIE

J. L. Dodd and W. K. Lauenroth

INTRODUCTION

Opuntia polyacantha Haw., plains prickly pear, is one of the major plant species of the shortgrass prairie (Costello, 1941; Klipple and Costello, 1960). It and other species of *Opuntia* are important sources of energy for several species of insects (Cook, 1942; Houston, 1963), rodents (Flake, 1973), and other consumers (Vaughan, 1967). Because of its rooting habits (Harvey, 1936), drought resistance, and growth habits (Turner and Costello, 1942), the prickly pear is also important in retarding erosion during drought periods.

Much of the knowledge relating to the ecology of *O. polyacantha* deals with its cover or frequency responses to grazing and variations in weather. Very little is known about its biomass response to these or other factors, and no literature is available concerning intraseasonal biomass dynamics.

Houston (1963) concluded that early workers were mistaken in attributing increases in *O. polyacantha* populations to grazing intensity. He found that in the grasslands of eastern Montana *O. polyacantha* populations were controlled largely by weather and soils and very little by grazing. Hyder et al. (1966) and Bement (1968) found similar results in eastern Colorado. Ground cover of *O. polyacantha* doubled during the period 1940-1964 as a result of fluctuations in weather, but no significant responses were found to light, moderate, or heavy summer grazing intensities. Hyder et al. (1975), also in eastern Colorado, found that heavy grazing in September or October increased *O. polyacantha* populations while heavy grazing in either April or July decreased them. They also reported an important relationship between *O. polyacantha* populations and weather, especially seasonal distribution of precipitation.

The objectives of this paper are to report: (1) response of *O. polyacantha* pad density and biomass to water and nitrogen treatments and (2) intraseasonal biomass dynamics of *O. polyacantha*.

STUDY AREA

The study site is located in Weld County, northeastern Colorado, on the western edge of the U.S.D.A., Central Plains Experimental Range. This location is near the western border of the Great Plains, and the climate is predominantly continental. Long-term annual precipitation and precipitation for the years of the study are presented in Table 1. Approximately 75% of the annual precipitation falls during the April to September growing season. This area has moderately cold winters although daytime air temperatures of 4 C have been recorded for each month. Mean monthly maximum air temperatures for the growing season range from 15.6 C in April to 29.4 C in July. Minimums for this period range from -1.1 C to greater than 10 C.

The natural vegetation of the study area is characteristic of a large portion of the shortgrass prairie and is basically a blue grama (*Bouteloua gracilis*) grassland with a mixed low shrub/half-shrub overstory. The major species in addition to blue grama are fringed sagewort (*Artemisia frigida*), scarlet globemallow (*Sphaeralcea coccinea*), plains prickly pear (*Opuntia polyacantha*), broom snakeweed (*Gutierrezia sarothrae*), and needleleaf sedge (*Carex eleocharis*).

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Table 1. Monthly precipitation (mm) for the shortgrass prairie site in northeastern Colorado for 1970-1973.

Month	1970	1971	1972	1973	CPER MEAN[a/]
Winter					
January	1.3	14.3	7.4	2.6	7.0
February	1.3	11.5	0.2	0.3	6.0
Spring					
March	30.2	23.0	8.5	25.2	14.5
April	33.5	64.5	14.2	29.0	26.0
May	22.3	50.0	27.5	9.9	55.5
Subtotal	86.0	138.0	50.2	64.1	96.0
Summer					
June	15.0	10.1	83.9	28.9	61.5
July	31.2	8.7	39.4	106.3	48.0
August	5.1	8.5	70.6	11.1	39.0
Subtotal	51.3	27.3	193.9	146.3	148.5
Fall					
September	33.0	53.9	21.6	64.8	26.0
October	20.3	13.3	10.3	1.1	17.0
November	5.3	3.1	14.0	30.5	6.5
Subtotal	58.6	70.3	53.5	96.4	49.5
Winter					
December	4.2	1.2	8.1	10.1	4.0
TOTAL	202.7	262.1	305.7	319.8	311.0

[a/] Central Plains Experimental Range Headquarters, 1932-1970.

METHODS

Experimental Design and Treatments

The experimental design consisted of two replications of each of four treatments. Each treatment replicate was located on a 1 ha plot. The treatments were as follows: control, water, nitrogen, and water plus nitrogen. The treatments were chosen with respect to their anticipated effects on the entire ecosystem and therefore were beyond the range of agronomic experimental criteria.

The nitrogen treatments consisted of maintaining a difference of at least 50 kg/ha of soil mineral nitrogen ($NH_4 + NO_3$) between the nitrogen and control treatments. This was accomplished initially by an application of 150 kg/ha of nitrogen as ammonium nitrate in the spring of 1970. In the spring of 1972 an additional 150 kg/ha of nitrogen were applied to the water plus nitrogen treatment and in 1973 100 kg/ha of nitrogen were applied to the nitrogen and nitrogen plus water treatments.

The water treatment, initiated in 1971, maintained soil water potential above -0.8 bars at a depth of approximately 10 cm. Soil water potential rarely went below -0.6 bars before watering was started. Soil water potential was monitored by tensiometers and checked daily. The supplemental water was applied mostly at night to minimize conflicts with sample collection activities and to avoid windy conditions. Water was applied by a sprinkler system on each 1 ha plot. The sprinkler system was designed to have a uniformity coefficient of 80% (Zimmerman, 1966).

In order to evaluate the intraseasonal biomass dynamics of *O. polyacantha* in 1972 data from the water and nitrogen experiment were combined with biomass data taken from a nearby grazing intensity study. The grazing intensity experiment was a long-term study in which two comparable shortgrass prairie pastures (each 128 ha in size) were grazed at light and heavy intensities from 1940 through 1972. The pastures were stocked with yearling cattle from early May through early November. The design of the study has been reported in more detail by Klipple and Costello (1960) and Bement (1968). Also included in the grazing intensity data for 1972 are data from a test area that had not been grazed since 1938 and another area, formerly part of the heavy grazed treatment, that was protected from grazing during 1972 only.

Pad Density Determinations

Pad density data were collected from 100 quadrats 0.25 m^2 in area from each of the treatments in the water and nitrogen experiment in 1971, 1972 and 1973. Sampling (once/year) occurred between 15 June and 15 July in all 3 years. All green pads occurring in a quadrat were counted.

Biomass Determination

Total aerial biomass (live plus attached dead) of *O. polyacantha* was harvested from randomly located quadrats in the water and nitrogen experiment in 1970, 1971, 1972 and 1973. Similar data were collected from the grazing intensity experiment in 1972. In 1970 10 quadrats 0.25 m^2 in area were harvested from each treatment and in the remaining years 12 quadrats 0.5 m^2 each were harvested from each treatment.

In 1971, 1972 and 1973 weight estimation (Pechanec and Pickford, 1937) of *O. polyacantha* biomass was performed concurrently with harvesting. The procedure for each sample date consisted of estimating the weight of *O. polyacantha* in 46 quadrats per treatment in each replicate (six of these were harvested and 40 were permanent plots). The harvest data supplied the correction factor (by linear regression) for the additional estimates. Separate regressions were prepared for each replicate of each treatment. The major problem encountered in using this method is related to the small number of quadrats harvested on each date. If *O. polya-*

cantha occurred in one or none of the quadrats, correction factors could not be derived for the estimates. Another less important problem was the precision of the estimator. The estimates were judged to be invalid when harvest and visual estimates for the calibration plots were in poor agreement ($r^2 < 0.51$). For these reasons those biomass data presented here are combinations of calibrated weight-estimate and harvest replicate means. Analysis of variance are based on replicate responses.

In 1970 samples were collected on 11 dates from April to September. In 1971 samples were collected on five dates beginning in March and ending in December. Nine samples were taken from the water and nitrogen experiment in 1972 from April to October and six from the grazing intensity pastures from May to August. Biomass samples were harvested on six dates in 1973 from May to September.

RESULTS AND DISCUSSION

Pad Density

Analysis of variance of the live pad density data (Table 2, Fig. 1) indicated that significant changes occurred as a result of both treatments and years. The significant treatment effects are probably attributable to the higher densities for the water and nitrogen (except 1973) and the nitrogen treatments. The year effect is probably a result of the high density for the nitrogen treatment in 1972.

Since the treatment x year interaction term was not significant, we have no statistical justification for discussing yearly changes in density by treatment but we feel that there are some interesting interpretations of these trends.

Our results indicate that soil water availability during the growing season is not a critical factor in determining the growth and maintenance of live cactus pads, but that the level of nitrogen fertility is critical. The intraseasonal dynamics data indicate that the important growing period for cactus is in March and April well ahead of the growing season for the other species in the community. If this is correct, there would be very little direct competition for either water or nitrogen between *O. polyacantha* and other species. Lauenroth and Sims (1973) present basal cover data for the same site that indicates total basal cover was similar for all treatments in 1971. In 1972 basal cover changed only slightly for the control and water treatments, but decreased 60% on the nitrogen treatment and increased 80% on the water and nitrogen treatment. In 1973 basal cover increased on both the nitrogen and water plus nitrogen treatments. In each instance basal cover and density appear to be negatively correlated. If this is correct the growth of *O. polyacantha* is influenced by increased or decreased competition from other species. The negative effects of this competition may be a result of shading, decreased soil temperatures in the spring, or a more favorable microclimate for insects that feed on *O. polyacantha*.

Biomass

Our evaluation of *O. polyacantha* biomass responses to the water and nitrogen treatments is based on changes in annual averages (Fig. 2). Analysis of variance results indicate significant treatment and treatment x year effects as well as significant replicate and replicate x treatment effects (Table 3). In our discussion of the results we assume consistent trends and large changes to be real.

Average biomass (Fig. 2) of *O. polyacantha* for the control treatment was 28 g/m^2 in 1970, decreased in 1971, and then increased in both 1972 and 1973 to 45 g/m^2 in 1973. The decrease in biomass on the control from 1970 to 1971 is associated with a very dry summer in 1970 and a normal spring in 1971. Contrary to the pad density response, this response agrees

Table 2. Analysis of variance for *Opuntia polyacantha* pad density (live pads/m^2) response to control, water, nitrogen, and water plus nitrogen treatments in 3 years (1971, 1972, 1973).

Source	d.f.	Sum of Squares	Mean Square	F	p
Replicates	1	28.167	28.167	2.216	0.16
Treatments	3	154.833	51.611	4.060	0.04
Years	2	77.250	38.625	3.038	0.09
T × Y	6	58.417	9.736	0.766	0.61
Pooled Error	11	139.833	12.712		
R × T	3	24.167			
R × Y	2	25.583			
R × T × Y	6	90.083			

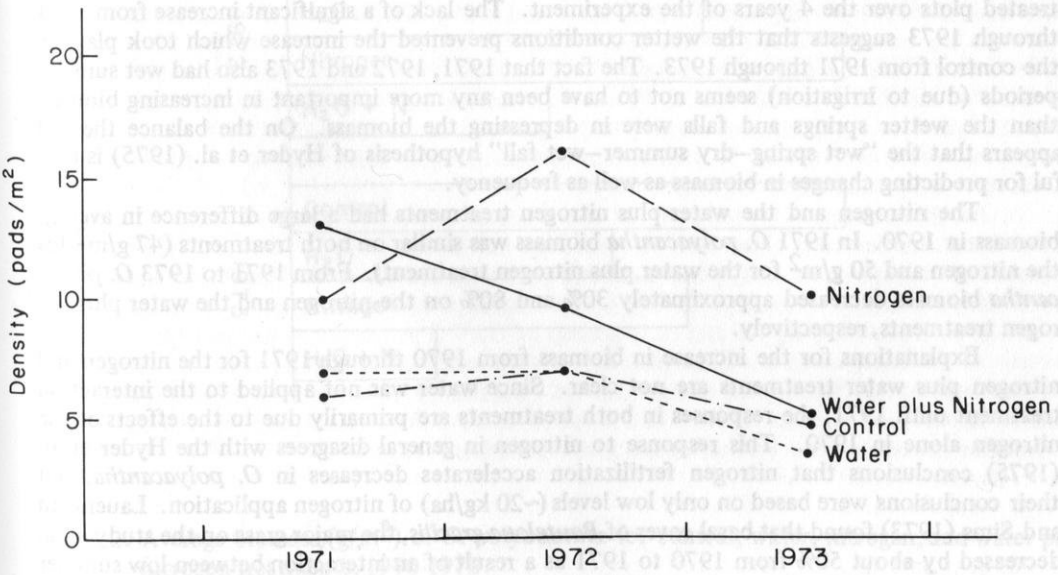

Fig. 1. Average pad density (live pads/m^2) of *O. polyacantha* for control, water, nitrogen, and water plus nitrogen treatments, 1971-1973.

Table 3. Analysis of variance for *Opuntia polyacantha* biomass (g/m^2) response to control, water, nitrogen, and nitrogen plus water treatments in 4 years (1970-1973).

Source	d.f.	Sum of Squares	Mean Square	F	p
Replicates	1	2701.125	2701.125	28.439	<0.01
Treatments	3	1249.750	416.583	4.386	0.03
Years	3	500.750	166.917	1.757	0.21
T × Y	9	2373.000	263.667	2.776	0.05
R × T	3	1591.125	530.375	5.584	0.01
Pooled Error	12	1139.750	94.979		
R × Y	3	90.625			
R × T × Y	9	1049.125			

with Hyder et al. (1975) multiple regression predictions for changes in frequency. The subsequent increase in biomass from 1972 to 1973 is also in general agreement with Hyder et al. (1975) projections since it appears to be the result of a dry spring and a wet summer in 1972.

Average seasonal biomass of *O. polyacantha* remained relatively constant on the water-treated plots over the 4 years of the experiment. The lack of a significant increase from 1971 through 1973 suggests that the wetter conditions prevented the increase which took place in the control from 1971 through 1973. The fact that 1971, 1972 and 1973 also had wet summer periods (due to irrigation) seems not to have been any more important in increasing biomass than the wetter springs and falls were in depressing the biomass. On the balance then, it appears that the "wet spring–dry summer–wet fall" hypothesis of Hyder et al. (1975) is useful for predicting changes in biomass as well as frequency.

The nitrogen and the water plus nitrogen treatments had a large difference in average biomass in 1970. In 1971 *O. polyacantha* biomass was similar on both treatments (47 g/m^2 for the nitrogen and 50 g/m^2 for the water plus nitrogen treatment). From 1971 to 1973 *O. polyacantha* biomass decreased approximately 30% and 80% on the nitrogen and the water plus nitrogen treatments, respectively.

Explanations for the increase in biomass from 1970 through 1971 for the nitrogen and nitrogen plus water treatments are not clear. Since water was not applied to the interaction treatment until 1971, the responses in both treatments are primarily due to the effects of the nitrogen alone in 1970. This response to nitrogen in general disagrees with the Hyder et al. (1975) conclusions that nitrogen fertilization accelerates decreases in *O. polyacantha*, but their conclusions were based on only low levels (~20 kg/ha) of nitrogen application. Lauenroth and Sims (1973) found that basal cover of *Bouteloua gracilis*, the major grass on the study area, decreased by about 50% from 1970 to 1971 as a result of an interaction between low summer precipitation and high nitrogen levels in 1970. The increase in *O. polyacantha* was an apparent positive response to less competition with *B. gracilis* for soil water or a direct response to increased soil fertility.

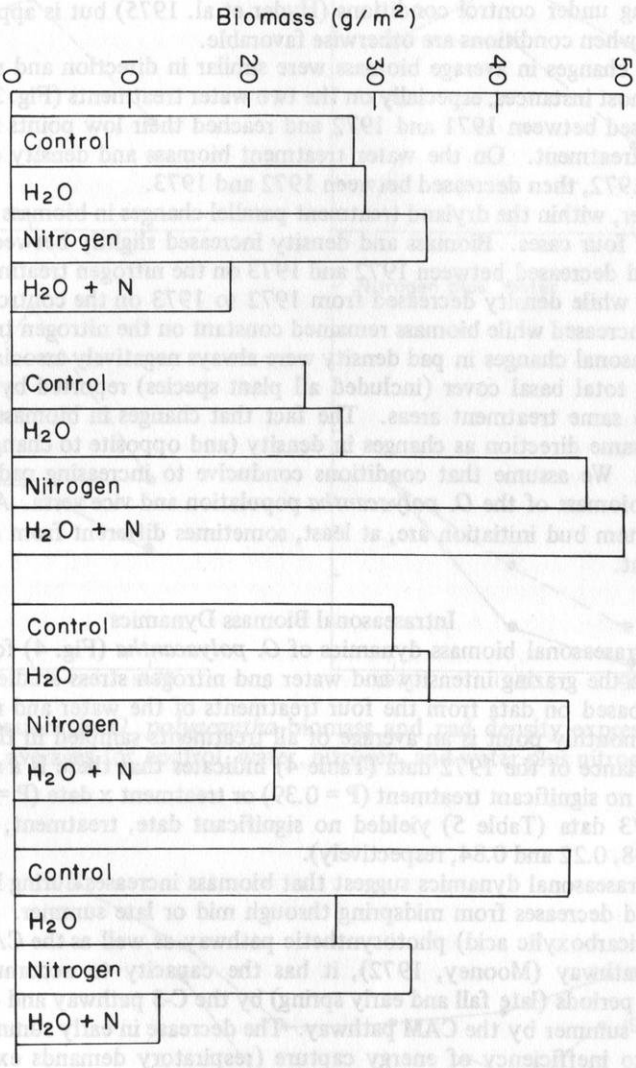

Fig. 2. Average biomass (g/m^2) of *O. polyacantha* for control, water, nitrogen, and water plus nitrogen treatments, 1970-1973.

The general decline of *O. polyacantha* biomass from 1971 through 1973 on the two nitrogen treatments is opposite to the control response. A possible explanation for the water plus nitrogen treatment is that the decrease was most likely a response to wetter conditions. The decline on the nitrogen treatment is harder to explain. This general response (more rapid decline due to nitrogen) has been noticed by other workers during years when *O. polyacantha* is also declining under control conditions (Hyder et al. 1975) but is apparently not observed during periods when conditions are otherwise favorable.

Annual changes in average biomass were similar in direction and magnitude to changes in density in most instances, especially on the two water treatments (Fig. 3). Both biomass and density decreased between 1971 and 1972 and reached their low points in 1973 on the water plus nitrogen treatment. On the water treatment biomass and density changed only slightly from 1971 to 1972, then decreased between 1972 and 1973.

However, within the dryland treatment parallel changes in biomass and density occurred in only two of four cases. Biomass and density increased slightly between 1971 and 1972 on the control and decreased between 1972 and 1973 on the nitrogen treatment. In contrast, biomass increased while density decreased from 1972 to 1973 on the control. And from 1971 to 1972 density increased while biomass remained constant on the nitrogen treatment.

Interseasonal changes in pad density were always negatively associated with corresponding changes in total basal cover (included all plant species) reported by Lauenroth and Sims (1973) for the same treatment areas. The fact that changes in biomass are usually, but not always in the same direction as changes in density (and opposite to changes in cover), is somewhat puzzling. We assume that conditions conducive to increasing pad numbers would also increase total biomass of the *O. polyacantha* population and vice versa. Apparently conditions favorable for stem bud initiation are, at least, sometimes different from conditions that favor pad enlargement.

Intraseasonal Biomass Dynamics

The intraseasonal biomass dynamics of *O. polyacantha* (Fig. 4) for 1972 are based on data from both the grazing intensity and water and nitrogen stress studies while for 1973 the dynamics are based on data from the four treatments of the water and nitrogen stress study. In 1972 each monthly point is an average of all treatments sampled in that particular month. Analysis of variance of the 1972 data (Table 4) indicates that there is a significant date effect ($P = 0.11$) and no significant treatment ($P = 0.39$) or treatment x date ($P = 0.77$) effect. Analysis of the 1973 data (Table 5) yielded no significant date, treatment, or treatment x date effects ($P = 0.38$, 0.22 and 0.84, respectively).

The intraseasonal dynamics suggest that biomass increases during late summer, fall, and early spring and decreases from midspring through mid or late summer. Since *O. polyacantha* has the C-3 (tricarboxylic acid) photosynthetic pathway as well as the CAM (crassulacean acid metabolism) pathway (Mooney, 1972), it has the capacity to accumulate biomass during relatively cool periods (late fall and early spring) by the C-3 pathway and during hotter but dry periods of late summer by the CAM pathway. The decrease in early summer possibly reflects a net loss due to inefficiency of energy capture (respiratory demands exceed assimilation by either pathway) and loss due to death as a result of insect damage (Houston, 1963; Cook, 1942) or loss due to consumption by insects and small mammals (Vaughan, 1967).

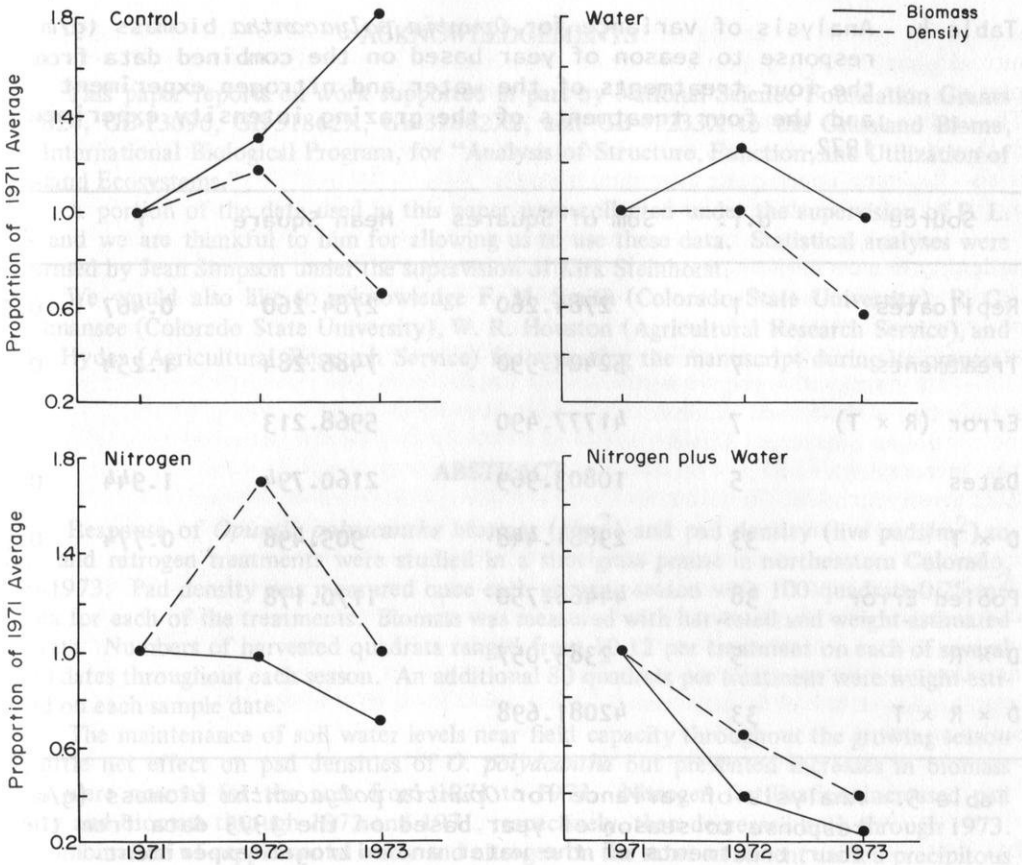

Fig. 3. Annual fluctuations in *O. polyacantha* biomass and pad density expressed as proportions of 1971 averages for control, water, nitrogen, and water plus nitrogen treatments.

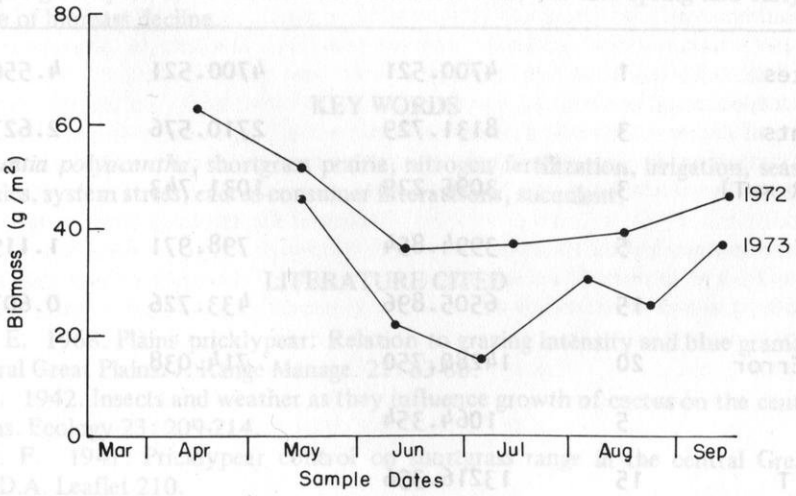

Fig. 4. Intraseasonal biomass dynamics (g/m^2) of *O. polyacantha* for 1972 and 1973.

Table 4. Analysis of variance for *Opuntia polyacantha* biomass (g/m) response to season of year based on the combined data from the four treatments of the water and nitrogen experiment and the four treatments of the grazing intensity experiment, 1972.

Source	d.f.	Sum of Squares	Mean Square	F	p
Replicates	1	2784.260	2784.260	0.467	0.52
Treatments	7	52403.990	7486.284	1.254	0.38
Error (R × T)	7	41777.490	5968.213		
Dates	5	10803.969	2160.794	1.944	0.11
D × T	33	29881.448	905.498	0.774	0.77
Pooled Error	38	44466.750	1170.178		
D × R	5	2385.057			
D × R × T	33	42081.698			

Table 5. Analysis of variance for *Opuntia polyacantha* biomass (g/m^2) response to season of year based on the 1973 data from the four treatments of the water and nitrogen experiment.

Source	d.f.	Sum of Squares	Mean Square	F	p
Replicates	1	4700.521	4700.521	4.556	0.12
Treatments	3	8131.729	2710.576	2.627	0.22
Error (R × T)	3	3095.229	1031.743		
Date	5	3994.854	798.971	1.119	0.38
D × T	15	6505.896	433.726	0.607	0.84
Pooled Error	20	14280.750	714.038		
D × R	5	1064.354			
D × R × T	15	13216.396			

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ABSTRACT

Response of *Opuntia polyacantha* biomass (g/m^2) and pad density (live pads/m^2) to water and nitrogen treatments were studied in a shortgrass prairie in northeastern Colorado, 1970-1973. Pad density was measured once each growing season with 100 quadrats 0.25 m^2 in area for each of the treatments. Biomass was measured with harvested and weight-estimated quadrats. Numbers of harvested quadrats ranged from 10-12 per treatment on each of several (5-11) dates throughout each season. An additional 80 quadrats per treatment were weight-estimated on each sample date.

The maintenance of soil water levels near field capacity throughout the growing season had little net effect on pad densities of *O. polyacantha* but prevented increases in biomass which were normal for the area from 1971 to 1973. Nitrogen fertilization increased pad density and biomass through 1972 and 1971, respectively, then decreased both through 1973. The combination of supplemental water and nitrogen on the same treatment caused precipitous decreases in both pad density and biomass.

The intraseasonal biomass dynamics of *O. polyacantha* suggest that late summer, fall, and early spring are periods of biomass accumulation while the late spring and early summer period is one of biomass decline.

KEY WORDS

Cactus, *Opuntia polyacantha*, shortgrass prairie, nitrogen fertilization, irrigation, seasonal biomass dynamics, system stress, cactus-consumer interactions, succulent.

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EFFECTS OF SOIL ENVIRONMENT ON ROOT GROWTH OF AGRICULTURAL CROPS IN PRAIRIE SOILS

W. B. Voorhees

The worldwide need for food and the United States' ability to produce a large portion of it are causing more and more previously uncropped land to be tilled for food production. The nationwide concern for preserving our environment has put some restrictions on crop production practices. The current energy crises is affecting food production due to shortages of fuel for processing and transportation, fertilizer, and other necessary chemicals. In addition to these, each year about 1 million acres of agricultural land are irreversibly lost to airports, highways, shopping centers, factories, and housing. The problem then is how can we more efficiently increase food production from decreasing land acreage in the face of an energy crises, and still preserve our environment?

There are many different approaches to solving this problem. Many scientists are attempting to increase both the quantity and quality of crop produce, and to improve plant production efficiency. For example, plant physiologists are increasing their knowledge of photosynthesis with hopes of increasing the efficiency of this basic process of converting raw materials into edible foodstuffs. Plant geneticists are improving crop varieties and increasing crop yields through selective breeding. Equally important examples in other disciplines could be cited.

One area of crop production that has not received widespread attention but has significant potential is the response of plant roots to soil environment under natural field conditions. Plant root systems perform many important functions such as those relating to water and nutrient uptake. Generally, the plant's root and aerial portion compete for the metabolic end products of these raw materials. The optimum partition should be when final yield of usable plant material is maximized. For most crops, this product is some portion of the shoot, generally the seed. However, for sugarbeets, potatoes, and other vegetables, the root itself (or some underground organ) is the usable portion of the plant. Nevertheless, a close interrelationship exists between root and shoot growth, and the soil and atmospheric environment (Aung, 1971). Modifying the soil environment to achieve optimum partition of metabolites between root and shoot will result in more than yield increase. Efficiency of plant material produced per unit of raw material used will likely also increase. Healthy, vigorous plants may withstand the attacks of pests which will help ease the energy crises and pollution concerns by using less fuel and farm chemicals. Data concerning the response of roots to soil environment, under field conditions, are sorely lacking. Unlike the shoot portion, the root system of a plant cannot be directly and nondestructively studied except by using hydroponic and rhizotronic methods. Various aspects of soil environment have been measured by new technical developments and new knowledge of basic plant-soil relationships.

This paper illustrates how root growth can be altered by normal cultural practices, and briefly discusses some important practical consequences. Although most of the discussion concerns row crop systems for agricultural crops, it can be applied to trees and grasses.

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I. Effects of Normal Cultural Practices on Soil Environment

A normal cultural practice can be defined as any manipulation of the soil and/or plant material commonly practiced during the production of a given crop. All agricultural crops involve a certain amount of soil manipulation during seeding and subsequent harvesting. This manipulation always has two general effects; (1) rearrangement of the soil matrix, and (2) deposition of plant residue on or near the soil surface.

The soil matrix consists of solid material, organic and inorganic. Water is held on the surfaces of this solid material and in some pore spaces between the solid particles. Thus, a soil volume consists of some definite ratio of solid, liquid, and air. The bulk density of the soil, expressed as weight of dry soil per unit volume of bulk soil mass, is an expression of the physical or spatial arrangement of the solid portion of the soil matrix. Generally, a soil with high bulk density has a small percentage of pore volume and a relatively small mean pore diameter, while the converse is true for low bulk density soil. These porosity characteristics strongly influence the quantity of water stored for root uptake and the ease with which water can infiltrate and move throughout the soil mass. Soil capacity to hold heat and the movement of heat through the soil is also a function of the porosity characteristics and the related water regimes. The diffusion of oxygen into, and carbon dioxide out of the soil depend on the porosity characteristics.

Depending on soil type and moisture content, various tillage practices can significantly affect soil environment. For example, moldboard plowing can increase porosity by about 60% in the upper 6-inch layer of soil (Allmaras et al., 1966), and thus significantly affect water storage capacity of the layer. Subsequent tilling or cultivating the soil may either decrease or increase the porosity.

Table 1 shows the effects of tillage on shallow soil temperatures. Although these temperature differences seem small, they are significant, since the optimum temperature for dry matter production of corn is about 27.4 C (Allmaras et al. 1964). Since soil temperatures at planting (about May 1) are usually much lower, tillage may significantly affect germination and early growth.

Soil matrix can be rearranged by other means than tillage. Wheel traffic, during normal field operations, exerts a compactive force on the soil mass, which may increase bulk density. Table 2 shows the bulk density with depth for soil subjected to wheel traffic (during the normal preparation and planting of soybeans) as compared with an adjacent row with no wheel traffic. Soil with the higher bulk density also had a higher volumetric water content and a slightly higher temperature.

As the bulk density of the soil increases, the soil strength increases. Soil strength is the physical resistance of the soil to displacement by a plant root. When a plant root develops turgor pressure sufficient to overcome the soil resistance, roots can elongate. Soil strength is often measured with a metal penetrometer probe and can be related to root elongation rates (Voorhees et al., 1974a). Since porosity decreases as bulk density increases poor aeration also limits root growth in high density soils. Thus, soil strength and soil aeration are closely related and difficult to delineate (Voorhees et al., 1974b). Since plant roots can exert only limited turgor pressure and require a certain minimal oxygen supply, the bulk density of the soil can profoundly affect root growth patterns.

The second general effect of normal cultural practices is deposition of plant residue on or near the soil surface. This residue effectively conserves water and reduces soil and wind erosion. Since it also reflects solar radiation and insulates soil against heat loss, the end result often is maintaining the upper foot of soil at a lower temperature than bare soil. Table 3 shows the effect of plant residue on the soil surface. The residue decreased soil temperature to 45-cm depths. Plant residue may also retard evaporation and increase infiltration, thus increasing the soil water content. While the latter is normally beneficial, the decreased soil temperatures may be detrimental in the northern latitudes.

Table 1. Shallow (8 cm) soil temperatures on June 30 produced by various tillages. (Lamberton, Minnesota, 1965).

Tillage	Temperature, °C
Plow	24.5
Plow-disk-harrow	26.4
Plow and wheel-tracked	27.7

Table 2. Effects of normal wheel traffic on bulk density during soil preparation and planting of soybeans, 1973.

Depth	Bulk density midway between rows	
	Wheel-tracked	Non wheel-tracked
inches	g cm^{-3}	
3	1.40	1.28
9	1.52	1.48
15	1.56	1.54
21	1.61	1.60
30	1.67	1.66
42	1.72	1.73
54	1.82	1.82

Table 3. Mean soil temperature for bare and mulched soil surfaces. (Allmaras and Nelson, 1971)

Depth	Mean soil temperature midway between rows	
	No mulch	4,500 kg straw/ha
cm	°C	
	Planting to 39 days after planting, 1968	
5	21.5	19.7
15	20.9	19.3
25	20.3	18.9
35	19.7	18.4
45	19.0	17.6
	Planting to 57 days after planting, 1969	
5	20.1	18.3
15	19.4	17.9
25	18.5	17.5
35	17.6	16.8
45	16.9	16.2

II. Effects of Soil Environment on Root Growth Patterns

The most important function of a plant root system is to supply water and nutrients for the plant's various metabolic processes. Thus, soil environment is important if it limits the roots' ability to extract water and nutrients from the soil. Most plants grown for food and fiber are often planted in soil prepared to have certain characteristics. All seedbeds are intended to promote fast germination, good emergence, and early growth. Many crops are seeded in distinct widely spaced rows, tilled and prepared for the desired soil environment. Exceptions are some cereal grains and grasses that may be seeded in a random fashion or in closely spaced rows without a distinct seedbed soil environment that differs from surrounding soil environment. More often, however, to support and produce a mature plant root growth must extend beyond its original soil environment at planting time to explore and exploit the soil for water and nutrients.

To measure the vertical and horizontal distribution of root systems, soil monoliths with plant roots intact, are extracted from the soil. For a mature corn plant the monolith is 5 feet deep, 3 feet wide, and 15 inches thick. The roots are held in place by a modified pin board technique while the soil is washed away (Nelson and Allmaras, 1969). The whole root system is photographed and then segmented for later, more detailed, laboratory analysis.

Figure 1 shows the root distribution of 6-week-old corn plants. The rows are orientated perpendicular to the plane of the photograph and are spaced 30 inches apart. The vertical dimension of the photograph corresponds to a soil depth of 3 feet. The corn plant on the left was subjected to an equal amount of wheel traffic from tractor and implements on both sides

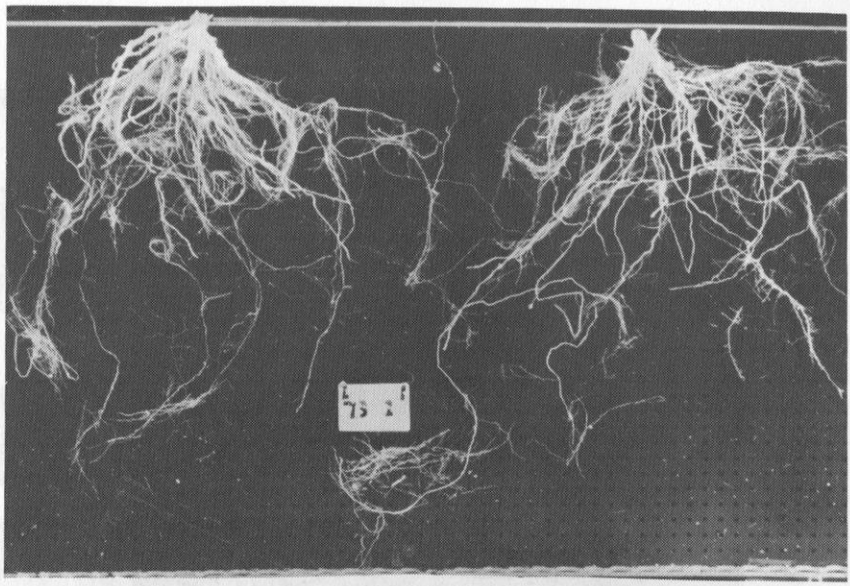

Fig. 1. Root distribution of corn as affected by wheel traffic-induced soil compaction, Lamberton, Minnesota, 1973 (Wheel traffic on both sides of left hand plant; wheel traffic on left side only of right hand plant).

of the row. The plant on the right had wheel traffic on the left side only. The increased bulk density, and soil strength prevented roots from the plant on the left from proliferating extensively into the surface 8 in. of soil, whereas roots on the right-hand side of the right plant grew freely into the noncompacted upper soil depths.

Figure 2 shows similar effects of soil compaction on soybean root growth patterns. The vertical depth in this photograph is 5 feet, and the horizontal width is 3 feet. Wheel traffic was confined to the right side of the row, and root growth was restricted in the compacted upper 8 to 10 in. of soil.

Figure 3 shows growth patterns of sugarbeet tap roots in relatively normal (3-A) and compacted (3-B) soil environments. The high soil strength was obtained by excessive wheel traffic. Since beets grown in dense soil were restricted in rooting depth, the main storage root was deformed and branched in response to the high soil resistance. Such root growth often results in a lower beet yield. Effects of soil compaction on potato tuber development have also been noted (Adams et al., 1960).

While the above figures illustrate the effect of high bulk density in restricting root growth, the bulk density may also be too low. Figure 4 shows similar age pea roots grown under laboratory conditions in soil cores with different bulk densities. For water and nutrient uptake, a relatively large total root length per unit volume of soil is desirable. Thus, a density of 1.4 g cm^{-3} (4-B) is better than a density of 1.2 g cm^{-3} (4-A). This principle has been observed under field conditions for corn.

The effects of plant residue mulch on soil temperature and soil water can influence root growth, depending on general climatic conditions. Figure 5-A shows root growth patterns of corn in a warm, dry season with a mulch placed over the rows only. Root growth between the rows was sparse as compared with 5-B where mulch was placed between the rows (rather than

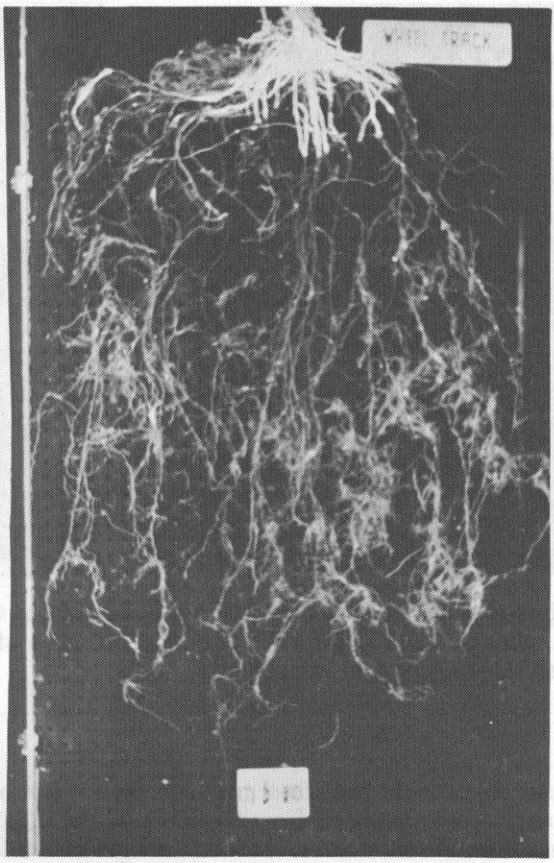

Fig. 2. Root distribution of soybean as affected by wheel traffic-induced soil compaction, Lamberton, Minnesota, 1973 (Wheel traffic on right hand side of row only).

over the rows). The mulch between the rows kept the soil cooler and wetter. The increased water supply promoted lateral root extension between rows. Opposite results have been observed for a cool, wet season (Figure 6, Allmaras and Nelson, 1971) when mulch placed between the rows (as compared with mulch placed over the rows) decreased soil temperature and suppressed lateral root extension. Under both climatic conditions, mulch placed over the row reduced the mass of root growth to a 5-cm depth for both corn and soybeans (Allmaras et al., 1973). This suggests that the optimum temperature for root initiation is relatively high and may be significantly affected by normal cultural practices in the north.

III. Practical Implications of Soil Environment on Root Growth

Normal cultural practices can create differences in soil environment which can affect root growth. These effects may be simply quantitative or may manifest themselves in terms of spatial distribution both vertically and horizontally. These root growth patterns can significantly affect final plant yield if water and nutrient uptake are restricted in some way by restricted root growth.

Experiments involving placement of plant residue (Figure 5) show that grain yields generally decreased, as early root growth at shallow depths decreased between the rows.

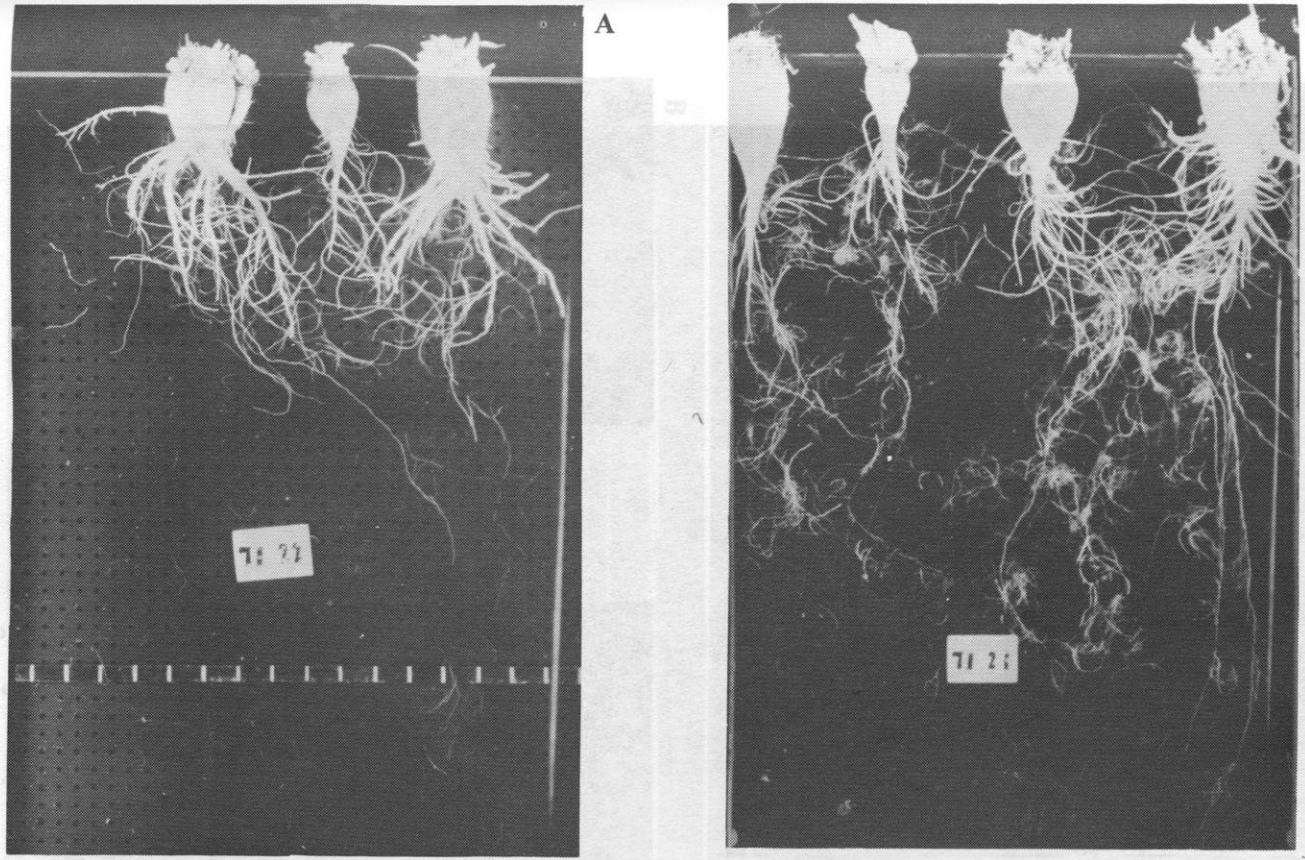

Fig. 3. Sugar beet root growth in normal soil (3-A), and in compacted soil (3-B) (Grand Forks, North Dakota, 1971).

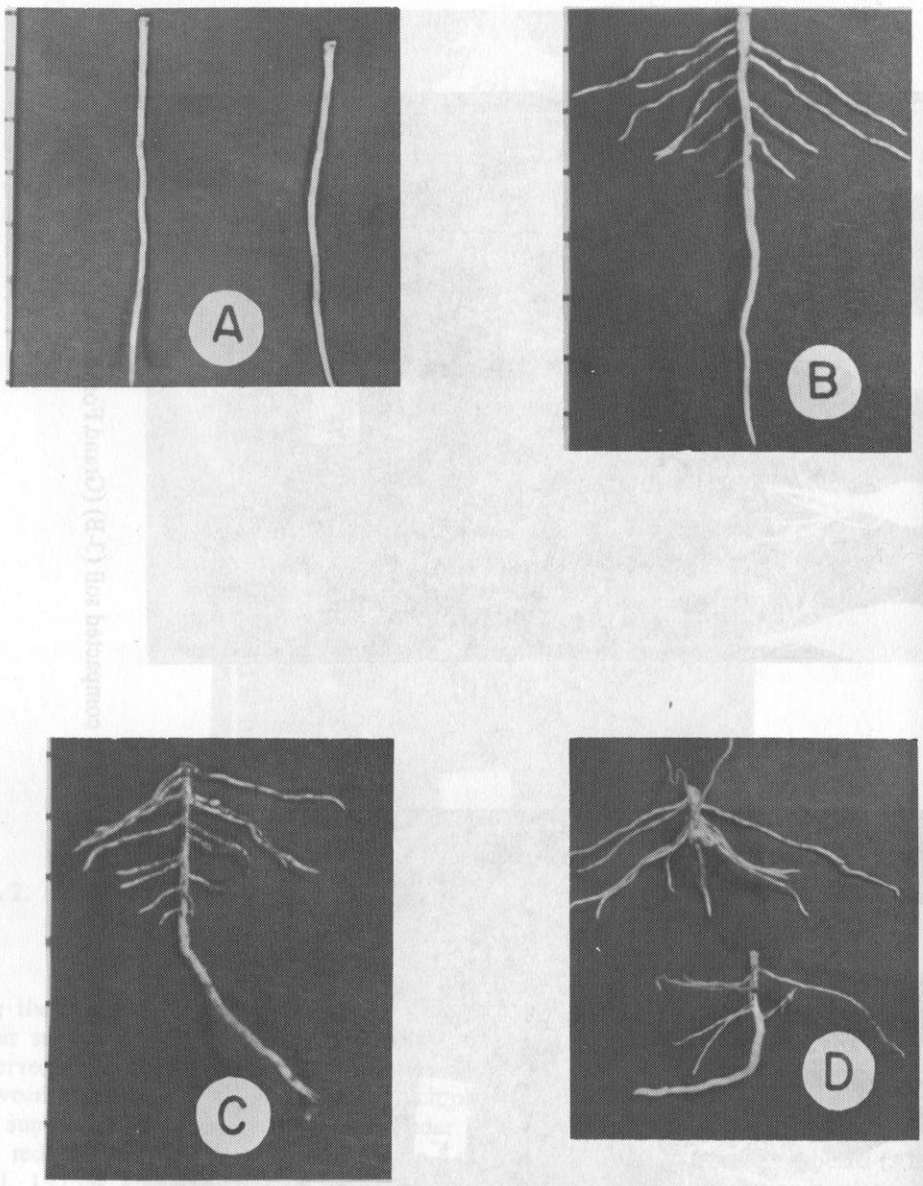

Fig. 4. Morphological features of pea seedling root growth in soil cores of varying bulk density.
A -- bulk density ≃ 1.2 g cm^{-3}
B -- bulk density ≃ 1.4 g cm^{-3}
C -- bulk density ≃ 1.6 g cm^{-3}
D -- bulk density ≃ 1.8 g cm^{-3}

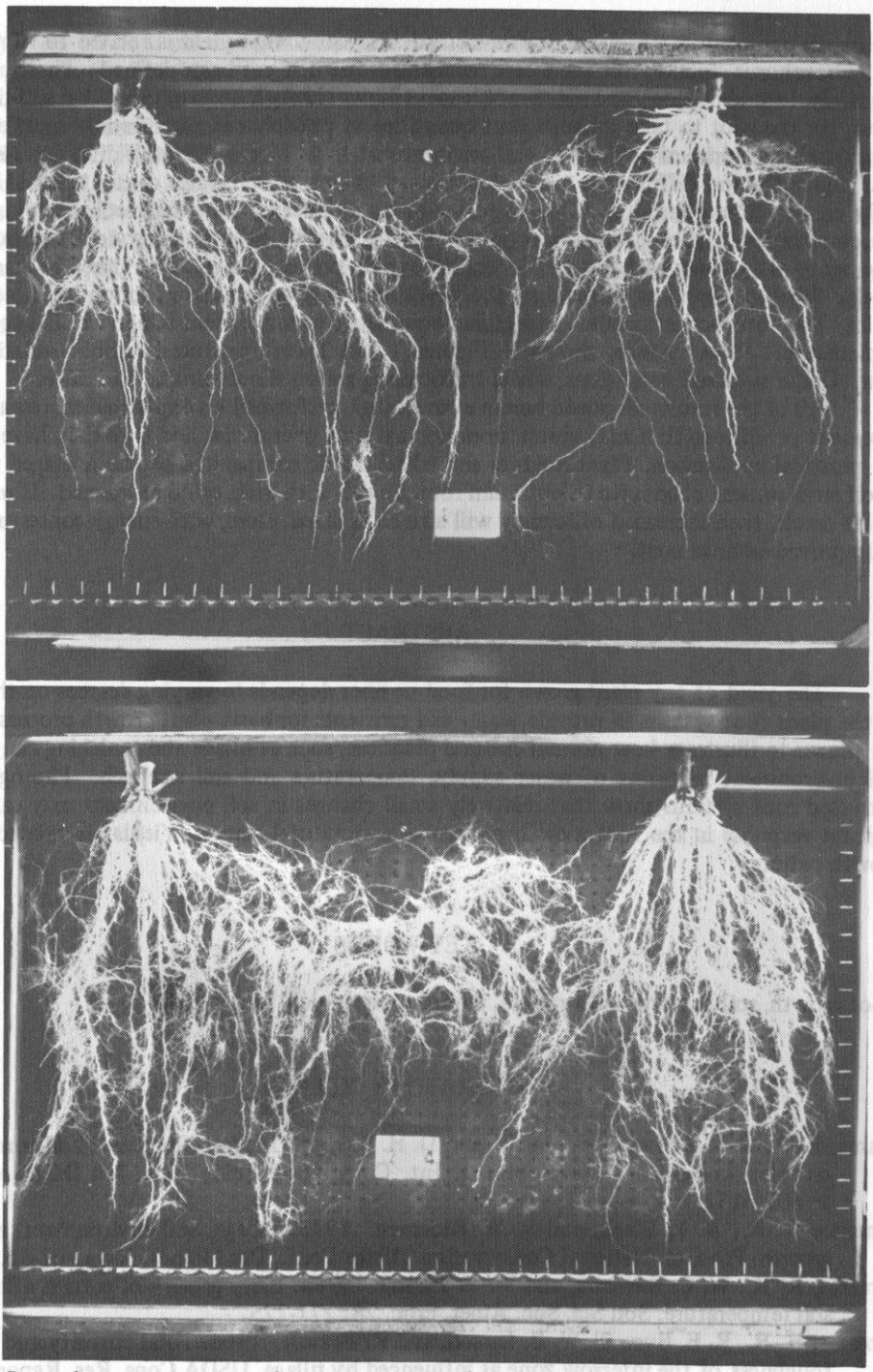

Fig. 5. Lateral root extension of corn in a warm dry year with mulch placed over the rows only (5-A) and with mulch placed only between the rows (5-B) (Allmaras and Nelson, 1971).

Experiments with wheel traffic compaction show that yield is related to root growth and phosphorus uptake, but the exact mechanism has not yet been defined. Phosphorus is a relatively immobile ion, and does not easily move through the soil mass by self-diffusion. Thus, for the root to take up sufficient quantities of phosphorus, either roots must explore a considerable volume of soil or the soil environment must increase the self-diffusion rate of the ion. Since the ion diffuses via a liquid pathaway, increased soil water content should theoretically increase phosphate ion diffusion to the root. This seems to be the mechanism involved in the compaction studies. The corn rows having wheel traffic on both sides yielded about 18 bu/acre more than rows with no traffic on either side on plots having low inherent phosphorus levels. When phosphorus was added, the yields increased but soil compaction had no effect on yield. The compaction resulted in a higher volumetric water content which would support this explanation. Root systems shown in Figures 1 and 2 were produced during a relatively dry year. Under such soil conditions, wheel traffic compaction should not be excessive.

All of the results discussed herein even though performed on experimental research basis represent conditions that may result from normal field operations, and thus they have immediate practical application. Plant residues and wheel traffic compaction can be managed to create a soil environment conducive to optimum root growth with little or no extra cost. If maximum yields result, then increased efficiency will also be realized, along with energy conservation and an improved environment.

ABSTRACT

The yield of any plant grown for food or fiber depends to varying degrees on the ability of the plant root system to provide water and nutrients for basic plant growth processes. Data are shown to illustrate how normal cultural practices, such as tillage and mulching can alter the soil environment in terms of water supply, temperature and soil strength. Photographs of extracted root systems show that relatively small changes in soil environment may cause a signigicant response in the root growth pattern of agricultural plants. Yields are related to root growth patterns.

KEY WORDS

Root growth, soil density, soil strength, compaction, mulch, crop yield.

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Section III: CYTOGENETICS AND TAXONOMY

The paper on the role of cytoplasmic inheritance in speciation re-examines a fundamental question in the light of author's own work of more than a decade. The vegetative key on the grasses of Nebraska should prove very useful even outside of that state. This section was better represented at the meetings than might be reflected by the number of papers included here.

CYTOPLASMIC VARIABILITY AND SPECIATION IN *TRITICINAE*

S. S. Maan

INTRODUCTION

The presence of mitochondrial and chloroplast DNA provides physical basis for cytoplasmic inheritance in higher plants (Granick and Gibor, 1967). Cytoplasmic inheritance is essentially maternal because cytoplasmic genes usually are not transmitted through the male gametes. Research on cytoplasmic inheritance in higher plants is limited to the study of cytoplasmic differences between and within species. Cytoplasmic differences are inferred from specific nucleo-cytoplasmic interactions between the cytoplasmic hereditary constituents and certain nuclear genes controlling the presence or absence of cytoplasmic effects. However, the prevalence of cytoplasmic variability among plant species and cytoplasmic homologies between certain polyploids and their related diploid progenitors indicate that cytoplasmic differences between and within species may have played a significant role in the evolution of species. Stebbins (1950) referred to hybrid sterility and reduction of plant vigor caused by nucleo-cytoplasmic interactions in the genus *Epilobium* (Michaelis, 1938, 1949, 1954; Lehmann, 1944) and concluded that "The explanation of these results is not clear. That, in contrast to the majority of plant species which have been compared by means of hybridization, the species of *Epilobium* differ markedly in their cytoplasm, is certain"...and..."The constancy of the plasma and its apparent partial independance of the genotype in *Epilobium* are as yet unique among known examples in the higher plants..." However, cytoplasmic variability in plants has since been shown to be pervasive and constancy of interspecific cytoplasmic differences has been demonstrated in many unrelated plant genera including *Solanum* (Grun, 1970), *Nicotiana, Gossypium* (see reviews by Edwardson, 1970; Harvey, Levings, and Wernsman, 1972). Relatively more extensive investigations of interspecific nucleo-cytoplasmic genetics of *Epilobium* (Michaelis, 1954), *Triticum*, and *Aegilops* (Mann, 1973a, b; and reported here) indicate that cytoplasmic variability often results in reduced fertility and plant vigor of backcross plants and may be involved in the development and operation of genetic isolating mechanisms which play an important role in the evolution of species.

In general, the available data indicate that the prevailing cytoplasmic characteristics among related diploid and polyploid species of *Triticum* and *Aegilops* correspond to their genomic relationships (Mann, 1973a, c). Also, the cytoplasmic differences between cultivated *T. timopheevi* or *T. zhukovskyi* and their putative wild progenitor *T. araraticum* indicate that incipient species may differ cytoplasmically, even though their nuclear genomes still have relatively close chromosomal pairing homology (Maan, 1973a). If cytoplasmic variability is only one of the several genetic, phenotypic or physiological characteristics which together determine ultimate development of subspecies into incipient species, then (like other genetic variables) cytoplasmic differences within species may equal or exceed those between related species or genera as in *Epilobium* (Michaelis, 1954). However, if the magnitude of cytoplasmic differences among related species corresponds to their overall genomic relationships, then cytoplasmic differences within species may not exceed those between related species, and nuclear

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genes controlling cytoplasmic effects or specific nucleo-cytoplasmic interactions may provide a measure of genomic affinities among certain polyploids and their diploid progenitors. Certain diploid species with a wider geographical distribution, greater antiguity, and adaptation to diverse environments may be cytoplasmically more diverse than their allopolyploid descendents of recent origin or restricted adaptation. Therefore, the present day diploids and related allopolyploids may have similar cytoplasms but not the 'same cytoplasm'.

The cytoplasmic differences within species or between subspecies may enhance the development of hybrid sterility isolating systems, and may raise them to a level of incipient species because their hybrids and backcross progenies would have male sterility and/or reduced plant vigor. Such hybrid combinations or their backcross progenies will be rapidly eliminated due to zygotic sterility, reduced male fertility and plant vigor, unless chromosomes or genes controlling the cytoplasmic effects from the female parent are transmitted through the functional female gametes produced by sterile F_1 hybrids. In such a situation, cytoplasmic variability may have an important role in the unilateral introgression of certain nuclear genes controlling cytoplasmic effects. If these genes have other epistatic effects they may influence the expression of still other nuclear genes controlling certain phenotypic or physiologic characteristics, because nucleo-cytoplasmic interactions often affect the expression of a whole syndrome of phenotypic characters. In some cases, the resulting plants may not resemble parental species.

This paper relates cytoplasmic variability to the development and operation of incompatibility and sterility barriers which lead to speciation in plants. The data presented and literature reviewed show that cytoplasmic similarities and differences among related *Triticum* and *Aegilops* species correspond to their genomic relationships. It is proposed that the magnitude of cytoplasmic differences and nucleo-cytoplasmic interactions, and not the nuclear components alone, determine the probable success of new allopolyploid species, and that crossability barriers between certain allopolyploids and their putative diploid progenitors indicate their phylogenetic relationships.

SPECIATION IN *TRITICUM*

Sakamura (1918) demonstrated three ploidy levels (n=7,14,21) among *Triticum* species. Kihara (1919, 1924) and Sax (1922) demonstrated that tetraploid and hexaploid *Triticum* species were allopolyploids, and Kihara (1924, 1954b) assigned genome symbols AA, AABB, and AABBDD to the *Triticum* species at three ploidy levels (Table 1). Since *T. boeoticum* had been identified as the A-genome donor to 4x and 6x *Triticum* species (Kihara, 1924), a search continued for the diploid B-genome donor to 4x and 6x species, and the diploid D-genome donor to 6x wheats. In 1924, the D-genome was first identified in 4x *Ae. cylindrica* (Sax and Sax, 1924; Gains and Aase, 1926), and 20 years later *Ae. squarrosa* was shown to be the 2x D-genome donor to 4x *Ae. cylindrica* (2n=28;CCDD) and 6x *T. aestivum* (2n=42, AABBDD) by Kihara (1944) and McFadden and Sears (1944, 1946). Kihara (1944) and McFadden and Sears (1944, 1946) reported the synthesis of hexaploid *T. aestivum* and demonstrated that *T. aestivum* originated from the natural hybridization between cultivated emmer (2x=28;AABB) and wild *Ae. squarrosa* (2x=14;DD).

However, the source of the B genome of wild *T. dicoccoides* Körn and cultivated 4x and 6x *Triticum* species remained controversial (McFadden and Sears, 1946; Riley, Unrau, and Capman, 1958; Sears, 1956a, b, 1969; Sarkar and Stebbins, 1956; Feldman, 1966; Kimber and Athwal, 1972; Johnson, 1972). Also, phylogenetic schemes for the origin of common wheat proposed by Kihara (1944) and McFadden and Sears (1944, 1946) did not emphasize relationships between the two wild tetraploid *Triticum* species complexes--the *T. timopheevi* complex

and the *T. dicoccoides* Körn complex. *T. timopheevi* remained an unsolved problem in the systematics of *Triticum* species (Harlan and Zohary, 1966) and was essentially ignored until recently because it was known to be endemic to a small isolated area in Georgia, and wild AG-genome tetraploids were not known to occur outside southern USSR (Svetozarova, 1939; Tanaka and Ichikawa, 1968). However, the two tetraploid *Triticum* species complexes with AB and AG genomes are now known to occur sympatrically in southern Turkey (Rao and Smith, 1968), northern Iraq (Sachs, 1953; Wagenaar, 1961, 1966), eastern Iran (Jakubzinger, 1958; Dagan and Zohary, 1970) and in Transcaucasia (Johnson and Hall, 1966; Johnson, 1967b, Waines, 1970). Therefore, a discussion of phylogenetic relationships among *Triticum* species should not ignore *T. timopheevi*.

Lilienfeld and Kihara (1934) assigned genome AG to *T. timopheevi* because the second genome had partial homology to the B-genome of emmers. Kostoff (1936) suggested that the G-genome was a modified B and designated it as β . Kihara (1966) proposed that *Ae. speltoides* contributed the cytoplasm (and B-genome) to tetraploid emmers (2x=28,AABB) and hexaploid *T. aestivum* (2x=42;AABBDD), because F_1 hybrids between *Ae. speltoides* and *T. boeoticum* were obtained only when *Ae. speltoides* was used as a female parent. At that time cytoplasmic sterility characteristics of *Ae. speltoides* cytoplasm were not conclusively established (Suemoto, 1968, 1973; Maan and Lucken, 1968b, 1969) and *Ae. speltoides* was generally assumed to be the B-genome donor to 4x emmers and 6x common wheats (Sears, 1956a, b; Kihara, 1966). Since then, *T. monococcum, T. boeoticum* (Maan and Lucken, 1967, 1968a, 1970) and *Ae. speltoides* (Maan and Lucken, 1971a) have been shown to have different male sterility inducing cytoplasms (Tables 1 & 2) and to have cytoplasms different from those of B-genome tetraploid or hexaploid *Triticum* species (Maan and Lucken, 1972). In view of this cytoplasmic evidence, Maan and Lucken (1971a, 1972) and Maan (1973a) suggested that *Ae. speltoides* contributed cytoplasm and G-genome to the *T. timopheevi* complex. Also, Shands and Kimber (1973) reported closer chromosome pairing homology in F_1 hybrids of *T. timopheevi* X *Ae. speltoides* than in those of *T. durum* X *Ae. speltoides* and redesignated the *T. timopheevi* genomes as AASS.

To account for the failure to find a diploid B-genome and cytoplasm donor to tetraploid emmers and hexaploid common wheats with B-genome, Maan (1973a) suggested that an amphidiploid progenitor of 4x *T. araraticum* (AAGG or AASS) hybridized as a male with an *Aegilops* species having cytoplasm like that of *Ae. squarrosa* and wild tetraploid *T. dicoccoides* Körn with emmer cytoplasm and AB genome developed from this cross (Fig. 1). Later, AB-genome emmer under domestication again crossed with *Ae. squarrosa* and produced hexaploid *T. aestivum* as proposed by Kihara (1944) and McFadden and Sears (1944, 1946). Possibly, this process was facilitated by a high frequency of unreduced restitution nuclei formation during meiosis as shown in hybrids of *T. durum* X *Ae. squarrosa*. The high frequency of unreduced gametes resulted in fertility of F_1 plants and production of amphidiploid F_2 plants with 2n=42; 21", AABBDD (Mitsuoka, 1953; Tanaka, 1959; Kihara and Lilienfeld, 1949).

The proposed phylogenetic scheme (Fig. 1) explains cytogenetic and cytoplasmic relationships among related *Triticum* and *Aegilops* species. An argument can be advanced against the proposed origin of AABB genomes and cytoplasm of *T. dicoccoides* Körn because inviable seeds are produced from *Ae. squarrosa* ♀ X *T. araraticum* ♂ (Maan, unpublished).

A genetic crossability or sterility barrier can be anticipated between a derived backcross fertile line from a sterile F_1 hybrid and the descendants of one or the other parental species. Without such a crossability or sterility barrier between the derived fertile line and the parental species, the two species will not remain distinct. A fertile line was experimentally obtained from the backcrosses of a highly sterile F_1 hybrid *Ae. speltoides* ♀ X *T. aestivum* ♂ with the latter species as the recurrent male parent. This fertile alloplasmic *T. aestivum* line with *Ae. speltoides* cytoplasm had normal fertility and produced fertile or partially fertile F_1 hybrids

Table 1. Triticum species, their genomic symbols, and nucleo-cytoplasmic interactions.

Triticum species	Chromosome no., and genome symbol	Nucleo-cytoplasmic interactions*		
		T. aestivum	T. durum	T. timopheevi
T. monococcum	2n=14;AA		S,W,Z^{8}	
T. boeoticum	2n=14,AA	S,W,Z^{16}	S,W,Z^{15}	S,W,Z^{8}
T. dicoccoides	2n=28,AABB	F,N^{10}	FN^{6}	FN^{10}
T. dicoccum	2n=28,AABB	F,N^{11}	F,N	
T. durum	2n=28,AABB	FN^{2}		F,N^{12}
T. aestivum	2n=42,AABBDD		FN^{3}	F,N^{7}
T. macha	2n=42;AABBDD	F,N^{13}	FN^{10}	FN^{6}
T. dicoccoides var. nudiglumis	2n=28,AAGG	S,N^{11}	S,N^{13}	S,N^{12}
T. timopheevi	2n=28,AAGG	S,N^{20}	S,N^{10}	
T. araraticum	2n=28,AAGG	S,N^{15}	S,N^{12}	F,N^{12}
T. Zhukovskyi	2n=42,AAAAGG	S,N^{8}	S,N^{16}	F,N^{8}

* F = male fertile, N = normal vigor, S = male sterile, W = weak or reduced vigor, and Z = inviable seeds or zygote elimination. Superscript indicates the number of backcrosses with the recurrent male parent.

from reciprocal crosses with euplasmic *T. aestivum*. However, sterile F_1 hybrids were obtained from crosses between male-sterile alloplasmic *T. aestivum* with *Ae. speltoides* cytoplasm and the derived fertile alloplasmic *T. aestivum* line with *Ae. speltoides* cytoplasm. These results show that a nucleo-cytoplasmic sterility barrier between the fertile and sterile lines derived from a sterile F_1 hybrid of *Ae. speltoides* X *T. aestivum* can be established (Maan, unpublished).

Meiotic chromosome pairing in certain 35 chromosone F_1 hybrids of *T. dicoccoides* (2n=28;AABB), *T. paleocolchicum* (2n=28;AABB), *T. araraticum* (2n=28,AABB), or *T. timopheevi* (2n=28;AAGG) X *T. aestivum* indicated that one or more D-genome chromosomes were involved in multivalent configurations, leaving fewer than the expected seven unpaired D-genome chromosomes (Maan, 1973a). This evidence of segmental interchanges between the D-genome and the AB- or AG-genome chromosomes suggests that the D-genome may have been involved in the origin of AB-genome of *T. dicoccoides*. Therefore, the crossability barrier between the 4x *Triticum* species and 2x *Ae. squarrosa*, and possible translocations between the D- and the AB-genomes, indicate that a progenitor of *Ae. squarrosa* was involved in the origin of cytoplasm and B-genome of the tetraploid *Triticum* species.

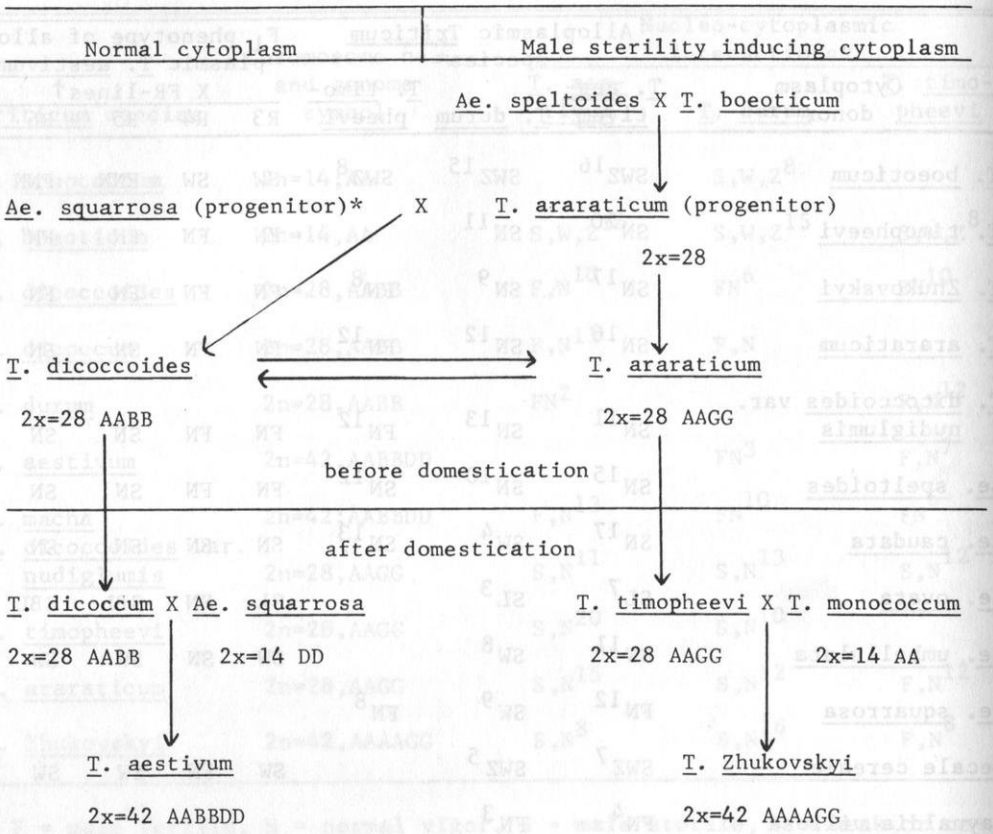
Table 2. Cytoplasmic differentiation among species of Triticum, Aegilops, Secale, and Haynaldia.

Cytoplasm donor	Alloplasmic Triticum species*			F_1 phenotype of alloplasmic T. aestivum X FR-lines†			
	T. aestivum	T. durum	T. timopheevi	R3	R4	R5	R6
T. boeoticum	SWZ^{16}	SWZ^{15}	SWZ^{8}	SW	SW	FNN	FNN
T. timopheevi	SN^{20}	SN^{11}		FN	FN	FN	FN
T. Zhukovskyi	SN^{17}	SN^{9}	FN^{8}	FN	FN	FN	FN
T. araraticum	SN^{16}	SN^{12}	FN^{12}	FN	FN	SN	SN
T. dicoccoides var. nudiglumis	SN^{11}	SN^{13}	FN^{12}	FN	FN	SN	SN
Ae. speltoides	SN^{15}	SN^{10}	SN^{12}	FN	FN	SN	SN
Ae. caudata	SN^{17}	SW^{4}	SN^{13}	SN	SN	SN	SN
Ae. ovata	SL^{7}	SL^{3}		SL	SN	SBL	SBL
Ae. umbellulata	SW^{11}	SW^{8}		SW	SN	SW	SW
Ae. squarrosa	FN^{12}	SW^{9}	FN^{8}				
Secale cereale	SWZ^{7}	SWZ^{5}		SW	FN	SW	SW
Haynaldia villosa	FN^{4}	FN^{3}					
T. aestivum (euplasmic)		FN^{3}	FN^{7}	FN	FN	FN	FN
T. durum (euplasmic)	FN^{2}			PFN	PFN	PFN	PFN

* Superscript indicates number of backcrosses with the recurrent male parent.

† R3 = T. timopheevi/3*T. aestivum 'Marquis'.
R4 = T. timopheevi-Ae. squarrosa/3*T. aestivum 'Dirk'.
R5 = T. Zhukovskyi/3*T. aestivum 'Justin'.
R6 = T. boeoticum-Ae. squarrosa/T. durum/T. aestivum.
B = bushy growth habit, F = male fertile, L = late or delayed maturity, N = normal plant vigor, NN = near normal vigor, PF = partially fertile, S = male sterile, W = weak or reduced vigor, Z = zygote elimination or inviable seeds.

Fig. 1. ORIGIN OF WHEAT



*Crosses involving Ae. squarrosa ♀ and T. timopheevi, T. araraticum, or T. durum ♂ result in shrivelled inviable seeds, indicating that F_1 hybrids may be obtained by embryo culture. Reciprocal crosses produce normal, semilethal, or lethal F_1 hybrids depending on the parental genotypes. T. timopheevi or T. aestivum with Ae. squarrosa cytoplasm have normal fertility and plant vigor, indicating that T. timopheevi genomes have homoeoallels of the D-genome chromosome genes, because addition of one D-genome chromosome to AB-genomes is necessary to develop T. durum with Ae. squarrosa cytoplasm.

SPECIATION IN *AEGILOPS*

Polyploidy has also played a significant role in the evolution of the genus *Aegilops*. Kihara (1949, 1954a) used meiotic chromosome pairing, male and female fertility, and morphology of the F_1 hybrids to analyze genome relationships among 2x, 4x, and 6x species of *Triticum* and *Aegilops*. Also, morphology of the synthetic allotetraploids, the amount of chromosome pairing, and fertility of hybrids of certain synthetic and natural allopolyploids were used for genome designations. These genome symbols indicate phylogenetic relationships among species and genera (Table 3).

Nine diploid *Aegilops* species were grouped according to the extent of genome homologies as following:

C-group included *Ae. caudata* (C), and *Ae. umbellulata* (C^u),

M-group included *Ae. comosa* (M), *Ae. uniaristata* (M^u), *Ae. mutica* (M^t), *and Ae. squarrosa* (D),

S-group included *Ae. speltoides* (S), *Ae. bicornis* (S^b), and *Ae. longissima* (S^l).

According to this grouping of the diploid *Aegilops* species, *Ae. squarrosa* with the D-genome was included in the M-group, *Ae. comosa* included *Ae. Heldreichii, Ae. longissima* included *Ae. sharonensis*, and *Ae. speltoides* included *Ae. auscheri* (Lilienfeld, 1951).

In general, 2x *Aegilops* species within the C-, M-, and S-groups had closer genome homologies than those between groups, but chromosome pairing data from crosses among diploid species alone were not conclusive enough for genome designations because of homologous pairing (Sears, 1948). Chromosome pairing data from 2x and 4x species crosses supplemented those from crosses between and within diploid species groups and showed relatively stronger genome hologies between certain allotetraploids and their respective diploid progenitors. However, in certain other cases the diploid genome donors were not conclusively identified because "It was not always possible to raise hybrids between the allotetraploid and the supposed parental species" (Kihara, 1954a). Also, one genome of certain 4x species may have been substantially modified from that of the likely diploid progenitor, or the current diploid progenitor has not been discovered. For example, the M-genomes of *Ae. ventricosa, Ae. ovata, Ae. triaristata, Ae. biuncialis*, and *Ae. columnaris* had substantially reduced chromosome pairing affinities in F_1 hybrids from crosses among these 4x species or with those of M-genome diploid *Aegilops* species which could be crossed with one or more of these tetraploids (Table 4).

The chromosome pairing affinities have not been studied in the F_1 hybrids from direct crosses of *Ae. squarrosa* X *Ae. cylindrica, Ae. bicornis* X *Ae. variabilis, Ae. comosa* or *Ae. umbellulata* X *Ae. triaristata, Ae. mutica* X *Ae. ovata,* and *Ae. uniaristata* X *Ae. biuncialis,* because of the crossability barriers (Kihara, 1954). Following sections report on cytoplasmic similarities and differences among *Ae. variabilis, Ae. cylindrica, Ae. triaristata, Ae. ovata, Ae. biuncialis,* and their respective diploid progenitors, and indicates that *Ae. bicornis, Ae. squarrosa, Ae. umbellulata, Ae. mutica,* and *Ae. uniaristata,* respectively, were the cytoplasm donors of these allotetraploids.

CYTOPLASMS OF *AE. VARIABILIS* AND ITS PROGENITORS

Chromosome pairing homology in F_1 hybrids from crosses between *Ae. variabilis* and *Ae. umbellulata* (Berg, 1931) and those between *Ae. caudata* and *Ae. variabilis* (Kihara and Nishiyama, 1937) indicated that *Ae. umbellulata* contributed C^u-genome to *Ae. variabilis. Ae. umbellulata* was crossed as a male with *Ae. speltoides, Ae. sharonensis,* and *Ae. bicornis,* and the morphology of the F_1 hybrids indicated that *Ae. bicornis* was the S-genome donor to *Ae. variabilis.* Reciprocal crosses involving *Ae. umbellulata* (as the female) and *Ae. speltoides, Ae.*

Table 3. Aegilops species, their genome symbols, and nucleo-cytoplasmic interactions involving Triticum genomes.

Aegilops species	Chromosome number and genome symbol	Nucleo-cytoplasmic interactions† T. durum	T. aestivum	T. timopheevi
Ae. speltoides Tausch	2n=14,SS	S,NN[11]	S,NN[16]	S,NN
Ae. bicornis (Forsk.) Jaub. Spach.	2n=14,S^bS^b	PF,W[17]	PF,W[16]	PF,W
Ae. longissima S. & M.	2n=14,S^1S^1	PF,NN[2]	♀ S,BN[8]*	
Ae. sharonensis Eig.	2n=14,S^1S^1	PF,NN[6]	♀ S,BN[8]*	
Ae. mutica Boiss.	2n=14,M^tM^t	S,L[2]	PF,NL[6]*	
Ae. comosa S. & S.	2n=14,MM	S,BN[2]	S,BN[2]	
Ae. Heldreichii Holzm.	2n=14,MM	S,BN[6]	S,BN[6]	
Ae. uniaristata Vis.	2n=14,M^uM^u	♀ S,W[4]*	PF,W[4]	
Ae. caudata L.	2n=14,CC	♀ S,W[4]*	S,NN[16]	S,N
Ae. umbellulata Zhuk.	2n=14,C^uC^u	S,W[8]	S,W[10]	
Ae. squarrosa L.	2n=14,DD	♀ S,W[9]*	F,N[12]	FN
Ae. cylindrica Host.	2n=28,CCDD	♀ S,W[3]*	FN[6]	
Ae. ventricosa Tausch	2n=28,DDM^uM^u	PF,BN[2]*	PF,BN[6]	
Ae. crassa Boiss.	2n=28,D^1D^1MM		FN[2]*	
Ae. ovata L.	2n=28,C^uC^uMM	S,L[3]	S,L[9]	
Ae. triaristata Willd.	2n=28,C^uC^uMM	S,W[4]	S,W[7]	
Ae. biuncialis Vis.	2n=28,C^uC^uMM	S,W[4]*	PF,W[4]*	
Ae. columnaris Zhuk.	2n=28,C^uC^uMM	S,W[2]*	S,W[2]*	
Ae. juvanalis (Thell.) Eig.	2n=42,$DDMMC^uC^u$		FN[7]	
Ae. variabilis Eig.	2n=28,$C^uC^uS^1S^1$	PF,W[8]	PF,W[15]	PF,NN
Ae. kotschyi Boiss.	2n=28,$C^uC^uS^1S^1$	F,N[3]*	F,N[8]	
Ae. triuncialis L.	2n=28,C^uC^uCC	S,W[2]*	S,W[4]*	

sharonensis, Ae. longissima, or *Ae. bicornis* as the male did not succeed. Also, *Ae. variabilis* or *Ae. kotschyi* did not hybridize with any of the S-genome 2x species (Table 4). Therefore, chromosome pairing affinities between the S-genome of *Ae. variabilis* (or *Ae. kotschyi)* and those of *Ae. bicornis* (or other *Sitopsis* species) were not determined (Kihara, 1937a, 1954).

However, nucleo-cytoplasmic interactions between *Triticum* genomes and the cytoplasm of *Ae. variabilis, Ae. kotschyi, Ae. longissima, Ae. sharonensis, Ae. speltoides* and *Ae. bicornis* indicate that *Ae. longissima* and *Ae. sharonensis* are cytoplasmically similar (Maan, 1974a), and differ cytoplasmically from *Ae. speltoides* or *Ae. bicornis. Ae. bicornis* is cytoplasmically similar to *Ae. variabilis* and *Ae. kotschyi* (Tables 3 and 7). Therefore, it was concluded that *Ae. variabilis* (and *Ae. kotschyi*) originated from a cross between *Ae. bicornis* ♀ and *Ae. umbellulata* ♂.

The results from experiments conducted to substitute *T. durum* or *T. aestivum* genomes into the cytoplasms of *Ae. variabilis, Ae. umbellulata,* and *Ae. bicornis* to study cytoplasmic relationships among these *Aegilops* species are given as following (Table 5):

Ae. variabilis cytoplasm

The F_1 hybrids from reciprocal crosses between *Ae. variabilis* and *T. aestivum* 'Chris' had complete male sterility. The metaphase-1 chromosome pairing in PMCs ranged from 1 to 4 open bivalents and 27 to 33 univalents. The F_1 hybrids were backcrossed with pollen from *T. aestivum,* and F_1 plants with *Ae. variabilis* cytoplasm set seven seeds (on five crossed heads), and F_1 plants from the reciprocal cross set four seeds (on three crossed heads), indicating a high degree of female sterility. Five BC_1 plants were obtained from *Ae. variabilis* ♀/2**T. aestivum* ♂. The BC_2 to BC_4 progenies had 24 fertile or partially fertile plants and one was completely male sterile. Several of the BC_4 plants had 21 normal chromosome pairs. These BC_4 and earlier generation plants were grown in the greenhouse. However, BC_5 plants were grown in the field where reduction in plant vigor became apparent for the first time, and subsequent data on BC_6 to BC_{12} plants grown under different environmental conditions indicated that plant vigor of alloplasmic wheat with *Ae. variabilis* cytoplasm ranged from about 50 to 60% of the normal in the field, 70 to 80% in the fall greenhouse, and from about 90% to near-normal in the spring greenhouse. These observations indicated that *T. aestivum* with *Ae. variabilis* cytoplasm was relatively more sensitive to the environmental conditions than normal wheat (Table 5). Appar-

* Complete chromosomal complement of the genome donor species has not been accomplished, due to insufficient backcrossing, preferential transmission of female gametes with critical chromosome from the cytoplasm donor species, or (zygotic sterility) elimination of homozygotes of the recurrent male genotype. Several plants in the backcross series involving Ae. triuncialis and T. aestivum as the recurrent parent had apparently normal anther extrusion and abundant functional pollen and set only a few seeds on the crossed or selfed heads. Similar results were obtained in backcross series involving Ae. longissima or Ae. sharonensis as the cytoplasm donors and T. aestivum as the genome donor.

† Superscript indicates the number of crosses with the recurrent male parent. Where only 2, 3, or 4 crosses are made, the results indicated are tentative. Additional backcrosses usually enhance the phenotypic effects of alien cytoplasms on the expression of Triticum genomes. B = bushy or stunted, F = male fertile, L = delayed maturity, N = normal plant vigor, NN = near normal plant vigor, PF = partially fertile, S = male sterile, W = weak or reduced vigor, and Z = zygote elimination or inviable seeds.

Table 4. Meiotic chromosome pairing in F_1 hybrids from crosses between 2x and 4x Aegilops species with M-C-genomes (Summary from Kihara, 1954).

Female \ Male	Ae. ovata	Ae. triaristata	Ae. biuncialis	Ae. columnaris	Ae. cylindrica (2n=28,CD)	Ae. variabilis 2n=28;C^uS^v
Ae. ovata 2n=28,C^uM^o		6-7(9) 6-9(7)	(R)		9-12(6) (R)3-8(1)	
Ae. triaristata 2n=28,C^uM^t	6-12(7)* (R)6-7(9)		(R)	11-14(5)	2-11(8)	5-9(4)
Ae. biuncialis 2n=28,C^uM^b	10-13(4)	5-10(4)		6-9(4)	(R)0-10(8)	-7(4)
Ae. columnaris 2n=28,C^uM^c		**(R)11-14(5)	7-9(4)			
Ae. caudata 2n=14,C	6-7(4) (R)7-10(3) (R)5-7(4)	3-6(9) (R)5-7(4)	4-8(5) (R)5-7(5)	6-7(4) (R)7-8(5)	(R)7(4) 7(7)	
Ae. umbellulata 2n=14,C^u	(R)7(4)				6-8(4)	(R)7-8(2)
Ae. comosa 2n=14,M	(R)6-7(5)		(R)5-7(5)	(R)3-7(5)		
Ae. uniaristata 2n=14,M^u	(R)1-7(5)	(R)2-6(5)		(R)4-6(5)	(R)6(4)	
Ae. bicornis 2n=14, S^b			(R)0-6(5)	(R)1-7(5)		

* 6 to 12 bivalents (reference to authors) as following: (1) Aase, H.C. 1930; (2) Berg, K. H. 1937; (3) Blier, H. 1928; (4) Kihara, H 1937b; (5) Kihara, H. 1949; (6) Kihara, H., and F. A. Lilienfeld, 1932; (7) Kihara, H. 1937a; (8) Lindschau, M., and E. Oehler, 1936; and Percival J. 1932.

** (R) = reciprocal cross.

Table 5. Substitution of T. durum or T. aestivum genomes into the cytoplasm of Ae. variabilis, Ae. bicornis, Ae. umbellulata, Ae. cylindrica, and Ae. squarrosa.

Pedigree	Back-cross generation	Number of seeds or plants: Grown (inviable seeds)	Fertile	Sterile or low seed set
Ae. variabilis/T. aestivum	F_1	5	0	5
Ae. variabilis/T. aestivum//T. aestivum	BC_{1-5}	25	23	2
" " "	BC_{6-10}	100 †	all	0
Ae. variabilis/5*T. aestivum//T. durum	F_1	8	8	0
" " "	BC_{1-6}	43	41	2
Ae. bicornis-T. boeoticum/T. durum	BC_{5-12}	100 †	all	0
Ae. bicornis-T. boeoticum/3*T. durum//T. aestivum	BC_{8-14}	100 †	all	0
Ae. umbellulata/T. durum	F_1	5	0	5
Ae. umbellulata/T. durum//T. aestivum	F_1	1	0	1
" " "	BC_{1-3}	12(2)	0	11
" " "	BC_{4-8}	50	0	50
Ae. umbellulata/T. durum//4*T. aestivum//T. durum	BC_{1-4}	20	0	20
Ae. cylindrica/T. aestivum	F_1	5	0	5
" "	BC_{1-5}	17	5	12
" "	BC_6	60	52	8
" "	BC_7	100 †	all	0
Ae. cylindrica/3*T. aestivum/T. durum	F_1	12	12	0
" " "	BC_2	20(8)	8 ±	4
" " "	BC_3	16(4)	1 ±	11
" " "	BC_4	16	0	16
Ae. squarrosa(4x)/T. durum//T. aestivum	BC_{5-15}	100 †	all	0
Ae. squarrosa(4x)/3*T. aestivum//T. durum	F_1	5 4 Bushy		9
" "	BC_{1-7}	59(22)	28 ±	9
" "	BC_{8-9}	64(18)	46 ±	0

† More than 100 plants were grown and data were not collected from individual plants because they were phenotypically similar.

± Complete T. durum genome was not substituted into the cytoplasm of Ae. squarrosa or Ae. cylindrica. The 29 chromosome plants with 14"+1' or 14"+ a telocentric of a D-genome chromosome produced plants with maternal chromosome number, and 28 chromosome adult plants with Ae. squarrosa or Ae. cylindrica cytoplasm were not obtained due to nonfunctional female gametes, zygote elimination, or lethal seedlings.

ently, low soil- and night-temperatures in the field, and lower light intensity and photoperiod in the fall season had adverse effect on wheat plants with *Ae. variabilis* cytoplasm.

A plant with the pedigree *Ae. variabilis*/5*T. aestivum* 'Selkirk' was crossed with *T. durum* Sel. 56-1 pollen to substitute emmer genome into *Ae. variabilis* cytoplasm. The F_1 plants (*Ae. variabilis*/5*Selkirk//*T. durum*) with 2n=14''+7' had nearly complete seed set on bagged heads. In BC_2 to BC_6 progenies 38 fertile or partially fertile and two male-sterile plants were obtained (Table 5). *T. durum* plants (2n=14'') with *Ae. variabilis* cytoplasm had reduced male fertility during fall season in the greenhouse, and were even more sensitive to the environmental conditions than *T. aestivum* plants with *Ae. variabilis* cytoplasm.

Ae. umbellulata cytoplasm

F_1 plants from *Ae. umbellulata* ♀ X *T. durum* ♂ had 2n=21 (0-2 pairs and 17-21 unpaired) chromosomes, complete male sterility and high degree of female sterility. One seed was obtained from crosses with *T. aestivum* pollen, and produced a completely male-sterile and highly female-sterile plant, and this plant set one seed from *T. aestivum* pollen. The resulting BC_2 plant set several seeds from crosses with *T. aestivum* pollen which produced one partially male-fertile and nine male-sterile BC_3 plants. The male-sterile plants had 2n=38, or 2n=39 chromosomes with 16-18 bivalents and 0-1 trivalent and 2-5 univalents. The partially male-fertile BC_3 plant had 2n=43 chromosomes with 21 bivalents + 1 univalent or 19 bivalents + 3 univalents. Subsequent backcrosses of this 43 chromosome plant resulted in BC_4, BC_5 and BC_6 plants with 2n=42 and 21 normal pairs of chromosomes (Table 5). These plants with *Ae. umbellulata* cytoplasm had reduced vigor and normal appearing anthers which were extruded at the time of anthesis but did not burst normally, and consequently resulted in a low seed set on the bagged heads (Table 7).

A partially-fertile 42 chromosome plant with the pedigree *Ae. umbellulata*/4*T. aestivum* was crossed with *T. durum* pollen to substitute emmer genome into *Ae. umbellulata* cytoplasm. The F_1 plants (2n=14''+7') had complete male sterility, and BC_2 plants with 2n=14 pairs of chromosomes were obtained and these plants also had complete male sterility. Subsequently, in BC_3 to BC_7 all *T. durum* plants with *Ae. umbellulata* cytoplasm had reduced vigor and complete male sterility (Table 5). These data indicated that alloplasmic *T. durum* plants with *Ae. umbellulata* cytoplasm had complete male sterility and reduced plant vigor, and *T. aestivum* plants with *Ae. umbellulata* cytoplasm had reduced fertility and plant vigor. Alloplasmic *T. aestivum* with *Ae. caudata* cytoplasm had complete male sterility (Kihara, 1951; 1959) and near-normal plant vigor. Therefore, differential phenotypic effects on the expression of *T. aestivum* genome indicate *Ae. caudata* and *Ae. umbellulata* have different cytoplasms.

Ae. bicornis cytoplasm

Maan and Lucken (1971a) reported that *T. durum* and *T. aestivum* with *Ae. bicornis* cytoplasm had reduced male fertility and plant vigor. Alloplasmic *T. durum* and *T. aestivum* plants with *Ae. bicornis* cytoplasm were grown for several years for observation and to make additional backcrosses (Table 5). These *T. durum* and *T. aestivum* plants with *Ae. bicornis* cytoplasm were similar to the alloplasmic *T. durum* and *T. aestivum* plants with *Ae. variabilis* cytoplasm regarding the reduction of plant vigor under the different greenhouse and field conditions. Apparently, *Ae. bicornis* and *Ae. variabilis* cytoplasms have similar effects on the manifestation of *T. durum* and *T. aestivum* genomes. By contrast, the other two *Aegilops* species of the *Sitopsis* group had different cytoplasms: *T. durum* and *T. aestivum* plants with *Ae. speltoides* cytoplasm had complete male sterility (Maan and Lucken, 1971a), *T. durum* with *Ae. sharonensis* cytoplasm had low partial fertility, and *T. aestivum* with *Ae. sharonensis* cytoplasm had complete sterility (Maan, 1974a). These data indicated that *Ae. bicornis* was the

most likely cytoplasm and S-genome donor to *Ae. variabilis*.

CYTOPLASMS OF *AE. CYLINDRICA* AND ITS PROGENITORS

Chromosome pairing in F_1 hybrids from crosses between *Ae. caudata* and *Ae. cylindrica* indicated that *Ae. caudata* contributed C-genome to *Ae. cylindrica* (Kihara and Mutsumara, 1941). However, crosses between *Ae. squarrosa* and *Ae. cylindrica* did not succeed in either direction. The morphology of F_1 hybrid from a cross between *Ae. caudata* X *Ae. squarrosa* (Kihara, 1944) and chromosome pairing in F_1 hybrids from a cross between a synthetic amphidiploid (*caudata-squarrosa*) and *Ae. cylindrica* proved that *Ae. squarrosa* contributed D-genome to *Ae. cylindrica* (McFadden and Sears, 1946). Electrophoretic analyses of the seed protein of several accessions of *Ae. caudata, Ae. squarrosa* and *Ae. cylindrica* further confirmed the allopolyploid origin of *Ae. cylindrica* (Johnson, 1967a).

Alloplasmic *T. aestivum* with *Ae. squarrosa* or *Ae. cylindrica* cytoplasms had normal fertility and plant vigor (Maan, 1973a). But *T. durum* genome was not compatible with the cytoplasm of *Ae. squarrosa* or *Ae. cylindrica* (Maan, 1973a). Addition of one D-genome chromosome to the emmer genome improved compatibility between *T. durum* genome and *Ae. squarrosa* or *Ae. cylindrica* cytoplasms (Table 5). However, *T. timopheevi* was compatible with *Ae. squarrosa* cytoplasm (Maan and Lucken, 1972). These data indicated that the AG-genome had homoeoalleles of the critical gene(s) on the additional D-genome chromosome, and these gene(s) were not present in the AB-genome of *T. durum*.

The results from experiments involving the substitution of *T. durum*, and *T. aestivum* genomes into the cytoplasms of *Ae. cylindrica*, and *Ae. squarrosa* are given as following (Table 5):

Ae. cylindrica cytoplasm

Emasculated spikes of *Ae. cylindrica* (P. I. 172358) were pollinated with *T. aesticum* cv. Chinese Spring pollen. The F_1 plants had 2n=35, and average meiotic chromosome pairing in PMC's was 5.1 (4-7) closed bivalents + 1.9 (1-4) open bivalents + 0.4 (0-1) trivalent + 0.1 (0-1) quadrivalent, + 21 (17-25) univalents. The F_1 plants had complete male sterility and set two seeds on 40 spikes crossed with *T. aestivum* pollen; one of these germinated and produced a completely male sterile BC_1 plant with 2n=48 (16''+16', 14''+20', etc.). This BC_1 plant set two seeds and produced two completely male-sterile BC_2 plants and one of them again set two seeds and produced two male-sterile BC_3 plants. These two BC_3 plants produced four partially-fertile and eight completely male-sterile BC_4 plants. In subsequent backcross generations (BC_5 and BC_6) 51 fertile or partially fertile, and eight male-sterile plants were obtained (Table 5). Most of the fertile plants had 2n=42 and 21 normal pairs of chromosomes in the PMC's at metaphase I of meiosis. The male-sterile plants had 2n=42 +1 or 2 chromosomes and incomplete chromosome pairing. These data indicated that *T. aestivum* plants with *Ae. cylindrica* cytoplasm had normal fertility and plant vigor.

A plant (2n=21'') with the pedigree *Ae. cylindrica*/5*T. aestivum* was crossed with *T. durum* to substitute AB genome into *Ae. cylindrica* cytoplasm. The *Ae. cylindrica*/5*T. aestivum//T. durum* plants had 2n=35 (14''+7') chromosomes. In subsequent backcross generations with *T. durum* pollen, a significant proportion of seeds were shrivelled or inviable and partially fertile plants with 2n=14''+1' or 2n=14''+2' were obtained (Table 5). These plants had relatively less vegetative growth and vigor than the normal *T. durum* plants.

Seedlings from selfed or backcrossed viable seeds on the 2n=29 (14''+1') and 2n=30 (14''+2') chromosome plants were examined for chromosome number and pairing in the PMC's. Large majority of the plants had 29 or 30 chromosomes and a few 28 chromosome plants were

obtained. These 28 chromosome plants had 13 pairs and 2 unpaired chromosomes at metaphase 1 of meiosis in PMC's, indicating that an addition or substitution of one D-genome chromosome to the *T. durum* genome in *Ae. cylindrica* cytoplasm largely restored nucleo-cytoplasmic balance.

Ae. squarrosa cytoplasm

Maan and Lucken (1971) reported that alloplasmic *T. aestivum* with *Ae. squarrosa* cytoplasm had normal fertility and plant vigor. A fertile plant with pedigree *Ae. squarrosa* (4x)/*T. durum*//*3*T. aestivum* was crossed with *T. durum* to substitute AB genome into *Ae. squarrosa* cytoplasm. In the third backcross progeny partially fertile plants with 2n=29 (14" +1') chromosomes were obtained. In subsequent backcross progenies plants with 2n=28 and 14 normal pairs of chromosomes were not obtained (Maan, 1973c). The BC_4 to BC_9 plants with 2n=29 chromosomes crossed with *T. durum* pollen produced a small proportion of plump and viable seeds and a larger proportion of relatively shrivelled non-viable seeds. The plump viable seeds produced 29 chromosome plants, indicating that 15-chromosome female gametes resulted in viable zygotes and shrivelled non-viable seeds had 28 chromosome zygotes (Table 5).

These data indicated that the addition of one D-genome chromosome to the AB genome was necessary to have alloplasmic *T. durum* plants with *Ae. squarrosa* or *Ae. cylindrica* cytoplasm(s). The zygotes with 28 AB genome chromosomes were eliminated as shrivelled inviable seeds or semi-lethal seedling of highly reduced vigor. Apparently, *Ae. squarrosa* and *Ae. cylindrica* are cytoplasmically similar, indicating that *Ae. squarrosa* contributed cytoplasm and D-genome to *Ae. cylindrica.*

CYTOPLASMS OF *AE. TRIARISTATA, AE. OVATA, AE. BIUNCIALIS,* AND THEIR DIPLOID PROGENITORS

A review of literature indicates that precise diploid M-genome donors to tetraploid *Ae. triaristata* (2n=28;$C^uC^uM^tM^t$), *Ae. ovata* (2n=28;$C^uC^uM^oM^o$), *Ae. biuncialis* (2n=28,C^uC^u M^bM^b), and *Ae. columnaris* (2n=28,$C^uC^uM^cM^c$) were not identified due to crossability barriers between the critical 2x and 4x species and different amounts of homologous and homoeologous chromosome pairing in F_1 hybrids from successful crosses (Table 4). For example, *Ae. triaristata* did not hybridize with its diploid putative progenitors, *Ae. umbellulata* (2n=14,C^uC^u) or *Ae. comosa* (2n=14,MM). However, a synthetic amphidiploid *Ae. uniaristata-Ae. umbellulata* (2n=28;$M^uM^uC^uC^u$) had a general morphological resemblance to *Ae. triaristata, Ae. ovata, Ae. columnaris,* and *Ae. biuncialis* (Kihara and Yamashita, 1956). Also, hybrids between *Ae. ovata* and *Ae. mutica; Ae. biuncialis* and *Ae. umbellulata, Ae. uniaristata* or *Ae. mutica;* and *Ae. columnaris* and *Ae. umbellulata* or *Ae. mutica* have not been reported (Kihara, 1954a). Therefore, Kihara's (1954b) designation of genome symbols to these *Aegilops* species and their putative diploid progenitors were based on indirect cytogenetical and morphological evidence and on available information on geographical distribution of these *Aegilops* species. These genome designations indicated general phylogenetic relationships among 2x and polyploid species and precise M-genome donors to the four tetraploids were not identified because of the crossability barriers or modification of the M-genome subsequent to incorporation in the 4x species.

Nucleo-cytoplasmic interactions between *Aegilops* cytoplasms and *Triticum* genomes were used to identify diploid progenitors of the polyploid *Aegilops* species. Experimental results from investigations of cytoplasmic relationships among these *Aegilops* species are discussed as following (Table 6):

Table 6. Substitution of Triticum genomes into the cytoplasm of Aegilops triaristata, Ae. Heldreichii, Ae. mutica, Ae. biuncialis, or Ae. uniaristata.

Pedigree	Back-cross generation	Total plants grown	Fertile or partially fertile plants	Sterile plants
Ae. triaristata/T. timopheevi	F_1	2	0	2
Ae. triaristata/T. timopheevi//T. aestivum	BC_1F_1	2	0	2
" " "	BC_2F_1	1	0	1
" " "	BC_3F_1	4	0	4
" " "	BC_4F_1	12	0	12
" " "	BC_5F_1	65	0	65
" " "	BC_6F_1	42	0	42
" " "	BC_7F_1	6	0	6
Ae. triaristata/T. durum//2*T. aestivum//T. durum	F_1	8	0	8
" " " "	BC_1F_1	40	0	40
" " " "	BC_2F_1	54	0	54
Ae. Heldreichii/T. durum	F_1	10	10	0
" " //T. aestivum	F_2	18	18	0
" " "	BC_1F_1	10	0	10
" " "	BC_2F_1	4	0	4
" " "	BC_3F_1	6	0	6
" " "	BC_4F_1	36	0	36
" " "	BC_5F_1	36	0	36
" " "	BC_6F_1	30	0	30
Ae. Heldreichii/T. durum	F_1	10	10	0
" " //T. durum	BC_1F_1	4	4	0
" " "	BC_2F_1	3	0	3
" " "	BC_3F_1	4	0	4
" " "	BC_4F_1	20	0	20
" " "	BC_5F_1	4	0	4

Table 6. (Continued)

Ae. mutica/T. durum	F_1		
" " //T. aestivum	BC_1F_1	29(13)*	6	13
" " "	BC_2F_1	12(1)	8	3
" " "	BC_3F_1	36(4)	28	4
" " "	BC_4F_1	58	58	0
" " "	BC_5F_1	18	18	5
Ae. biuncialis/T. durum	F_1	4	0	4
" " //T. durum	BC_1F_1	2	0	2
" " "	BC_2F_1	6(4)	0	2
" " "	BC_3F_1	22	0	22
" " "	BC_4F_1	34	2	32†
Ae. uniaristata/T. durum	F_1	2	0	2
" " //T. durum	BC_1F_1	6	0	6
" " "	BC_2F_1	20	0	2
" " "	BC_3F_1	54(21)	0	33+
" " "	BC_4F_1	25	0	25

* 29 seeds planted and 13 did not grow. Numbers in parentheses indicate inviable seeds.

† All plants had 14"+1' or more univalents. Three plants with 14"+3' or 4' univalents had good anther extrusion and a few seeds on the bagged heads. Plants with 14"+1' when pollinated with T. durum pollen had complete seed set but only a few viable plump seeds were produced which again resulted in 14"+1' progeny. T. durum plants with 14" and Ae. uniaristata cytoplasm were not obtained. Most plants with Ae. biuncialis cytoplasm and T. durum chromosomal complement had 14"+1' or more univalents. A few 2n=14"-chromosome male-sterile plants having Ae. biuncialis cytoplasm had highly reduced vigor.

Table 7. Cytoplasmic relationships among Aegilops species based on phenotype of alloplasmic T. aestivum and T. durum.

Phenotypic characteristics	Genome donor (and genome substituted)	Cytoplasm donor
1. Full fertility, normal plant vigor	T. aestivum (2n=42;21")	Ae. juvenalis*
"	"	Ae. crassa*
partial fertility, reduced vigor	T. durum (29-chromosome plants	
28-chromosome zygotes inviable	"	Ae. squarrosa
28-chromosome seedlings semi-lethal	"	Ae. cylindrica
2. Partial fertility, reduced plant vigor	T. aestivum (2n=42;21")	Ae. ventricosa*
reduced fertility, reduced vigor	T. durum (2n=28;14")	Ae. variabilis
"	"	Ae. bicornis
complete sterility, reduced vigor	T. durum (29-chromosome plants	
28-chromosome zygotes inviable	"	Ae. uniaristata
28-chromosome seedlings weak	"	Ae. biuncialis
3. Good anther development and extrusion, indehiscent anthers, occasional seed set	T. aestivum (2n=42;21")	Ae. triuncialis*
complete male sterility, weak plants	T. durum (2n=28;14")	Ae. triaristata
"	"	Ae. umbellulata
4. Complete male sterility, normal plants	T. aestivum (2n=42;21")	
male sterility, reduced vigor	T. durum (2n=28;14")	Ae. speltoides
male sterility, or inviable seeds	"	Ae. caudata
partial male fertility	"	Ae. sharonensis
5. Very late plants male sterility, tall plant growth	T. aestivum " (2n=42;21")	Ae. ovata
partial fertility, tall plant growth	" "	Ae. mutica*
complete male sterility, plant height reduced	" (2n=42;21")	Ae. Heldreichii

* Additional data from T. durum crosses may indicate a precise cytoplasmic relationship between a polyploid and diploid species.

Ae. triaristata cytoplasm

Emasculated florets of *Ae. triaristata* plants were crossed with *T. timopheevi, T. durum,* and *T. aestivum,* and all F_1 hybrids were backcrossed with pollen from each of the three *Triticum* species. The F_1 hybrids had complete male and female sterility, except that *Ae. triaristata/T. timopheevi//T. aestivum* set two seeds, and these produced two plants. One of these two backcross F_1 plants set one seed with *T. aestivum* pollen, indicating a high degree of female sterility. In subsequent backcross generations all plants had complete male sterility, but improved female fertility (Table 6). In the fifth backcross generation male-sterile plants with 21 pairs of *T. aestivum* chromosomes were obtained.

The alloplasmic *T. aestivum* plants with *Ae. triaristata* cytoplasm resembled those with *Ae. umbellulata* cytoplasm in having reduced plant vigor, partial anther extrusion, a small amount of stainable pollen grains, and an occasional seed or two in the bagged heads.

Ae. Heldreichii cytoplasm

Emasculated florets of *Ae. Heldreichii* were crossed with *T. durum* pollen. The F_1 plants were partially male and female fertile, and set seeds on the bagged heads. Cytological examination of chromosome behavior during meiosis indicated that a majority of the pollen mother cells matured to functional pollen with unreduced chromosome number (Maan and Whited, 1973). Apparently, similar meiotic events in megaspore mother cells produced functional female gametes with an unreduced chromosome number. The resulting fertile F_2 hybrids had the doubled chromosome number of 2n=42. Tanaka (1959) also reported similar male and female fertility of F_1 hybrids of *T. durum* X *Ae. squarrosa*, resulting in amphidiploid F_2 progeny.

Substitution of *T. durum* genome into the *Ae. Heldreichii* cytoplasm produced completely male-sterile plants of reduced vigor (Table 6). Similarly, alloplasmic *T. aestivum* with *Ae. Heldreichii* cytoplasm had complete male sterility and reduced plant vigor (Table 6). These alloplasmic *T. durum* or *T. aestivum* plants with *Ae. Heldreichii* cytoplasm were morphologically similar to those having *Ae. triaristata* cytoplasm. But, *Ae. Heldreichii* cytoplasm induced complete male sterility and these plants (in contrast to those with *Ae. triaristata* cytoplasm) had no anther extrusion and no seed set on the bagged heads.

Ae. ovata cytoplasm

Alloplasmic *T. durum* and *T. aestivum* with *Ae. ovata* (2n=28;$C^UC^UM^OM^O$) cytoplasm had male sterility and delayed maturity (Fukasawa, 1953, 1959; Maan and Lucken, 1972). Alloplasmic *T. aestivum* with *Ae. caudata* (Kihara, 1951) or *Ae. umbellulata* (Maan, 1972) cytoplasms had male sterility and reduced plant vigor. These cytoplasmic relationships indicated that *Ae. ovata* must have received its cytoplasm from a diploid *Aegilops* species with M-genome. This M-genome 2x progenitor was tentatively identified as *Ae. mutica* (Table 7).

Ae. mutica cytoplasm

Substitution of *T. aestivum* genome into *Ae. mutica* cytoplasm resulted in partially fertile plants with highly delayed maturity and robust growth like those with *Ae. ovata* cytoplasm (Table 6). These plants had one or more *Ae. mutica* chromosomes indicating incomplete substitution of *T. aestivum* genome. However, delayed maturity effect of *Ae. mutica* cytoplasm on the *T. aestivum* genome indicated that *Ae. ovata* received its cytoplasm and M-genome from *Ae. mutica*. Alloplasmic *T. aestivum* with cytoplasms of other M-genome diploid species, *Ae. comosa, Ae. Heldreichii,* or *Ae. uniaristata* did not resemble alloplasmic *T. aestivum* with *Ae. mutica* cytoplasms (Table 2).

Ae. biuncialis cytoplasm

Four F_1 plants grown from *Ae. biuncialis* ♀ X *T. durum* ♂ had complete male sterility and high degree of female sterility. Two backcross plants from pollination with *T. durum* had 2n=42 (16"+10'; 18"+6') and complete male sterility, indicating that F_1 plants produced 28 chromosome functional female gametes. From further backcrosses with *T. durum* pollen, six BC_2 and 22 BC_3 plants were grown. These BC_2 and BC_3 plants had complete male sterility and 2n=29 + one or more (14"+1' + one or more) chromosomes, indicating that 14 chromosome female gametes were not transmitted (Maan, 1974b). These 29 chromosome *T. durum* plants with *Ae. biuncialis* cytoplasm had complete male sterility, reduced plant vigor and delayed maturity, and resembled alloplasmic 29 chromosome *T. durum* plants having *Ae. uniaristata* cytoplasm (Table 6).

Ae. uniaristata cytoplasm

F_1 plants from *Ae. uniaristata* ♀ X *T. durum* ♂ had complete male sterility and an average of 0.37 (0-1) bivalents, and 20-22 (19-21) univalents at metaphase I of meiosis in pollen mother cells. The F_1 set six seeds from backcrosses with *T. durum* pollen, and six BC_1 plants obtained had 2n=35 (14"+7'), indicating F_1 plants produced 21 chromosome functional female gametes. Twenty BC_2 plants were grown and these plants had complete male sterility and 2n= 29 or more chromosomes. Fifty-four BC_3 seeds were planted and 33 mature plants were obtained. All 33 BC_3 plants had complete male sterility (Table 6) and 2n=14"+1' or more unpaired chromosomes, indicating that 14 chromosome female gametes were not transmitted (Maan, 1974b). These data indicated that *Ae. uniaristata* and *Ae. biuncialis* are cytoplasmically similar and the latter tetraploid species received cytoplasm and M-genome from *Ae. uniaristata*.

Cytoplasmic relationships among *Aegilops* species based on the phenotype of alloplasmic *T. aestivum* or *T. durum* are summarized in Table 7.

GENERAL DISCUSSION AND CONCLUSIONS

Prevalence of cytoplasmic variability in *Triticinae* indicates that cytoplasmic similarities and differences between certain allopolyploids and their putative diploids may provide phylogenetic information that cytogenetic data alone do not provide (Maan, 1973a; Maan and Lucken, 1971a, 1972). For example, cytogenetic and crossability relationships among *Triticum* and *Aegilops* species indicate that certain natural or synthetic allopolyploids do not produce viable seeds from crosses with their diploid progenitors. Kihara (1966) assumed that *Ae. cylindrica* (2n=28;CCDD) had *Ae. caudata* (2n=14;CC) cytoplasm, because F_1 could be obtained only when *Ae. caudata* was crossed as a female parent with *Ae. squarrosa*. Also, Kihara (1966) proposed that *Ae. triuncialis* (2n=28;CCC^uC^u) had *Ae. caudata* cytoplasm because *Ae. caudata* could be crossed only as a female with *Ae. umbellulata*, and the synthetic amphidiploid *Ae. caudata-Ae. umbellulata* was "almost identical to natural *Ae. triuncialis*". However, the chromosome pairing and differential fertility of F_1 hybrids from reciprocal crosses between synthetic allotetraploid *Ae. caudata-Ae. umbellulata* (CCC^uC^u) and two subspecies of *Ae. triuncialis* (CCC^uC^u) reported by Kihara and Kondo (1943), indicates that *Ae. caudata* and *Ae. triuncialis* differ cytoplasmically, and *Ae. umbellulata* may be the cytoplasm and C^u-genome donor to *Ae. triuncialis*. *Ae. caudata* (Kihara, 1951) and *Ae. umbellulata* (Muramatsu, 1965; Maan, 1972) are known to differ cytoplasmically (Table 2) and preliminary data indicates that *T. durum* and *T. aestivum* plants with *Ae. triuncialis* cytoplasm have reduction in vigor comparable to those with *Ae. umbellulata* cytoplasm (Tables 3, 7). Also, cytoplasmic relationships indicated that *Ae. squarrosa* contributed the cytoplasm and D-genome to *Ae. cylindrica* (Maan, 1973c). Similarly, hybrids were obtained from *Ae. speltoides* ♀ X *T. boeoticum* ♂, and recip-

rocal crosses did not succeed. Kihara (1966) suggested that *Ae. speltoides* may have contributed the cytoplasm and B-genome to 4x emmer and 6x common wheats. However, nucleocytoplasmic interactions between *Triticum* genomes and *Aegilops* cytoplasm indicate that *Ae. squarrosa, Ae. cylindrica, T. durum* and *T. aestivum* apparently have a closer cytoplasmic similarity, but the likely diploid cytoplasm donor *Ae. squarrosa* does not produce viable seeds when crossed as a female with any one of these three allopolyploids. All of the other twenty or more *Aegilops* species, except *Ae. squarrosa,* cross readily as females with one or more of the *Triticum* species. Similarly, other examples of immediate crossability barriers between the diploid cytoplasm donors and their incipient synthetic amphidiploids show that a failure to obtain hybrids between certain diploids and their polyploid descendants may indicate that such crosses did indeed result in the origin of those polyploids. Therefore, cytoplasmic relationships may identify precise diploid progenitors of the polyploid species for which cytogenetic data are inconclusive or unavailable because F_1 hybrids were not obtained due to crossability barriers.

Interspecific and intergeneric F_1 hybrids from reciprocal crosses involving *Triticum* species do not differ morphologically, even though parental species may have cytoplasmic differences. Usually, the F_1 hybrids have complete male sterility. Unreduced functional female gametes result from the restitution nuclei formed during megasporogenesis and produce backcross plants from outcrosses with pollen from parental or other related species. The frequency of functional unreduced gametes differs widely in different hybrid combinations and can often be estimated from meiotic chromosome behavior in the F_1 (Aase, 1930; Maan and Whited, 1973) or the chromosome number and pairing in the backcross plants.

The unreduced functional female gametes may not always have a complete chromosonal complement of an F_1 hybrid, because one or more chromosomes may be excluded from certain restitution nuclei. Possibly, preferential transmission or exclusion of unreduced gametes with certain critical chromosome(s) may determine the relative ease or difficulty of getting backcross plants, because female gametes without a critical chromosome may not function (Maan, 1974a, b). Also, if parental species differ cytoplasmically and a critical maternal chromosome with genes controlling cytoplasmic effects is excluded from the unreduced functional female gametes, the resulting backcross plants may have male sterility, reduced plant vigor, delayed maturity and other phenotypic and physiological alterations. These male-sterile plants will produce seed (and the line may be perpetuated) only if they are outcrossed to male fertile sister plants or parental species. Even when the critical maternal chromosome is transmitted through the female gamete, most of the backcross plants may still have partial or complete sterility because the critical unpaired chromosome is excluded from the majority of functional male and female gametes during meiosis. The sterility of early generation backcross plants can result also from structural heterozygosity, homoeologous chromosome pairing, aneuploidy and associated meiotic irregularities. However, plants with improved fertility and normal phenotype can be selected and maintained by alternate selfing and backcrossing of partially fertile plants, if large populations are grown after each substitution backcross and relatively fertile plants are selected for additional backcrosses.

If chromosomes of the parental species do not pair, and critical genes controlling cytoplasmic effects are not transferred to the chromosomes of the recurrent male parent, then resulting fertile plants with alien cytoplasm will have an alien chromosome added to the chromosomal complement of the recurrent male parent. Therefore, cytoplasmic characteristics of the female parent can determine the unilateral introgression of certain critical nuclear genes or chromosome segments into the genome of the recurrent male parent.

The choice of a suitable genome donor is an important consideration for a successful study of cytoplasmic relationships among related species, because cytoplasmic differences can be inferred only from their interactions with certain critical nuclear genes or genotypes. The successful substitution of the nucleus of one species into the cytoplasm of a series of related species depends on several factors, including the ease of hybridization as a male, female fertility

of the F_1 hybrids, and viability and vigor of plants in early backcross generations, until the chromosomal complement of the recurrent male parent is established within the alien cytoplasm. The genome donor species should be phylogenetically close enough to cross with other related species, but distinct enough to provide a spectrum of nucleo-cytoplasmic interactions which indicate cytoplasmic similarities and differences. Both for biological and economic considerations the fortuitous selection of cultivated allopolyploids, *T. aestivum* and *T. durum*, meets most of these requirements for study of cytoplasmic relationships among species of *Triticum, Aegilops, Secale,* and *Haynaldia*. During substitution backcrosses, a combination of allopolyploidy and cytoplasmic variability favors a unilateral introgression of chromosome(s), chromosome segment(s), or gene(s) controlling cytoplasmic effects from the genome of cytoplasm donor into the substituted *T. aestivum* genome (Maan and Lucken, 1971b). These alloplasmic alien chromosome addition or substitution lines have normal fertility and plant vigor and can be crossed with a series of other alloplasmic lines with cytoplasms from other related species to study nucleocytoplasmic interactions which indicate cytoplasmic similarities or differences among the cytoplasm donor species (Maan and Lucken, 1972).

Alloplasmic *T. durum* and *T. aestivum* wheats (wheats having alien cytoplasms) with or without the cytoplasm differentiating nuclear genes from the cytoplasm donor species allow freedom from the effects of aneuploidy and hybrid sterility in the study of interspecific and intergeneric cytoplasmic differences in *Triticinae*. Since all 12 diploid species examined (9 *Aegilops*, 1 each of *Triticum, Secale,* and *Haynaldia*) differ cytoplasmically (Tables 1, 2, 3), and cytoplasmic similarities have been demonstrated between certain allopolyploids and their putative diploid cytoplasm donors (Table 7), we may conclude that cytoplasmic variability among diploids antedated allopolyploidy, and cytoplasmic and nuclear hereditary systems are relatively stable over a long period of time. Possibly, cytoplasmic variability at the diploid level appear to be a genetic prerequisite for the evolutionary processes leading to allopoloyploidy in *Triticinae*, and for a stepwise increase (or decrease) of chromosome numbers in certain other plant groups. If so, both the cytoplasmic and nuclear gene mutations can play an important role in the evolutionary processes in plant species groups.

Allopolyploidy

Allopolyploidy provides a 'bridge' or a 'by-pass' to the cytoplasmic and nuclear sterility isolating mechanisms because critical homozygous nuclear genes controlling cytoplasmic effects can be incorporated into the allopolyploid from the diploid cytoplasm donor progenitor. Since allopolyploids from reciprocal crosses between species with cytoplasmic differences may differ in fertility and other plant and grain characteristics, the magnitude of cytoplasmic differences between diploid progenitors may determine the (evolutionary) success of the natural and synthetic allopolyploids. Triticales from reciprocal crosses between *Triticum* and *Secale* differ morphologically and in the amount of seed fertility; those with rye cytoplasm are less fertile and set fewer seeds per head than those with wheat cytoplasm (Röbbelen and Smutkupt, 1968). Also, triticales with *T. aestivum* cytoplasm have higher fertility and better grain characteristics than those with *T. durum* cytoplasm (Larter and Hsam, 1973).

Possibly, crossability barriers between the cytoplasm donor progenitor and its allopolyploid provide a genetic isolating mechanism allowing stability of the host genome and the evolution of a compatable 4x-nucleocytoplasmic combination involving major adaptive changes in the foreign genome only. Relative stability and strong pairing affinity between the D-genomes of *Ae. squarrosa* and the allopolyploids *T. aestivum* and *Ae. cylindrica* parallels cytoplasmic similarity of these 2x, 4x and 6x species. Relatively significant differences between the A-genomes of *T. boeoticum* and 4x or 6x *Triticum* species may correspond to parallel cytoplasmic differences between these 2x and polyploids. Evolutionally, numerical changes involving the genomes of diploid progenitors and segmental allopolyploidy may be the necessary steps

resulting in a compatable nucleo-cytoplasmic system at the 4x or higher ploidy levels. For example, selection for higher seed fertility and agronomic improvement in hexaploid triticale resulted in the substitution of certain rye chromosomes with D-genome chromosomes of *T. aestivum*. These hexaploid triticales have 14 chromosomes of *T. durum* and seven D- and R-genome chromosomes (Gustafson and Qualset, 1974).

Aneuploidy and Introgression

The changes involving an increase or decrease of one chromosome at a time may produce species with different haploid numbers. Darlington (1937) described mechanisms involving unequal translocations between nonhomologous chromosomes which could result in a stepwise increase or decrease of one chromosome at a time. The unequal translocations could result in an increase or decrease of chromosome numbers only if regions close to the centromere were genetically inactive (heterochromatic). However, an increase or decrease of chromosome numbers among cytoplasmically different (related) species may result from an obligate unilateral introgression (addition or substitution) of a critical nonhomologous chromosome from the genome of a cytoplasm donor species following interspecific hybridization and backcrossing. Since F_1, F_2, or backcross progenies from reciprocal crosses between cytoplasmically different species may have differential fertility and plant vigor, the segregates with relatively improved fertility and plant vigor may carry critical chromosomes with nuclear genes controlling cytoplasmic effects from the cytoplasm donor species. This kind of addition or substitution of alien nonhomologous chromosomes into the genomes of the *Triticum* species with alien cytoplasms occur frequently under experimental conditions. In addition to the genes controlling cytoplasmic effects, these critical chromosomes carry genes for delayed or early maturity and for other phenotypic alterations which may result in genetic isolation of alloplasmic plants in hybrid populations under natural conditions.

This kind of unilateral introgression of a critical chromosome or a critical chromosome segment from the cytoplasm donor species was essential for the development and maintenance of certain alloplasmic lines of *T. durum* or *T. aestivum* with cytoplasm from *Ae. squarrosa* (Table 5), *Secale cereale* (Maan and Lucken, 1971b), *Ae. longissima*, or *Ae. sharonensis* (Maan, 1974b). Similar introgression of nonhomologous chromosomes may result in further cytoplasmic differentiation, and subsequent cycles of interspecific hybridization and chromosomal introgression may produce species with a series of haploid chromosome numbers. Experimental proof of such an evolutionary process may become available if cytoplasmic differences can be demonstrated among related plant species groups having a series of haploid chromosome numbers and allopolyploids from these progenitors differing in their basic chromosome numbers by one as in *Brassica*. In backcross progenies of *Raphanus sativum* ♀ X *Brassica oleracea* ♂ hybrids with latter species as the recurrent male parent, raddish chromosome(s) carrying genes for white flower color are preferentially transmitted from the female parent, indicating unilateral introgression of raddish chromosome(s) into the cabbage genome in the raddish cytoplasmic background (Bannerot, personal communication). Apparently, female gametes or zygotes without the critical raddish chromosomes were eliminated due to nucleo-cytoplasmic incompatibility. Similar gametic or zygotic elimination due to nucleo-cytoplasmic interactions occurs frequently in interspecific and intergeneric hybrids (Kihara and Yamada, 1948).

Since cytoplasmic variability is a general occurrence among certain groups of related species, the nucleo-cytoplasmic interactions at the genic, chromosomal, and genome levels may involve parallel changes in the nuclear and cytoplasmic hereditary constituents. If so, both the cytoplasmic and nuclear gene mutations and not the nuclear genes alone may determine genetic variability and speciation in related plant groups.

ABSTRACT

Prevalence of cytoplasmic variability among diploid species, and cytoplasmic homologies between certain allopolyploids and their putative diploid progenitors indicate that cytoplasmic differences at the diploid level antedated polyploidy in Triticinae. Cytoplasmic relationships provide phylogenetic information that was not directly obtainable due to crossability barriers between certain polyploids and their putative diploid progenitors. For example, hybrids were not obtained between *Aegilops squarrosa* L. (2n=14, DD) and *Ae. cylindrica* Host. (2n=28, CCDD), *Ae. bicornis* Jaub. and Spach. (2n=14, S^bS^b) and *Ae. variabilis* Eig. (2n=28, C^uC^uSS), *Ae. mutica* Boiss. (2n=14, M^tM^t) and *Ae. ovata* L. (2n=28, $C^uC^uM^oM^o$), *Ae. umbellulata* Zhuk. (2n=14, C^uC^u) and *Ae. triaristata* Willd. (2n=28, $C^uC^uM^tM^t$), or *Ae. uniaristata* Vis. (2n=14, M^uM^u) and *Ae. biuncialis* Vis. (2n=28, $C^uC^uM^bM^b$). Cytoplasmic homologies were shown between these tetraploids and their respective diploid progenitors. Also, it is proposed that cytoplasmic differences among related species can result in unilateral hybrid introgression in derived polyploids, and cytoplasmic variability within species may contribute to the development and operation of incompatibility and sterility barriers leading to speciation.

KEY WORDS

Polyploidy, phylogenetic relationships, nucleo-cytoplasmic combinations, crossability barriers, cytoplasmic sterility, hybrid introgression, *Triticum, Aegilops.*

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A VEGETATIVE KEY TO NEBRASKA GRASSES

David M. Sutherland

INTRODUCTION

This key is intended for use locally by those who need to identify grasses which lack flowers, either because the specimens have been collected before the flowers have formed or because they have been topped by grazing or mowing. It is not intended for use with young seedlings. The key requires the use of a good microscope and a few tools, although it is designed so that the distinctions which need to be made are increasingly fine, and one can often arrive in the correct section of the correct group with the aid of only a hand lens. In this case, common sense and the included notes about distribution and habitat can often enable one to make a reasonably positive determination. The key requires fully expanded leaves, complete underground parts, and, sometimes, mature culms.

The project was suggested by Dr. C. L. Hitchcock, and the organization owes much to his key (1969) to the Pacific Northwest grasses. The characters used are basically his with the addition of a few anatomical features.

The major separations in the key are based on the following features:

The ligule

The ligule of a grass leaf is a projection which occurs at the junction of the blade and the sheath. Whether the ligule is principally a fringe of hairs or principally a membrane provides one of the best vegetative features. See Figs. 1 and 2.

Auricles

The presence of ear-like projections, auricles, at the margins of the leaf in the collar region is often a useful character, but one must check carefully on several leaves to make sure that these have not been broken off. See Fig. 3.

Sheaths

Some grasses have the sheath margins fused together, and this is a reliable feature for the recognition of some taxa. Grasses vary in the degree to which the closure occurs and in whether or not the fused margins overlap. This feature is most readily observed on fresh material. See Figs. 1 and 4.

Plants annual or perennial

Annual grasses have shallow root systems which pull up readily, and they lack the remains of previous years' culms and leaves which are usually found on perennial grasses. Annual grasses are never rhizomatous, although some species may have decumbent culms which root at the nodes. Perennial grasses may or may not be rhizomatous. It seems logical that first-year perennial plants might cause some problem in the key since they may be mistaken for annuals. In practice this problem does not often arise, probably because first-year perennials are much less common in nature than older, established plants.

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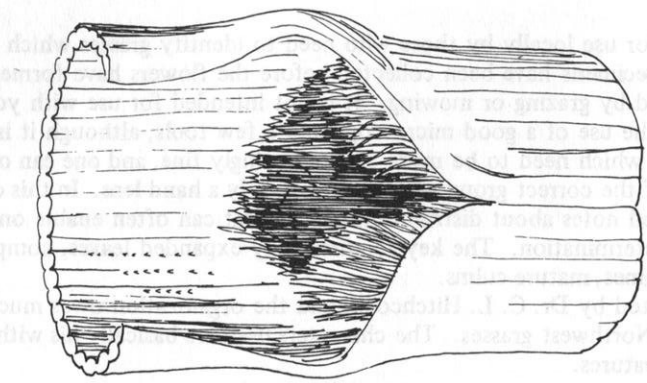

Fig. 2. Sketch of *Redfieldia flexuosa*, showing a hairy ligule

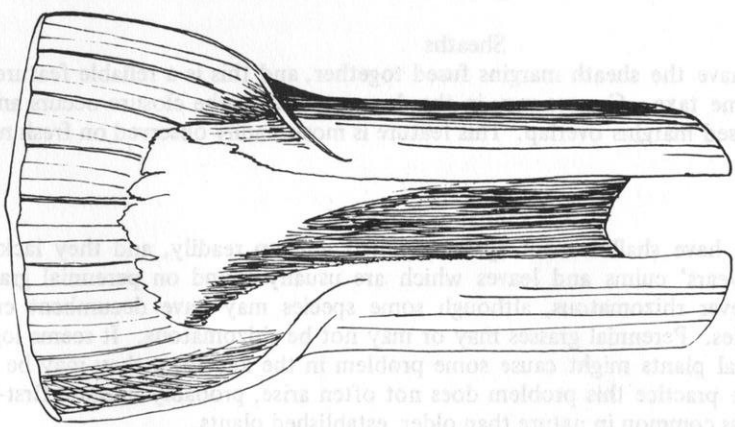

Fig. 1. Sketch of *Poa sylvestris*, showing membranous ligule and open sheath

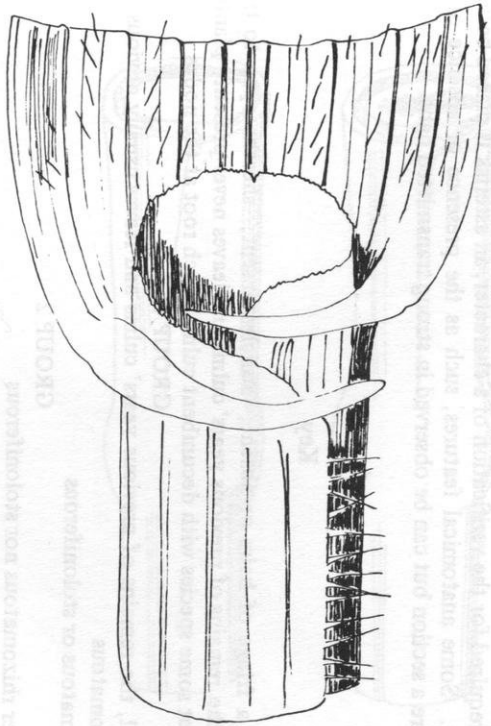

Fig. 3. Sketch of *Elymus villomus*, showing auricles

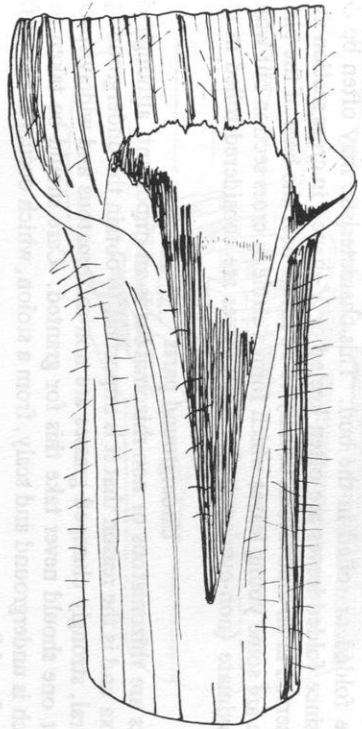

Fig. 4. Sketch of *Bromus pubescens*, showing closed sheath

Culms

Mature culms may be solid, pith-filled or hollow. See Fig. 5. This is a variable feature and has been used with caution in this key. It may be difficult to determine if culms are solid in young annual grasses, so this feature has been used sparingly in separating annual species. With perennial grasses one can examine culm bases persisting from the growth of the previous year.

Ptyxis

Leaves may be folded or rolled in the bud. This characteristic may often be deduced from a mature leaf, since folded leaves are often keeled or V-shaped in cross section at maturity, but it is best observed in an innovation, usually to be found near the base of the plant. See Figs. 6 and 7. There are some young leaves which form a circle in cross section but which have the two edges approximate (non-overlapping). Such leaves are considered rolled in this key.

Underground parts

Whether plants are rhizomatous or non-rhizomatous is an important, although variable, character in some taxa and is the reason that it is important to obtain the underground parts of a specimen. In general, strongly clumped grasses are non-rhizomatous and widely spaced ones are rhizomatous, but one should never take this for granted. Care should be taken to distinguish a rhizome, which is underground and scaly, from a stolon, which occurs at the surface and is not scaly. See Figs. 8 and 9.

Anatomical features

A number of anatomical features are used in the key, often as a last resort or for final verification of an identification. If these characters require an explanation, this appears in the key, although some users may occasionally need to refer to a good plant anatomy text (for example, Esau, 1960). Anatomical features usually require crude hand sections, which can be made most easily by using a new razor blade against a microscope slide. Dried material may be softened first in a tissue softener or the type described by Pohl (1962). I have found it most satisfactory to mount sections in Hoyer's Medium (Humason, 1972), since that medium clears the section enough for one to make out cellular details even when the section is relatively thick. If a section is required for the verification of a character, an asterisk is placed beside that character in the key. Some anatomical features, such as the presence or absence of cross-septae, may not require a section but can be observed in strong transmitted light.

Key

1. Ligule principally a fringe of hairs or absent; auricles absent; sheaths open to the base
   2. Plants annual, the remains of previous years' culms and leaves never present; plants never rhizomatous, but some species with decumbent culms which root at the nodes
      GROUP 1
2. Plants perennial, the remains of previous years' culms and leaves usually obvious; plants sometimes rhizomatous
   3. Plants rhizomatous or stoloniferous
      GROUP 2
   3. Plants neither rhizomatous nor stoloniferous
      GROUP 3

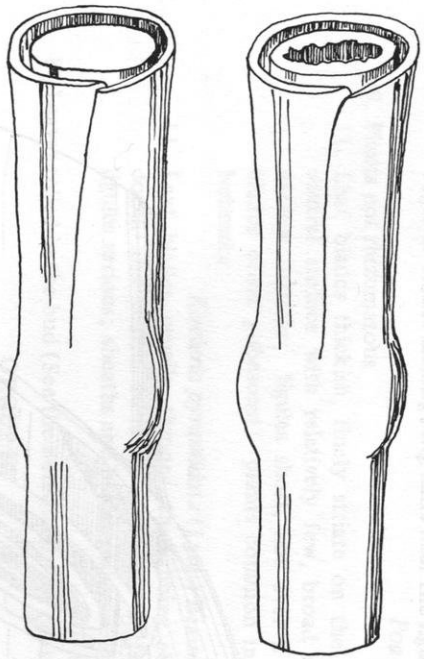

Fig. 5. Diagram showing a solid or pith-filled culm (left) and a hollow culm (right)

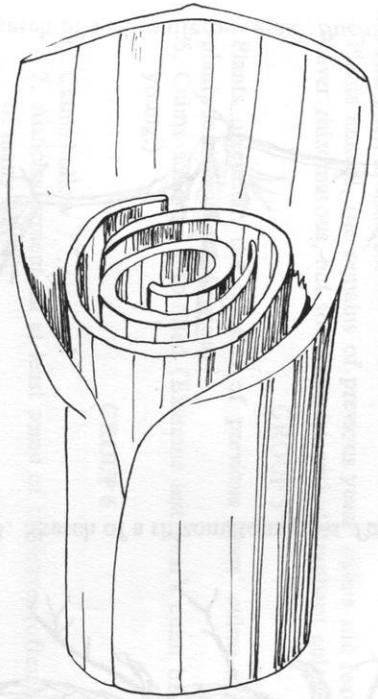

Fig. 6. Diagram showing leaves rolled in the bud

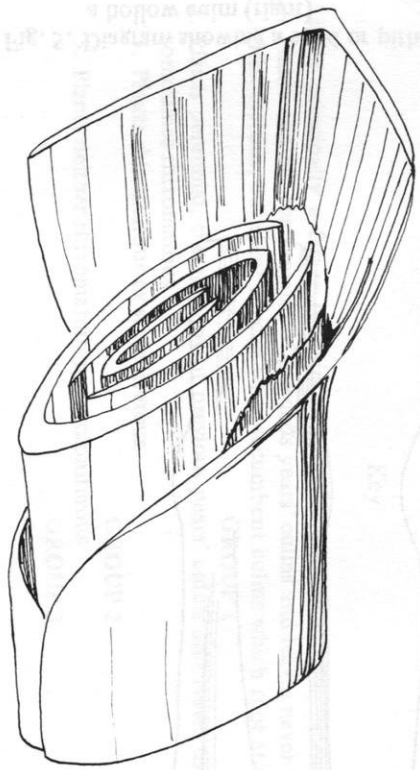

Fig. 7. Diagram showing leaves folded in the bud

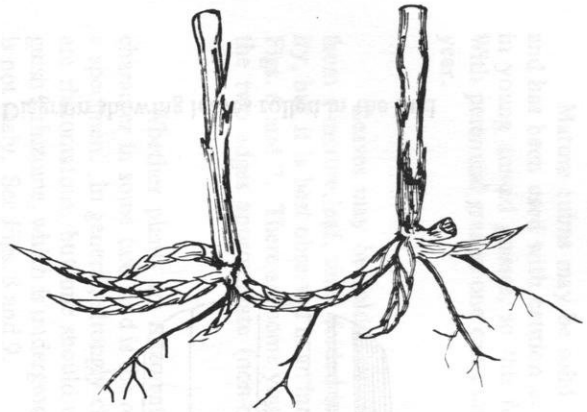

Fig. 8. Sketch of a rhizomatous grass, *Panicum virgatum*

Fig. 9. Sketch of a stoloniferous grass, *Buchloe cactyloides*

1. Ligule principally a membrane, this sometimes very short; auricles absent or present; sheaths open to the base or closed
   4. Sheaths entirely or partly closed

GROUP 4

   4. Sheaths open to the base
      5. Plants annual, the remains of previous years' culms and leaves never present; plants never rhizomatous, but some species with decumbent culms which root at the nodes

GROUP 5

      5. Plants perennial, the remains of previous years' culms and leaves usually obvious; plants sometimes rhizomatous
         6. Culms solid or pith-filled (Examine last year's culm bases if this year's are still young.)

GROUP 6

         6. Culms hollow
            7. Auricles present on at least some of the leaves (often absent from or broken off of many leaves)

GROUP 7

            7. Auricles lacking
               8. Leaves folded in the bud (In this key young leaves which form a circle in cross section, but which have the two edges approximate, are considered rolled in the bud.)
                  9. Plants strongly rhizomatous
                     10. Ligules fringed with hairs; leaf tips narrow, not prow-shaped; edges of blades pilose with long hairs near the ligule

Distichlis stricta (Torr.) Rydb.

                     10. Ligules sometimes ciliolate but not fringed; leaf tips prow-shaped; edges of blades lacking long hairs near the ligules

Poa (Go to Group 4, lead 18

                  9. Plants not rhizomatous
                     11. Leaf blades thickish, finely striate on the dorsal surface, but the ventral surface with relatively few, broad ribs separated by deep, narrow furrows; ligules short, not over 2 mm long; sheaths and blades often pubescent; plants common in dry prairie throughout Nebraska

Koeleria pyramidata (Lam.) Beauv. (*K. cristata* of authors)

                     11. Leaf blades usually thinner, the ribbing about equally spaced on dorsal and ventral surfaces or neither surface prominently ribbed; ligules various; sheaths and blades glabrous to scabrous

Poa (Go to Group 4, lead 24.

               8. Leaves rolled in the bud (See the note under the contrasting lead.)

GROUP 8

                  12. Leaves rhizomatous

GROUP 9

                  12. Plants not rhizomatous

GROUP 1

ANNUALS WITH THE LIGULES PRINCIPALLY A FRINGE OF HAIRS OR ABSENT, AURICLES ABSENT, AND SHEATHS OPEN TO THE BASE

1. Ligules absent — *Echinochloa crusgalli* (L.) Beauv. *sens. lat.*
   2. Plants not over 1 dm tall, more or less matted and spreading; leaves tufted at the nodes; many internodes bare; nodes often rooting
      3. Blades usually folded, sharp-pointed, the margins thick and whitish; plants of prairie in the western half of Nebraska — *Munroa squarrosa* (Nutt.) Torr.
      3. Blades not as above; plants of mudflats or sandflats near lakes, ponds, or streams
         4. Plants common; leaves up to 1 mm (1.5 mm) wide; decumbent culms up to about 0.5 mm thick; internodes 2-3.5 cm long — *Eragrostis hypnoides* (Lam.) B. S. P.
         4. Plants relatively rare, recorded from Lancaster, Cass, and Nemaha counties, more robust than *E. hypnoides*; leaves 1-2 mm wide; decumbent culms often 1-1.5 mm thick; internodes 2.5-6 cm long — *Eragrostis reptans* (Michx.) Nees
   2. Plants taller or not spreading or not otherwise as above
      5. Plants with disc-shaped glands on the blade margin and sheath; throat with hairs up to 2 mm long; blades flat to folded, mostly 2-7 cm long; ligules up to about 1 mm long — *Eragrostis cilianensis* (All.) Lutati
      5. Plants with blade margins and sheaths not as above
         6. Pustular-based hairs present, at least on the ventral surface of the blade near the ligule or on the leaf margin
            7. Leaves less than 2 mm wide; pustular-based hairs restricted to the margin of the blade; culms solid
               8. Ligule 0.5-0.6 mm long on most leaves; the purplish sheath generally with a whitish projection at the collar — *Triplasis purpurea* (Walt.) Chapm.
               8. Ligule shorter, usually under 0.2 mm long; sheath not as above — *Sporobolus neglectus* Nash; *Sporobolus vaginiflorus* (Torr.) Wood
               Note: These two species are not easily distinguished vegetatively, although *S. vaginiflorus* is slightly more robust than *S. neglecta*.
            7. Leaves under 2 mm wide; pustular-based hairs not restricted to the margin of the blade; culms usually hollow
               9. Sheaths glabrous; blades with the pustular-based hairs on the ventral surface near the base and 4-11 mm wide — *Setaria lutescens* (Weig.) Hubb.
               9. Sheaths pilose, often with many hairs pustular-based; pustular-based hairs not restricted to the ventral surface at the base of the blade
                  10. Plants not over 3 dm tall; hairs of the ventral surface of the blade usually restricted to the midvein and margin; culms usually not much over 2 mm in diameter, often somewhat decumbent at the base; plants very common weeds — *Panicum capillare* L.
                  10. Plants usually over 3 dm tall; hairs general on the ventral surface of the blade; culms to 7 mm in diameter, erect; plants uncommon, known only as occasional waifs from cultivated fields — *Panicum miliaceum* L.
         6. Pustular-based hairs absent
            11. Sheaths strongly keeled, 4-6 mm broad, glabrous; blades flat or folded, 2-6 mm wide; collar region constricted and usually pubescent — *Cenchrus longispinus* (Hack.) Fern.
            11. Sheaths not keeled; plants not otherwise as above
               12. Blades over 2 mm wide, with a prominent midvein for at least part of their length, usually flat

14. Leaves with a line of short hairs at the collar interrupted dorsally at the midvein

Setaria italica (L.) Beauv.

14. Leaves not as above

15. Plants generally pilose, not common

Setaria faberi Herrm.

15. Plants not pilose, very common

Setaria viridis (L.) Beauv.; *Setaria verticillata* (L.) Beauv.

13. Sheath margins not ciliate

16. Ligule up to 1.7 mm long; some culms often geniculate at the base; plants common weeds, especially in Southeast Nebraska

Panicum dichotomiflorum Michx.

16. Ligule not over 1 mm long; culms various; plants less common

17. Ligule up to about 0.7 mm; culms usually somewhat zigzagged; blades 3-4 mm wide; plants uncommon weeds, recorded from Douglas and Lancaster counties

Eriochloa contracta Hitchc.

17. Ligules shorter; culms relatively straight; blades 2-3 mm wide; plants rare weeds, recorded from Douglas and Hall counties

Eragrostis capillaris (L.) Nees

12. Blades under 2 mm wide and lacking a prominent midvein, often involute

18. Blades not bordered when viewed in strong transmitted light

19. Culms solid; blades very deeply furrowed on the ventral surface, *the furrows well over half the section in depth; plants rare, known from the vicinity of Minden

Aristida desmantha Trin. & Rupr.

19. Culms, at least in part, hollow; blades less deeply furrowed, *most furrows not over half the section in depth

Eragrostis pectinacea (Michx.) Nees; *Eragrostis pilosa* (L.) Beauv.

Note: *E. pectinacea* is very common throughout Nebraska, while *E. pilosa* is evidently rare, being known from a few scattered locations.

18. Blades with a wide, dark border when viewed in strong transmitted light

20. Thickened margins associated with one zone of fibers dorsally, this apparent in cross-section (or in surface view under good optics as a single light band near the dorsal margin)

21. The outer four veins alternatingly small and large

Aristida intermedia Scribn. & Ball

21. The outer four veins all about the same size

Aristida basiramea Engelm. ex Vasey

20. Thickened margins associated with two zones of fibers dorsally, these apparent in cross-section (or in surface view under good optics as a double light band near the dorsal margin)

22. Leaves with long hairs at the edge of the ligule; plants rare, known from an old collection at Lincoln

Aristida adscensionis L.

GROUP 2

RHIZOMATOUS OR STOLONIFEROUS PERENNIALS WITH THE LIGULE PRINCIPALLY A FRINGE OF HAIRS, AURICLES ABSENT, AND SHEATHS OPEN TO THE BASE

1. Plants robust; most blades over 5 mm broad at the base
   2. Blades with a strong, white midrib on the ventral surface, this one fifth or more of the width of the blade in the basal part; ligule about 1 mm long and with a basal membrane almost as long as the fringe portion; an introduced ornamental grass escaped from cultivation in Eastern Nebraska

      Miscanthus sacchariflorus (Maxim.) Hack.
   2. Blades with a narrower midrib or lacking a midrib; ligule not as above
      3. Culms usually solid; sheaths lacking regularly arranged air chambers between major veins at maturity
         4. Blades prominently keeled, often over 8 mm broad; rhizomes stout, short; plants rare in moist ground in Southeast Nebraska; *midrib of blade with a prominent zone of achlorophyllous parenchyma ventrally, this zone spanning more than 6 veins

            Tripsacum dactyloides L.
         4. Blades not prominently keeled, not over 8 mm broad; rhizomes long, creeping; plants common throughout the state in sandy ground; *midrib not as described above

            Calamovilfa longifolia (Hook.) Scribn.
      3. Culms often hollow; at least in the lower parts; sheaths with regularly arranged air chambers between the major veins, these often traversed by cross-septae
         5. Most ligules over 1.5 mm in length; blades well over 5 mm broad at the base; plants common in moist habitats throughout Nebraska
            6. Rhizomes stout, usually over 5 mm in diameter (including scales), often yellowish; ridges of the blade's ventral surface of various sizes, *corresponding to vascular bundles of various sizes; furrows of the blade's ventral surface up to one half of the section in depth

               Spartina pectinata Link.
            6. Rhizomes more slender, usually 5 mm or less in diameter (including scales), not yellowish; ridges of the blade's ventral surface more nearly equal (except for the midvein), *corresponding to vascular bundles which are more uniform in size; furrows of the blade's ventral surface shallow

               Panicum virgatum L.
         5. All ligules under 1.5 mm in length; blades barely 5 mm broad at base; plants restricted to the western and southern parts of the state, often on alkaline soil

            Spartina gracilis Trin.

1. Plants less robust; blades under 5 mm broad at the base
   7. Leaves without long hairs in addition to those of the ligule in the collar region (check several leaves to be sure that these have not broken off); plants of the sandhills or of moist ground in Western and Southern Nebraska
      8. Plants of moist areas and meadows, often where more or less alkaline; culms usually hollow; sheaths with air chambers between the major veins, lacking narrow furrows between the veins on the dorsal surface

         Spartina gracilis Trin.

8. Plants of sandhills, often found in blowouts; culms solid; sheaths lacking regularly spaced air chambers, with narrow furrows between the veins on the dorsal surface
   9. Blades over 10 cm in length, flexuous, folled in the bud; culms widely spaced along the rhizomes; plants not matted
      Redfieldia flexuosa (Thurb.) Vasey
   9. Blades under 10 cm in length, straight, pungent, folded in the bud; culms crowded; plants forming extensive mats
      Muhlenbergia pungens Thurb.
7. Leaves bearing few to many long hairs in addition to those of the ligule in the collar region; plants of various habitats
   10. Sheaths with regularly arranged air chambers between the major vascular bundles at maturity; culms solid; blades with the two margins touching in the bud, not really rolled; blades stiff, sharp-pointed; plants of moist, often alkaline areas
      Distichlis stricta (Torr.) Rydb.
   10. Sheaths more or less solid, lacking regularly arranged air chambers at maturity; culms solid or hollow; blades usually with the two margins overlapping in the bud, otherwise variable; plants of drier associations
      11. Ligules about 1 mm long or longer (Be sure to measure ligules and not the hairs behind them or at the margins.)
         12. Plants rhizomatous and also strongly stoloniferous; blades less than 10 cm in length and often under 3 mm wide; ligules usually 2-4 mm long; plants escaped from cultivation and doubtfully established in Nebraska
            Cynodon dactylon (L.) Pers.
         12. Plants strongly rhizomatous but not stoloniferous; blades more than 10 cm in length and often more than 3 mm in width; ligules about 1 mm long; plants native, common in sandy ground throughout the state
            Calamovilfa longifolia (Hook.) Scribn.
      11. Ligules shorter than 1 mm
         13. Blades mostly 2-4 mm wide
            14. Plants mat-forming; ligules backed by a zone of long hairs, a similar zone running around the collar dorsally; the second vascular bundle from each margin of the blade with a zone of fibers above and below it, this most easily seen in section but appearing under 50X in transmitted light as a clear band just inside the margin of the leaf; plants commonly used as a lawn grass, but seldom escaped and seldom blooming in our range
               Zoysia japonica Steud.
            14. Plants usually clumped; collar not exactly as described above; the second vein from each margin of the blade similar to the other veins; plants common throughout Nebraska in dry prairie
               Bouteloua curtipendula (Michx.) Torr.
         13. Blades 0.4-2 mm wide
            15. Blades delicate, usually under 1 mm wide and not over 3 cm long; an introduced grass cultivated to a minor extent as a lawn grass
               Cynodon transvaalensis Burrt-Davy
            15. Blades less delicate, many 1-2 mm wide and over 3 cm long; native grasses of dry prairie, but coming into increasing cultivation as lawn grasses

16. Plants extensively creeping by means of stolons, non-rhizomatous; sheaths and blades pilose

Buchloe dactyloides (Nutt.) Engelm.

16. Plants spreading by means of short rhizomes, not stoloniferous; sheaths and blades not often pilose

Bouteloua gracilis (H.B.K.) Lag. ex Steud.

GROUP 3

NON-RHIZOMATOUS, NON-STOLONIFEROUS PERENNIALS WITH THE LIGULE PRINCIPALLY A FRINGE OF HAIRS, AURICLES ABSENT, AND SHEATHS OPEN TO THE BASE

1. Leaves with a clearly marked line or zone of pubescence on the dorsal surface in the collar region; ligule short, less than 0.3 mm long in most plants
   2. Culms solid; mature sheaths with regularly arranged air chambers between the vascular bundles
      3. Blades with a prominent white margin wider than the adjacent ventral ridges, number of ridges roughly equal on the dorsal and ventral surfaces, *most vascular bundles corresponding to ventral ridges, and ventral furrows not equal to one-half the section in depth

Sporobolus cryptandrus (Torr.) Gray

      3. Blades lacking white margins, the number of ridges greater dorsally than ventrally, *vascular bundles present between and opposite the ventral ridges, ventral furrows usually over one-half the section in depth

Sporobolus airoides (Torr.) Torr.

   2. Culms generally hollow, at least below; mature sheaths lacking regularly arranged air chambers between vascular bundles
      4. Midrib prominent throughout much of the blade, appearing as a broad whitish band ventrally *because of a ventral zone of achlorophyllous parenchyma; plants common, especially on sandy soil

Eragrostis trichodes (Nutt.) Wood.

      4. Midrib absent or less prominent, not appearing as a broad whitish band ventrally, except sometimes at the base of the blade; plants scattered throughout Nebraska, often weedy
         5. Sheaths keeled; pubescence of the dorsal collar region in a triangular zone on either side, the hairs neither straight nor especially long (under 3 mm); long hairs absent on the ventral surface in the vicinity of the ligule

Tridens flavus (L.) Hitchc.

         5. Sheaths not keeled; pubescence of the dorsal collar region in a line, the hairs straight and long (many over 4 mm), similar hairs present on the ventral surface in the vicinity of the ligule

Eragrostis spectabilis (Pursh) Steud.

1. Leaves lacking a clearly marked line or zone of pubescence on the dorsal surface in the collar region, although general pubescence may be present, and the region of the ligule may have a clearly marked zone of ventral or marginal hairs; ligules short to long
   6. Ligules collar-like, short, less than 0.6 mm in length

7. Mature blades flat, broad, averaging well over 5 mm broad; some parts of blades or sheaths generally pilose with pustular-based hairs; culms hollow
   8. Ligule short, less than 0.3 mm in length; plants uncommon, in Eastern Nebraska
      Panicum leibergii (Vasey) Scribn.
   8. Ligule longer, 0.3-0.6 mm in length; plants general
      Panicum oligosanthes Schultes var. *scribnerianum* (Nash) Fern.
7. Mature blades involute to folded (flat), narrow, well under 5 mm broad except sometimes at the base; pilosity usually confined to the collar region, except in one narrow-leaved species; culms usually solid
   9. Blades relatively broad, although strongly involute, some over 4 mm broad at the base; mature sheaths generally with prominent, regularly-spaced air chambers between major vascular bundles; plants found throughout Nebraska, but most common in the west, usually on alkaline soil
      Sporobolus airoides (Torr.) Torr.
   9. Blades mostly narrower; mature sheaths lacking air chambers or with a few, irregularly-spaced ones
      10. Blades with raised margins, the three ridges at each edge fused together and the margins thicker than the central part of the blade; plants low, mat-forming or clumped; blades narrow, usually 1-2 mm wide
          Bouteloua hirsuta Lag.
      10. Blades lacking raised margins; plants various, but often not as above
          11. Blades of bud and mature plant folded when dry, V-shaped in cross-section; ridges not especially prominent dorsally or ventrally; plants scattered, most common in upland prairie in Eastern Nebraska
              Sporobolus heterolepis (A. Gray) A. Gray
          11. Blades usually rolled in the bud, although the margins may not be overlapped, but if, as rarely, folded in the bud, then not folded at maturity; ridges often prominent on the dorsal or ventral surface
              12. Ridges of blade more prominent dorsally than ventrally or of about equal prominence on each surface, the scabrosity or pubescence mostly confined to the margins and dorsal midrib; plants mat-forming, of general distribution in Nebraska, now used to some extent as a lawn grass
                  Bouteloua gracilis (H.B.K.) Lag.
              12. Ridges of blade more prominent ventrally than dorsally, the ventral surface usually scabrous or pubescent
                  13. Blades, when unrolled, revealing fewer than 10 ventral ridges; ventral scabrosity prominent, the individual projections often exceeding 0.05 mm in length
                      14. Blades short, mostly less than 8 cm in length, curly, basally distributed; plants of Western Nebraska
                          Aristida fendleriana Steud.
                      14. Blades longer, not curly, not predominently basal; plants of Western and Central Nebraska
                          Aristida longiseta Steud.
                  13. Blades, when unrolled, revealing more than 10 ventral ridges, the ventral scabrosity less prominent

15. Blades short, less than 10 cm in length, straight; culms spreading; plants rare, known from salt flats west of Lincoln
Sporobolus texanus Vasey

15. Blades longer, culms erect; plants general
Sporobolus asper (Michx.) Kunth

6. Ligules longer, more than 0.6 mm in length
16. Ligules 2-6 mm in length
17. Hairs of middle sheaths under 2 mm long or sheaths glabrous
Panicum lanuginosum Ell. *sens. lat.*

17. Hairs of middle sheath longer
Panicum praecocius Hitchc. & Chase

16. Ligules 0.6-2 mm in length
18. Ligules under 1 mm long; blades mostly less than 12 times as long as broad; plants branching at middle and upper nodes; *blades with ventral ridges scarcely apparent in cross section
Panicum oligosanthes Schultes var. *scribnerianum* (Nash) Fern.

18. Ligules over 1 mm long; blades mostly more than 12 times as long as broad; branching various; *blades with ventral ridges obvious in cross section
19. Leaves mostly arising at the base of the plant; ligules about 1 mm long
Panicum perlongum Nash

19. Leaves distributed up the culm; plants branching above; ligules 1-1.5 mm long
Panicum wilcoxianum Vasey

GROUP 4

GRASSES WITH THE LIGULE PRINCIPALLY A MEMBRANE AND THE SHEATHS PARTLY OR ENTIRELY CLOSED

1. Auricles present on at least some of the leaves (often absent from or broken off of many leaves)
2. Plants not rhizomatous, native, of woodlands
Bromus latiglumis (Shear) Hitchc.

2. Plants strongly rhizomatous, cultivated or weedy
Bromus inermis Leyss.

1. Auricles absent
3. Leaves rolled in the bud, the tips not prow-shaped
4. Plants annual, the remains of previous year's culms and leaves never present, weedy
5. At least the upper sheaths glabrous; culms glabrous, except sometimes at the nodes; ligules mostly over 1.5 mm long
Bromus secalinus L.

5. Sheaths strongly pubescent or culms pubescent or ligules shorter
Bromus japonicus Thunb.; *Bromus tectorum* L.; *Bromus mollis* L.; *Bromus commutatus* Schrad.; *Bromus brizaeformis* Fisch. & Mey.

Note: The above five grasses cannot easily be distinguished even with the use of cross-sections, but only the first two are common, the others being known from very few collections. *B. japonicus* can usually be distinguished from *B. tectorum* by its shorter ligules (under 1.5 mm long).

4. Plants perennial, the remains of previous years' culms and leaves usually obvious, native or weedy
   6. Plants rhizomatous
      7. Plants growing in or near water; both blades and sheaths with abundant air chambers, these cross-septate (Use strong transmitted light to see the septae, or make a cross section of the blade to see the air chambers.)
         8. Ligules relatively short, mostly less than 3 mm long; blades mostly under 5 mm wide; sheaths not flattened; plants growing throughout Nebraska
            Glyceria striata (Lam.) Hitchc.
         8. Ligules usually more than 3 mm long; blade sometimes wider, sheaths sometimes flattened
            9. Blades usually under 5 mm broad, finely papillate on the ventral surface; sheaths flattened; plants rare, in Northwest Nebraska
               Glyceria borealis (Nash) Batchc.
            9. Blades usually more than 5 mm broad, not noticeably papillate; sheaths not flattened; plants common throughout Nebraska
               Glyceria grandis S. Wats. ex A. Gray
      7. Plants of dry land, often planted as cover or for forage and widely escaped; sheaths, but not blades, with air chambers and cross-septae
         Bromus inermis Leyss.
   6. Plants not rhizomatous
      10. Sheaths closed only at the base; blades flat to involute, few-ribbed, not over 3.5 mm wide; plants of alkaline areas
          Puccinellia distans (L.) Parl.
      10. Sheaths closed more than half-way to the summit; blades usually flat, often over 3.5 mm wide; habitats various but seldom alkaline
          11. Sheaths closed to the summit and ligules hence usually tubular, often highest in front, less than 1 mm long; blades seldom much over 4 mm wide; plants uncommon, in Northwest Nebraska
              Schizachne purpurascens (Torr.) Swallen
          11. Sheaths not usually closed to the summit and ligules not usually tubular; blades wider than 4 mm
              12. Plants known from eastern Nebraska woodland, rare; ligule lacerate, not ciliate, often over 2 mm long; *all vascular bundles of blade and sheath joined to dorsal and ventral epidermis by sclerenchyma zones
                  Melica nitens (Scrib.) Nutt. ex Piper
              12. Plants either known only from Western Nebraska or else the ligule clearly ciliate under 30X magnification; ligule often shorter than 2 mm in length; *bundles of blade and sheath sometimes as above, but more often with some of the sclerenchymatous connections lacking or incomplete (The following four species are not easily separated, but only *Bromus ciliatus* and *B. pubescens* are common, the others being known from few collections.)
                  13. Grasses found in woodlands throughout the state but most common in the eastern part; *blades and sheaths not or only slightly ribbed in cross section (except for a few major veins); *some bundles lacking either a dorsal or a ventral sclerenchyma connection to the epidermis (or both)
                      Bromus pubescens Muhl. ex Willd.

13. Grasses mainly of wet places and open areas in the western part of the state; *sheaths, at least, very strongly ridged in cross section; *bundles of the blade and sheath as above or almost all with dorsal and ventral sclerenchyma zones
    14. *Virtually all bundles of the blade, even the small ones, with both dorsal and ventral sclerenchyma zones; plants of wet places in Western and Central Nebraska
        Bromus ciliatus L.
    14. *The smaller bundles of the blade lacking either dorsal or ventral sclerenchyma zones (or both); habitats various; specimens seen all from western counties
        15. *Blades smooth (unridged or only slightly ridged except for major veins) when viewed in cross section
            Bromus carinatus Hook. & Arn.
        15. *Blades obviously ridged dorsally and ventrally when viewed in cross section
            Bromus porteri (Coult.) Nash
3. Leaves folded in the bud, the tips often prominently prow-shaped
    16. Plants annual, usually found in wet places or lawns during fall or spring
        Poa annua L.
    16. Plants perennial, the remains of previous years' culms and leaves usually obvious
        17. Plants rhizomatous or strongly stoloniferous
            18. Plants aquatic; blades flat; sheaths with regularly arranged air chambers; *blades strongly papillate, this obvious in cross sections
                Catabrosa aquatica (L.) Beauv.
            18. Plants not aquatic, although sometimes growing in wet ground and perhaps sometimes where temporarily flooded; blades flat to folded; sheaths with or without air chambers; *blades often scabrous but seldom papillate
                Poa

Note: Species in this group are difficult to distinguish and identification should be considered tentative. Other poas may be present in Nebraska.

            19. Culms compressed (noticeable especially at the nodes); sheaths compressed; plants common, often weedy
                Poa compressa L.
            19. Culms not compressed; sheaths seldom compressed
                20. Plants stoloniferous but lacking scaly rhizomes; *blades not prominently ribbed (except for the midrib) when viewed in cross section; plants growing in wet places
                    Poa palustris L.
                20. Plants rhizomatous; blades variable, but sometimes strongly ribbed; habitats various
                    21. Sheaths closed for about half their length; plants strongly rhizomatous; *blades variable, but often unribbed or not strongly ribbed when viewed in cross section; plants commonly planted and escaped throughout Nebraska; the most common lawn grass
                        Poa pratensis L.

21. Sheaths open nearly to the base; plants sometimes only weakly rhizomatous; *blades sometimes rather strongly ribbed when viewed in cross section; plants native
    22. Ligules short in new growth, often less than 1 mm long, blunt; *sheaths not usually sclerenchymatous beneath the epidermis; plants uncommon, in Western Nebraska
        Poa juncifolia Scribn.
    22. Ligules often longer, acute, or plants not otherwise as above
        23. Plants general in Nebraska, especially in saline soil; *sheaths lacking a continuous sclerenchyma zone beneath the dorsal epidermis
            Poa arida Vasey
        23. Plants restricted to Western Nebraska, not common; *sheaths with a more or less continuous zone of sclerenchyma beneath the dorsal epidermis
            Poa glaucifolia Scribn. & Williams

17. Plants neither rhizomatous nor strongly stoloniferous
    24. Blades broad (3-11 mm in mature leaves), not prow-shaped at the tip, when mature with air chambers between major vascular bundles; sheaths flattened, also with air chambers; plants widely cultivated and escaped
        Dactylis glomerata L.
    24. Blades narrower on the average, prow-shaped at the tip, lacking air chambers; sheaths not prominently flattened, with or without air chambers; plants either native or, rarely, escaped
        Poa

Note: Species in this genus are difficult to distinguish and identifications should be considered tentative. Other poas may be present in Nebraska.

25. Plants of woodlands or escaped from cultivation in moist areas; blades flat and lax; plants most common in Eastern Nebraska
    26. Ligules blunt, collar-like, and mostly under 0.5 mm long; plants rare escapes from cultivation in moist ground
        Poa nemoralis L.
    26. Ligules longer, often acute, or lacerate; plants of woodlands
        Poa sylvestris A. Gray; *Poa wolfii* Scribn.

Note: *Poa sylvestris* is the common woodland poa in Nebraska; *P. wolfii* is rare.

25. Plants of open ground, not usually where very moist, in Western Nebraska
    27. Ligules short, especially on the young growth, less than 1 mm long, blunt
        Poa juncifolia Scribn.
    27. Ligules often longer, acute to lacerate
        Poa sandbergii Vasey; *Poa scabrella* (Thurb.) Benth. ex Vasey

Note: The two above species are interpreted in the broad sense although a still more inclusive interpretation would combine them under the latter name. Taller plants with leaf blades over 1 mm broad are usually assignable to *P. scabrella*; shorter ones with blades under 1 mm broad, to *P. sandbergii.*

GROUP 5

ANNUALS WITH THE LIGULE PRINCIPALLY A MEMBRANE AND SHEATHS OPEN TO THE BASE

1. Culms solid or pith-filled
   2. Plants small, the leaf blades less than 2 mm wide, rare or overlooked, known from sandy riverbanks and moist areas in western counties
      3. Plants matted; culms rooting at the lower nodes, not pubescent below the nodes
         Muhlenbergia filiformis (Thurb.) Rydb.
      3. Plants not matted; culms not rooting at the lower nodes, sometimes pubescent below the nodes
         Muhlenbergia minutissima (Steud.) Swallen
   2. Plants larger, the leaf blades well over 2 mm wide, lawn weeds or escapes from grainfields
      4. Leaves averaging 1 cm or more in width; plants tall, occurring as waifs from grainfields; blades rolled in the bud
         5. Leaves at least 2 cm wide
            Sorghum bicolor (L.) Moench.
         5. Leaves not averaging more than 1.5 cm in width
            Sorghum sudanense (Piper) Stapf
      4. Leaves averaging less than 1 cm in width; plants low, occurring mostly as weeds in cultivated ground; blades basically folded in the bud, although the margins may roll in
         Eleusine indica (L.) Gaertn.

1. Culms hollow
   6. Auricles present on at least some of the leaves
      7. Blades under 5 mm wide, usually conspicuously pilose on both surfaces; plants introduced rather recently, but becoming common as weeds in Eastern Nebraska
         Aegilops cylindrica Host
      7. Blades wider, not pilose
         8. Ligules 4-8 mm long; auricles short (less than 0.3 mm long); plants rare weeds
            Phalaris canariensis L.
         8. Ligules shorter; auricles often longer
            9. Blades with prominent scabrous ridges on the ventral surface, the dorsal surface smooth or with fewer, very low ridges, *the ventral furrows at least half the leaf section in depth; plants uncommon weeds, doubtfully established in Nebraska
               Lolium temulentum L.
            9. Blades less prominently ridged or the ridges about equally prominent on dorsal and ventral surfaces; plants waifs from cultivation (Identification of the following three species should be considered tentative.)
               10. Blades rather obviously ridged and usually somewhat scabrous on both surfaces, *bulliform cells not prominent on ventral surface between veins
                  11. Blades usually 5-10 mm wide, *more prominently ridged ventrally than dorsally
                     Secale cereale L.
                  11. Blades often over 10 mm wide, *about equally ridged on both surfaces
                     Hordeum vulgare L.

10. Blades not obviously ridged, especially when fresh, the scabrosity usually confined to the margins, *zones of bulliform cells very obvious on the ventral surface between the veins

Triticum aestivum L.

6. Auricles absent on all of the leaves
12. Ligules short, less than 1 mm in length; *midribs, if present, without a prominent zone of achlorophyllous parenchyma ventrally
13. Blades filiform, with fewer than 10 ventral ridges; plants common in waste areas

Festuca octoflora Biel.

13. Blades not filiform, with more than 10 ventral ridges
14. Blades pilose with stiff spreading hairs on both surfaces, many of the hairs 0.5 mm long or longer; plants recently introduced weeds in Eastern Nebraska

Aegilops cylindrica Host

14. Blades not pilose, the pubescence lacking or sparse and the hairs shorter; plants general

Hordeum pusillum Nutt.

12. Ligules longer than 1 mm; *midribs with or without a ventral zone of achlorophyllous parenchyma
15. Leaves with a zone of appressed pubescence on the dorsal surface at the collar region; plants stout aquatics often with at least some of the leaves floating and over 1 cm broad; sheaths with prominent air spaces and stout cross-septae, these usually visible to the naked eye, even without transmitted light; plants known from the northern two-thirds of Nebraska but now uncommon

Zizania aquatica L.

15. Leaves lacking a zone of appressed pubescence in the collar region although sometimes with general appressed pubescence there; plants sometimes aquatic but then often lacking floating leaves and with narrower blades; sheaths with or without air spaces, but cross-septae, if present, usually visible only under transmitted light
16. Blades strongly keeled, the midrib strong, appearing ventrally as a white band more than 0.2 mm wide, *the cross section revealing a large hollow zone of achlorophyllous parenchyma ventral to the midrib

Leptochloa fascicularis (Lam.) A. Gray

16. Blades not keeled or only weakly keeled, the midrib less prominent, *sometimes with a ventral zone of achlorophyllous parenchyma, but this not hollow
17. Leaves with few to many stiff hairs (over 1 mm long) in or near the collar region; sheaths lacking air chambers
18. Blades bearing numerous pustular-based hairs

Digitaria sanguinalis (L.) Scop.

18. Blades glabrous except near the ligule

Digitaria ischaemum (Schreb.) Schreb. ex Muhl.

17. Leaves lacking long, stiff hairs in the collar region; sheaths with air chambers when mature
19. Leaves obviously more deeply ridged ventrally than dorsally *and* with additional lines of scabrosity on the dorsal surface so that the number of dorsal ridges greatly exceeds the number of ventral ones in a dried leaf; plants of moist areas

20. Ligules puberulent externally, variable in length but often over 4 mm; blades variable in width, but often over 4 mm broad

Polypogon monspeliensis (L.) Desf.

20. Ligules glabrous externally, variable in length but often under 4 mm; blades variable in width but often under 4 mm broad

Alopecurus carolinianus Walt.

19. Leaves with ridges of the dorsal and ventral surface about the same height *or* the ridges of the dorsal and ventral surfaces about the same in number; plants of moist to dry areas

21. Ligule glabrous externally, usually 4-8 mm long; plants rare weeds, in Western Nebraska

Phalaris canariensis L.

21. Ligule scabrous to pubescent externally, sometimes longer than 8 mm or shorter than 4 mm

22. Plants of wet areas, usually in standing water; cross-septae obvious in sheaths in strong transmitted light; ligules usually over 6 mm long; plants of Western Nebraska

Beckmannia syzigachne (Steud.) Fern.

22. Plants of dry areas; cross-septae not obvious in sheaths in transmitted light; ligules usually under 6 mm long; plants general, escaped from cultivation

23. Herbage pilose, at least below

Avena fatua L.

23. Herbage glabrous

Avena sativa L.

GROUP 6

PERENNIALS WITH SHEATHS OPEN TO THE BASE, MEMBRANOUS LIGULES, AND SOLID CULMS

1. Plants rhizomatous

2. Auricles present on at least some leaves

3. Rhizomes extensive; culms arising singly; ligules short, less than 1 mm long; plants scattered in distribution, introduced throughout Nebraska

Agropyron intermedium (Host) Beauv.

3. Rhizomes short; plants clumped, ligules longer, more than 1 mm long; plants native to Western Nebraska

Elymus cinereus Scribn. & Merr.

2. Auricles lacking

4. Leaf blades under 4 mm broad

5. Leaves pubescent in or near the collar region

6. Plants truly rhizomatous; sheaths not keeled, with regularly spaced air chambers between the vascular bundles; blades stiff, sharp-pointed; plants of moist, often alkaline environments

Distichlis stricta (Torr.) Rydb.

6. Plants not truly rhizomatous but freely rooting at the decumbent lower culm nodes; sheaths slightly keeled, lacking air chambers; blades not stiff and sharp-pointed; plants of a variety of moist habitats, often weedy
Muhlenbergia schreberi Gmel.

5. Leaves not pubescent in the collar region except sometimes on the ligule
7. Culms irregularly nodulose-roughened; leaves about 1-2 mm wide; plants relatively uncommon, in Western Nebraska
Muhlenbergia richardsonis (Trin.) Rydb.

7. Culms not noticeably nodulose-roughened; leaves 1-4 mm broad
8. Plants clumped, not very strongly rhizomatous; leaf blades keeled, Y-shaped in section at maturity, about 2-4 (or more) mm wide; ligules usually over 1 mm long; plants common throughout Nebraska
Andropogon scoparius Michx.

8. Plants more or less matted, strongly rhizomatous; leaf blades V-shaped in section at maturity, about 1-2 mm wide; ligules usually less than 1 mm long; plants of Western and Central Nebraska
Muhlenbergia asperifolia (Nees & Mey.) Parodi

4. Leaf blades mostly more than 4 mm broad
9. Sheaths obviously keeled; blades usually under 5 mm wide, folded in the bud and at maturity, Y-shaped in cross section; plants weakly rhizomatous
Andropogon scoparius Michx.

9. Sheaths not keeled; some blades usually over 5 mm wide; blades usually rolled in the bud (sometimes folded) and usually flat at maturity; plants weakly to very strongly rhizomatous
10. Midrib very prominent ventrally, white, one fifth or more of the width of the blade in the lower part; ligule about 1 mm long, with a fringe of hairs only slightly shorter than the membranous lower portion; plants introduced ornamental grasses escaped in Eastern Nebraska
Miscanthus sacchariflorus (Maxim.) Hack.

10. Midrib narrower and plants not otherwise as above
11. Culms stout; sheaths with air chambers at maturity; blades more than 10 mm wide; plants escaped from cultivation in various parts of the state
Sorghum halepense (L.) Pers.

11. Culms stout to slender; sheaths lacking air chambers; blades of varying widths, but if broader than 10 mm, then culms slender
12. Plants uncommon woodland species of extreme Eastern Nebraska; blades broad, often 10-15 mm; culms slender
Brachyelytrum erectum (Schreb.) Beauv.

12. Plants usually of open ground, relatively common; blades mostly under 10 mm broad, culms stout
13. Plants very strongly rhizomatous, usually growing on sand
Andropogon hallii Hack.

13. Plants weakly rhizomatous, usually not on sand
Andropogon gerardii Vitm.

Note: *Andropogon gerardii* and *A. hallii* sometimes hybridize in Nebraska and intermediate plants are not uncommon.

1. Plants not rhizomatous
14. Dried blade strongly ribbed ventrally and relatively smooth dorsally (veined but not ribbed or only weakly ribbed)

15. Major ridges of blade relatively few, usually fewer than 9; blades involute, the edges often approximate in the bud, usually under 2 mm broad; auricles lacking
    16. Ligules over 5 mm long in most leaves; *each bundle in the blade not corresponding to a ventral ridge; plants of Western Nebraska
    Oryzopsis hymenoides (Roem. & Schult.) Ricker
    16. Ligules often under 5 mm long; *each bundle in the blade corresponding to a ventral ridge; plants found throughout Nebraska
    Stipa comata Trin. & Rupr.
15. Major ridges of the blade 9 or more, especially near the base; blades flat to involute, the edges generally overlapping in the bud, usually over 2 mm broad; auricles usually present on at least some leaves
    17. Ligules short, under 1.5 mm long, erose-ciliolate
        18. Some ridges of ventral blade surface very prominent, ridges not equal in height (*some ridges in section twice the height of others); plants glaucous, coarse, introduced in various parts of Nebraska, especially in saline soil
        Agropyron elongatum (Host) Beauv.
        18. Ridges of blade less prominent, mostly about equal in height (*the furrows between them shallow in section); plants not usually glaucous, not coarse, commonly introduced for forage in Western Nebraska, uncommon in the eastern part of the state
        Agropyron cristatum (L.) Gaertn. *sens. lat.*
    17. Ligules longer than 1.5 mm, not erose-ciliolate; plants uncommon, native to Western Nebraska
    Elymus cinereus Scribn. & Merr.
14. Dried blade obviously ribbed on both sides, or more heavily ribbed dorsally than ventrally, or not obviously ribbed on either side
    19. Blades clearly folded in the bud or obviously V-shaped or Y-shaped in cross section at maturity
        20. Internodes puberulent
            21. Ligules short, truncate, under 1 mm long, ciliolate; plants scattered in dry prairie
            Muhlenbergia cuspidata (Torr.) Rydb.
            21. Ligules longer, over 1 mm long, not ciliolate; plants of dry, disturbed to undisturbed habitats
            Schedonnardus paniculatus (Nutt.) Trel.
        20. Internodes glabrous
            22. Plants stout, at least some blades over 4 mm broad; sheaths not keeled; blades sometimes folded in the bud but not V-shaped in cross section; plants common throughout Nebraska
            Andropogon gerardii Vitm.
            22. Plants smaller, most of the blades under 4 mm broad, or if approaching or exceeding 4 mm, the sheaths very clearly keeled and the blades V-shaped or Y-shaped in cross section
                23. Long hairs present in or near the collar region (longer than the ligule); plants of disturbed habitats
                Chloris verticillata Nutt.
                23. Long hairs absent in or near the collar region

24. Ligules usually under 1.5 mm long, truncate, ciliolate; sheaths strongly keeled; blades Y-shaped in cross section; plants common in dry prairie throughout Nebraska
Andropogon scoparius Michx.

24. Ligules over 1.5 mm long, acute, not ciliolate; sheaths not keeled or only weakly keeled; blades V-shaped in cross section; plants common in both native and weedy habitats
Schedonnardus paniculatus (Nutt.) Trel.

19. Blades rolled in the bud and flat to somewhat involute at maturity

25. Culms slender, weak, rooting at the lower nodes and forming mats; plants weedy; blades relatively lax, flat, slender, mostly less than 3.5 mm broad and under 8 cm long; plants of moist ground in Eastern Nebraska
Muhlenbergia schreberi Gmel.

25. Culms slender to stout, not rooting at the lower nodes; blades mostly more than 3.5 mm broad and 8 cm long; habitats various

26. Auricles present; plants coarse, native bunchgrasses of Western Nebraska, uncommon
Elymus cinereus Scribn. & Merr.

26. Auricles absent

27. Plants uncommon in woodland in eastern Nebraska; internodes pubescent; many blades over 10 mm broad; ligules often over 1.5 mm long
Brachyelytrum erectum (Schreb.) Beauv.

27. Plants common in open habitats throughout Nebraska; internodes glabrous; blades often under 10 mm broad; ligules usually about 1.5 mm long or shorter

28. Blades bearing large, pustular-based hairs, especially on the wavy margin; sheaths ciliate, with air chambers at maturity; plants forming small bunches, often on sandy soil
Paspalum setaceum Michx. var. *stramineum* (Nash) D. Banks

28. Blades with the pustular-based hairs, if present, confined to the region of the ligule, the margins straight; mature sheaths lacking air chambers, not ciliate; plants forming large clumps, usually not on sand (See lead 13, this group.)
Andropogon gerardii Vitm.

GROUP 7

PERENNIALS WITH THE LIGULE PRINCIPALLY A MEMBRANE, SHEATHS OPEN TO THE BASE, CULMS HOLLOW, AND AURICLES PRESENT

1. Plants rhizomatous

2. Blades flat, with both dorsal and ventral surfaces unridged or about equally slightly ridged, mostly more than 5 mm broad
Agropyron repens (L.) Beauv.

Note: Hybrids between *A. repens* and *Hordeum jubatum*, which are of rare occurrence in Nebraska, may key here.

2. Blades flat to involute, with the ventral surface more obviously ridged than the dorsal, sometimes less than 4 mm broad

3. Blades involute, the ventral ridges of varying sizes corresponding to vascular bundles of varying sizes, some ridges broader than the furrows in the dried leaf; *blades with zones of sclerenchyma joining each bundle to both the ventral and the dorsal epidermis; mature sheaths usually lacking air chambers
   4. Leaves strongly pubescent on the lower sheaths, the blades often puberulent or strongly scabrous; plants of Western Nebraska
      Agropyron dasystachyum (Hook.) Scribn.
   4. Leaves weakly pubescent or glabrous on the lower sheaths, the blades often glabrous to scabrous; plants common throughout Nebraska
      Agropyron smithii Rydb.
3. Blades flat to involute in part, but ventral ridges relatively uniform in size and often appearing narrower than the furrows between them in the dried leaf
   5. Blades usually under 5 mm wide; rhizomes not extensive; auricles not ciliate; plants introduced, common
      Festuca pratensis Huds.
   5. Blades usually over 5 mm broad; rhizomes extensive; auricles ciliate; plants introduced, not common
      Festuca arundinacea Schreb.

1. Plants not rhizomatous
   6. Ligules more than 2 mm long; blades flat, under 10 mm wide; auricles small, not developed on many leaves; an introduced grass commonly escaped in moist sites
      Phleum pratense L.
   6. Ligules never more than 2 mm long except on rare robust individuals which have blades over 10 mm wide; blades and auricles various
      7. Blades relatively unridged, especially when fresh, or with dorsal and ventral ridges about equally prominent or the dorsal more prominent than the ventral; blades sometimes over 8 mm wide
         8. Leaf blades yellowish green, 2-5 mm broad; plants weedy, growing in clumps; *blades more prominently ridged ventrally than dorsally when viewed in section, although this may not be obvious in surface views; *at least some of the smaller veins lacking a sclerenchymatous connection to the ventral epidermis; *bulliform cells obvious, in the furrows of the ventral surface
            Hordeum jubatum L.

         Note: Occasional sterile hybrids between this species and species of the genera *Elymus* and *Agropyron* occur in Nebraska and may key here.

         8. Leaf blades dark green or glaucous; blades variable in width but often over 5 mm wide; plants native, growing in clumps or scattered; *blades unridged or not very much more prominently ridged ventrally than dorsally, or if so, then well over 5 mm wide; *vascular bundles (except in one species) mostly with sclerenchymatous connections to the ventral surface; *bulliform cells sometimes not obvious or level with the essentially unridged ventral surface
            9. Leaves decidedly pubescent on the ventral surface of the blade; plants confined to woodland habitats
               10. Leaf blades 8-15 mm wide, often sparsely pilose; *most veins joined to both dorsal and ventral epidermis by sclerenchyma in both blade and sheath
                  Hystrix patula (L.) Moench.
               10. Leaf blades 6-10 mm wide, usually densely pilose, *most veins of the sheath and some veins of the blade lacking a sclerenchymatous connection to the ventral epidermis
                  Elymus villosus Muhl.

9. Leaves glabrous or subglabrous; plants found in a variety of habitats and polymorphic

Elymus canadensis L.; *Elymus virginicus* L.

7. Blades prominently ridged ventrally, the dorsal ridges less prominent; blades not over 8 mm wide

11. Blades clearly folded in the bud; the culms slightly flattened

Lolium perenne L.

11. Blades rolled in the bud; culms not flattened

12. Blades at once broad (mostly 6-8 mm wide) and strongly pubescent on the ventral surface; ridges of the ventral surface pale and much narrower than the dark green furrows between them; plants native, growing in woodlands

Elymus villosus Muhl.

12. Blades narrower or not strongly pubescent or plants not otherwise as in the opposing choice

13. Ligules erose-ciliolate (this feature visible under 30X magnification)

14. *Each vascular bundle corresponding to a ventral ridge in the blade; grasses of weedy habitats

15. Ventral ridges standing out sharply in the dried blade, broader than the furrows between them; blades often slightly V-shaped in cross-section

Sitanion hystrix (Nutt.) J. G. Smith var. *brevifolium* (J. G. Smith) C. L. Hitchc.

15. Ventral ridges less prominent, in the dried leaf apparently narrower than the furrows between them (See note under lead 8, this group.)

Hordeum jubatum L.

14. *Some vascular bundles corresponding to ventral furrows rather than to ridges; grasses weedy or native

16. Plants cultivated or introduced; ligule clearly erose-ciliolate under 30X magnification; culms often partly pith-filled, *less than half of the culm's subepidermal layer consisting of sclerenchyma cells

Agropyron cristatum (L.) Gaertn. *sens. lat.*

16. Plants native; ligule weakly erose-ciliolate under 30X magnification; culms hollow, strongly sclerenchymatous, *more than half of the culm's subepidermal layer consisting of sclerenchyma cells

Agropyron caninum (L.) Beauv. *sens. lat.*

13. Ligules not erose-ciliolate

17. Plants native; ridges on ventral surface of blade prominent, many of them wider than the furrows between them; *alternating vascular bundles of the blade joined to the epidermis dorsally and ventrally by sclerenchyma, some vascular bundles corresponding to furrows rather than to ridges ventrally

Agropyron caninum (L.) Beauv. *sens. lat.*

17. Plants introduced; ridges on ventral surface of blade less prominent, often slightly narrower than the furrows between them; *none of the vascular bundles of the blade joined to the epidermis by sclerenchyma, all vascular bundles usually corresponding to ventral ridges

18. Ligule usually under 0.3 mm in length; plants strongly perennial and often shortly rhizomatous
Festuca pratensis Huds.

18. Ligule over 0.3 mm in length; plants non-rhizomatous and often short-lived
Lolium multiflorum Lam.

GROUP 8

RHIZOMATOUS PERENNIALS WITH THE LIGULE PRINCIPALLY A MEMBRANE, THE SHEATHS OPEN TO THE BASE, AURICLES ABSENT, AND CULMS HOLLOW

1. Plants with a clearly-marked zone of pubescence at each node (Plants having pubescent nodes but with pubescence continuous with sheath or culm pubescence should be keyed under the opposing lead.)
   2. Midrib unusually broad, about a fifth or more the width of the blade on the ventral surface near the base; ligule with a fringe of hairs almost equal in length to the basal membranous portion; plants ornamentals escaped in Eastern Nebraska
   Miscanthus sacchariflorus (Maxim.) Hack.
   2. Midrib not unusually broad; ligule often erose and sometimes ciliate but lacking a fringe as long as the membranous portion; plants not otherwise as above
      3. Plants of woodlands, weak-stemmed; sheaths without air chambers
      Leersia virginica Willd.
      3. Plants of wet areas or open prairie; sheaths with regularly spaced air chambers at maturity
         4. Sheaths with cross-septae obvious in transmitted light; blades with prominent marginal scabrosity, especially near the base; plants growing near water; stems often partly decumbent
         Leersia oryzoides (L.) Sw.
         4. Sheaths without obvious cross-septae in transmitted light; blades without prominent marginal scabrosity; plants of open prairie; stems erect
         Sorghastrum avenaceum (Michx.) Nash (*S. nutans* of authors)

1. Plants with nodes not pubescent or if pubescent, then the pubescence continuous with that of the sheath or culm
   5. Ligule very short (less than 0.5 mm long) and higher on the sides than at the back; blades narrow, usually less than 1.5 mm wide, strongly involute, few-ridged; plants grown as lawn grasses, sometimes escaping
   Festuca rubra L.
   5. Ligule short to long, but if short, not generally highest at the sides; blades variable in width, but usually over 1.5 mm wide, involute to flat
      6. Sheaths with prominent air chambers between vascular bundles, these traversed by numerous cross-septae (obvious in transmitted light); blades averaging over 5 mm in width; plants tall, growing in wet places
         7. Ligules prominently fringed with hairs, these often nearly as long as the membranous lower portion; blades very coarse, usually 10-40 mm in breadth
         Phragmites australis (Cav.) Steud. (*P. communis* of authors)
         7. Ligules at most slightly ciliolate, generally entire or erose
            8. Cross-septae common and obvious in even the upper part of the sheath

9. Grasses of standing water, known in Nebraska only from Grant County; blades usually 5-10 mm wide, the widest part not more than 40-ridged, the tips narrow, almost filiform

Scolochloa festucacea (Willd.) Link

9. Grasses of wet places, but not usually of standing water, general in distribution and common; blades often over 10 mm wide and more than 40-ridged in the widest part, the tips not filiform

Phalaris arundinacea L.

8. Cross-septae not apparent in the upper parts of the sheaths and few or scattered in the lower parts

Calamagrostis canadensis (Michx.) Beauv.

6. Sheaths without numerous cross-septae, if these obvious at all, then the blades averaging less than 5 mm in width

10. Blades broad, some of them over 10 mm wide; ligules very short, less than 0.5 mm long (although sometimes the margins of the sheath extended into a longer tooth adjacent to the ligule); stems usually unbranched; grasses of woodland areas in Eastern Nebraska

11. Rhizomes short, knotted; leaves not distributed toward the culm base, some nodes hence usually visible; sheaths with regularly spaced air chambers between vascular bundles at maturity; *blades without narrow ventral grooves corresponding to the zones of bulliform cells; plants rare

Oryzopsis racemosa (J. E. Sm.) Ricker

11. Rhizomes elongate, slender; leaves mostly distributed toward the culm base, the sheaths overlapping, most nodes not visible; sheaths lacking air chambers; *blades with narrow ventral grooves corresponding to the zones of bulliform cells; plants limited in distribution but not rare

Diarrhena americana Beauv.

10. Blades narrower, not usually over 10 mm wide, but if wider, then the ligules longer than 0.5 mm; stems branched or unbranched; grasses of various habitats

12. Ligule short, less than 0.5 mm long, truncate

13. Collar region and often the ventral surface of the blade with long hairs exceeding 1 mm in length; plants with stiffly erect, unbranched culms and stiff, sharp-pointed, often involute blades, growing in alkaline soils, usually where moist

Distichlis stricta (Torr.) Rydb.

13. Collar and blade not hirsute; culms often branched; blades often lax and flat; plants usually growing in woodland, but sometimes weedy

14. Internodes glabrous and shining, but sometimes slightly scabrous at the very apex

Muhlenbergia bushii Pohl; *Muhlenbergia sobolifera* (Muhl.) Trin.

Note: The above grasses are not readily distinguished vegetatively. Both species are uncommon and restricted to Eastern Nebraska

14. Internodes dull and puberulent, especially above

15. Sheaths retrorsely puberulent; species uncommon, found in Eastern Nebraska

Muhlenbergia tenuiflora (Willd.) B. S. P.

15. Sheaths glabrous

16. Nodes glabrous; culms usually branched; plants general, common

Muhlenbergia mexicana (L.) Trin.

16. Nodes puberulent; culms unbranched; plants relatively uncommon
Muhlenbergia glomerata (Willd.) Trin.

12. Ligule longer, on most leaves more than 0.5 mm long, truncate to obtuse or acute

17. Sheaths more or less pilose, many of the hairs exceeding 1.5 mm in length; plants tufted, the rhizomes very short, many of the culms decumbent at the base; *sheath with an uninterrupted sclerenchyma layer inside the ventral epidermis, solid
Leptoloma cognatum (Schultes) Chase

17. Sheaths not pilose, sometimes pubescent with shorter hairs; plants usually with longer rhizomes and often erect at the base; *an uninterrupted ventral sclerenchymatous hypodermis lacking in the solid to air-chambered sheath

18. Culms unbranched or branched only from the base; grasses of moist associations, or sometimes weedy; sheaths with at least some air chambers between veins; ligules often over 2 mm long

19. Blades involute, usually 2-4 mm broad, the ventral ridges very strong, *the ventral furrows often half the section in depth
Calamagrostis inexpansa A. Gray

19. Blades flat or involute, 2-10 mm broad, the ventral ridges apparent but not strong, *the ventral furrows not approaching half the section in depth

20. Plants of wet places, not weedy; culms erect; blades rather tough and fibrous; *each vascular bundle connected to the epidermis by dorsal and ventral zones of sclerenchyma
Calamagrostis canadensis (Michx.) Beauv.

20. Plants of wet to dry places, often weedy; culms sometimes prostrate or decumbent below; blades lax, not so tough and fibrous; *many of the smaller vascular bundles lacking either the ventral zone of sclerenchyma or both the dorsal and ventral zones
Agrostis stolonifera L.

18. Culms branching above; grasses of woodlands or sometimes weedy; ligules often under 2 mm long but sometimes longer; sheaths lacking air chambers

21. Internodes glabrous and shining, but sometimes slightly scabrous at the apex

22. Ligules of many leaves longer than 3 mm; plants common
Muhlenbergia racemosa (Michx.) B. S. P.

22. Ligules all less than 3 mm long

23. Rhizomes with the scales loosely imbricated; plants common in Nebraska
Muhlenbergia frondosa (Poir.) Fern.

23. Rhizomes with the scales tightly appressed; plants rare in Nebraska
Muhlenbergia bushii Pohl.

21. Internodes dull, puberulent, especially above
24. Ligules of many leaves longer than 1 mm; plants of Eastern Nebraska, not common
Muhlenbergia sylvatica (Torr.) Torr.

24. Ligules of all leaves less than 1 mm long; plants general, common
Muhlenbergia mexicana (L.) Trin.

GROUP 9

NON-RHIZOMATOUS PERENNIALS WITH THE LIGULE PRINCIPALLY A MEMBRANE, THE SHEATHS OPEN TO THE BASE, AURICLES ABSENT, AND CULMS HOLLOW

1. Blades, at least the basal ones, involute or under 3 mm wide
2. Ligules collar-like, truncate, less than 0.6 mm long, usually erose-ciliolate to ciliate
3. Blades with ridges of ventral surface and vascular bundles few in number (often 5); ligules usually higher on the sides than at the center; *all vascular bundles of the blade lacking both dorsal and ventral sclerenchymatous connections to the epidermis; plants seldom-collected escapes (probably from lawns) in our range
4. Lower sheaths thin, splitting into brown fibers, the innovations breaking through them; plants forming loose clumps
Festuca rubra L.

4. Lower sheaths persistent, innovations arising within them; plants in dense clumps
Festuca ovina L.

3. Blades with ridges of ventral surface and vascular bundles more numerous; ligules not usually markedly higher at the sides than at the back (sometimes so); *some or all of the vascular bundles of the blade with both dorsal and ventral sclerenchymatous connections to the epidermis
5. Low ridges of the blade's dorsal surface more numerous and closely spaced than the higher ridges of the ventral surface (most obvious in dried leaves) *because some vascular bundles are opposite ventral furrows or because sclerenchyma zones are present between the bundle regions dorsally but not ventrally; plants native
6. Blades involute, often under 1 mm wide; *some dorsal sclerenchyma zones not opposite vascular bundles; plants often in rocky soil of wooded areas
Oryzopsis micrantha (Trin. & Rupr.) Thurb.

6. Blades flat to involute, wider than 1 mm; *all dorsal sclerenchyma zones opposite vascular bundles; plants of various habitats
Agropyron caninum (L.) Beauv. *sens. lat.*

5. Ridges of the blade's dorsal and ventral surfaces approximately equal in number, *nearly all the bundles opposite ventral ridges and no sclerenchyma zones present between bundle regions dorsally; plants native or weedy
7. Ventral ridges standing out sharply in the dried blade, broader than the furrows between them; blades often slightly V-shaped in cross section
Sitanion hystrix (Nutt.) J. G. Smith var. *brevifolium* (J. G. Smith) C. L. Hitchc.

7. Ventral ridges less prominent, apparently narrower than the furrows between them (See note under lead 8, Group 7.)
Hordeum jubatum L.

2. Ligules not especially collar-like, over 0.6 mm long, entire to erose-ciliate or lacerate
   8. Leaf villous near the margin at the collar region, the hairs 0.5-1 mm long; ligule 0.6-3 mm long; sheath usually ciliate on one margin; plants found throughout Nebraska but most common westward
      Stipa viridula Trin.
   8. Leaf not as above; plants not otherwise as above
      9. Average length of ligule approaching or exceeding 3 mm, especially on culm leaves
         10. Blades flat, with margins evidently overlapping in the bud; plants of moist areas in Western Nebraska
            Agrostis exarata Trin.
         10. Blades involute, with margins approximate in the bud; plants tough, fibrous perennials of dry prairie
            11. Ligules often over 5 mm long; *not all bundles corresponding to ventral ridges in the blade; *culms with a distinct band of chlorenchyma interrupted by zones of fibers in the outermost cortex; blades usually densely pubescent on the ventral surface; plants common in Western Nebraska
               Oryzopsis hymenoides (Roem. & Schult.) Ricker
            11. Ligules mostly 3-5 mm long; *each bundle in the blade corresponding to a ventral ridge; *culms with a fibrous outer cortex; blades with the ventral surface puberulent to scarcely scabrous
               12. Blades, when unrolled, 1-2 mm wide; ligules acute; ventral surface of blade strongly scabrous or lightly puberulent; plants most common in Western Nebraska
                  Stipa comata Trin. & Rupr.
               12. Blades, when unrolled, 2-5 mm wide; ligules acute or sometimes higher at the sides than at the center; ventral surface of blade somewhat scabrous; plants most common in Eastern Nebraska
                  Stipa spartea Trin.
      9. Average length of ligules under 3 mm
         13. Plants of Western Nebraska, often found in rocky soil in dry woodland; ligules truncate, seldom over 1 mm long; blades often 10-30 cm long, *with sclerenchyma zones between and opposite the vascular bundles dorsally
            Oryzopsis micrantha (Trin. & Rupr.) Thurb.
         13. Plants often of moist soil, sometimes of moist, alkaline soil; ligules sometimes over 1 mm long, obtuse to acute; blades sometimes shorter than 10 cm, *lacking sclerenchyma zones between the bundle regions dorsally
            14. Plants of alkaline soils, uncommon; mature sheaths lacking air chambers
               Puccinellia distans (L.) Parl.
            14. Plants not characteristically of alkaline soil, relatively common; mature sheaths with air chambers
               15. Blades strongly fibrous, with heavy scabrous ridges, *sclerenchyma present above and below most bundles joining the bundles to both dorsal and ventral epidermis
                  Agrostis scabra Willd.
               15. Blades weakly fibrous, *fibers not numerous, not joining the bundles to dorsal and ventral epidermis
                  Agrostis hiemalis (Walt.) B. S. P.

1. Blades mostly flat and over 3 mm wide
16. Blades mostly 3-5 mm wide
17. Leaf villous near the margin at the collar region, the hairs 0.5-1 mm long; ligule 0.6-3 mm long, sheaths usually ciliate on one margin; plants found throughout Nebraska but most common westward

Stipa viridula Trin.

17. Leaf not as above; plants not otherwise as above
18. Ligules collar-like, most of them under 0.6 mm long
19. Ridges on the ventral surface of the dried leaf more prominent than those of the dorsal surface, often as broad or broader than some of the furrows between them
20. Grasses of weedy habitats; blades often slightly V-shaped in section; *each vascular bundle of the leaf generally corresponding to a ventral ridge; *fibers prominent at the edge of the blade, extending farther in on the dorsal side than on the ventral

Sitanion hystrix (Nutt.) J. G. Smith var. *brevifolium* (J. G. Smith) C. L. Hitchc.

20. Grasses not weedy; blades not usually V-shaped in section; *some vascular bundles not corresponding to ventral ridges

Agropyron caninum (L.) Beauv. *sens. lat.*

19. Ridges on the ventral surface of the dried leaf not much more prominent than those of the dorsal surface, narrower than the furrows between them
21. Grasses weedy, not growing in woodland or native prairie, yellowish-green; leaves usually under 10 cm long (See note under lead 8, Group 7.)

Hordeum jubatum L.

21. Grasses native, often growing in woodland or native prairie; leaves often over 10 cm long

Festuca obtusa Bieler; *Festuca paradoxa* Desv.

Note: *Festuca obtusa* is a common woodland species throughout the eastern two thirds of the state. *F. paradoxa*, a prairie species, is rare. I have seen one old specimen, from near Omaha.

18. Ligules not usually collar-like, over 0.6 mm long
22. Ligules mostly over 4 mm long; sheaths prominently cross-septate in transmitted light; the numerous ridges on the ventral surface of the blade sharp and prominent, *acute in cross section; plants of moist places, often in standing water

Alopecurus aequalis Sobol.

22. Ligules shorter, or if some of them exceeding 4 mm, then plants not as above in other respects
23. Plants of dry, often sandy, open slopes or fields; midribs not prominent on the dorsal surfaces of the blades; ligules often under 2 mm long
24. Plants with stems arising from decumbent, knotty bases; leaves under 10 cm long, distributed up the culm; sheaths more or less pilose with hairs often exceeding 1.5 mm in length; *sheath with an uninterrupted sclerenchyma layer inside the ventral epidermis, solid; plants of Eastern and Central Nebraska

Leptoloma cognatum (Schultes) Chase

24. Plants usually with erect stems arising in dense clumps; leaves often over 10 cm long, many of them basal; sheaths glabrous to puberulent with short hairs; *sheaths sometimes with a sclerenchyma zone but lacking a clearly marked hypodermis; plants of extreme Western Nebraska

Hesperochloa kingii (S. Wats.) Rydb.

23. Plants of moist habitats or not otherwise as above

25. Plants weedy; culms bulbous-based; ligules entire to lacerate, 2-4 mm long

Phleum pratense L.

25. Plants weedy to native; culms not bulbous-based; ligules usually toothed to erose or erose-ciliolate, sometimes also lacerate

26. Plants robust, most blades nearly 5 mm broad (or broader); culms often rooting at the lower nodes; grasses introduced in Eastern Nebraska; *ventral blade surface rather deeply furrowed, the furrows up to half the depth of the section

Alopecurus pratensis L.

26. Plants ordinarily less robust or else confined to Western Nebraska

27. Ligules usually over 3 mm long; plants of Western Nebraska

Agrostis exarata Trin.

27. Ligules less than 3 mm long; plants general

Sphenopholis obtusata (Michx.) Scribn. var. *obtusata* and var. *major* (Torr.) Erdm.

16. Blades mostly over 5 mm wide

28. Ligules backed by a zone of long hairs, many of them 1.5 mm or more in length; blades with pustular-based hairs, especially on the margins; plants of dry or sandy soil

Paspalum setaceum Michx. var. *stramineum* (Nash) D. Banks

28. Ligules not backed by long hairs, although sometimes by shorter pubescence

29. Leaf villous near the margin at the collar region, the hairs 0.5-1 mm long; ligule 0.5-3 mm long; sheath usually ciliate on one margin; plants of dry prairie throughout the state but most common westward

Stipa viridula Trin.

29. Leaf not as above; plants not otherwise as above

30. Ligules short, collar-like, under 0.6 mm long

31. Leaves mostly under 7 mm wide, *rather obviously ridged on the ventral surface when viewed in cross section (See note under lead 21, this group.)

Festuca obtusa Bieler; *Festuca paradoxa* Desv.

31. Leaves mostly over 7 mm wide, *not obviously ridged on the ventral surface when viewed in cross section

32. Ventral surfaces of blades with double or single rows of whitish dots (stomatal guard cells) on each side of each vein (apparent under 30X magnification); plants rather common in the woodland of Eastern Nebraska

Hystrix patula Moench.

32. Ventral surfaces of blades lacking the obvious stomatal rows on each side of each vein; plants rare in extreme Eastern Nebraska, not recently collected
Oryzopsis racemosa (J. E. Sm.) Ricker

30. Ligules longer, usually well over 0.6 mm long
33. Plants of dry, often sandy, open slopes or fields; midribs not prominent on the dorsal surfaces of the blades; ligules often under 2 mm long; blades relatively narrow, not over 6 mm wide
Go to lead 24, this group.
33. Plants of moist habitats or not otherwise as above
34. Ligules truncate and relatively short, not over 2 mm long, strongly erose-ciliate and puberulent; blades usually puberulent on the ventral surface; base of the plant sometimes with a series of somewhat swollen internodes; plants uncommon weeds, known only from a few introductions
Arrhenatherum elatius (L.) Presl.
34. Ligules longer or else not otherwise as above; blades often glabrous; plants sometimes bulbous-based but not with a series of swollen internodes at the base
35. Plants with ligules not ciliate or ciliolate, but often lacerate; culms usually somewhat bulbous-based
36. Plants weedy, midribs not prominent on the ventral surface of the blade near the base; stomates not prominent on the ventral blade surface under 30X magnification
Phleum pratense L.
36. Plants not weedy, of woodlands, midrib very prominent on the ventral surface near the base of the blade; stomatal guard cells apparent as whitish dots on each side of each vein (apparent under 30X magnification)
Cinna arundinacea L.
35. Plants with ligules ciliate or ciliolate and sometimes also lacerate
37. Ligules usually over 3 mm long; plants of Western Nebraska
Agrostis exarata Trin.
37. Ligules often under 3 mm long, at least on the basal leaves; plants introduced in Eastern Nebraska
Alopecurus pratensis L.

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THE FLORISTIC COMPOSITION OF PRAIRIE STANDS IN SOUTHERN MICHIGAN

Paul W. Thompson

INTRODUCTION

Early settlers (Butler, 1947) tell of the colorful prairies that they found scattered throughout southern Michigan. However, because these prairies were excellent farm lands, they were soon plowed for agricultural purposes. Today only a few remnants remain of these interesting prairielands. Most of them are located in areas quite close to former prairies but are considerably reduced in size and consist of only a small part of the original acreage that existed.

METHODS

In 1969 the Michigan Natural Areas Council initiated a study of prairie remnants in Michigan to determine which areas were best suited for preservation. Those exhibiting the least disturbance, a wide assortment of prairie species, and fairly extensive coverage, were chosen for further consideration. From this select group, several stands were chosen for further study which were representative of wet, dry or intermediate site conditions. Later this rating was verified by comparison with selected indicator species (Curtis, 1959). The study tracts selected are scattered throughout southern Michigan within the natural range of former prairies in Lower Michigan (Fig. 1).

During the period 1971-74 each area was visited periodically during the growing season - spring, early summer and late summer. The species of plants found in each tract were cataloged and a floristic listing was compiled (Table 3). Classification of the soil series for each tract was made by soil scientists from the Soil Conservation Service (see acknowledgements).

DESCRIPTION OF STUDY TRACTS

A brief discussion of the various tracts is given below:

Indian Bowl Prairie

This prairie, located at Berrien Springs, lies on a flat alluvial plain between a very strong moraine and the St. Joseph River. The entire area is moist and is bisected by several cold streams which originate at the base of the adjoining moraine. Although the area is relatively flat, small elevations that exist along stream courses vary in moisture conditions which are reflected by the composition and richness of the vegetation (Medley, 1972). Large areas are dominated by Indian grass (*Sorghastrum nutans*); some are dominated by sedges.

It is of interest that queen-of-the-prairie (*Filipendula rubra*), a rare plant in Michigan, is quite common at this location. Wolf Prairie, an early historical prairie, was located at Berrien Springs.

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Table 1: Character and Location of Prairie Stands

Prairie Name	Symbol[c]	Type	Soil Series	Location
Indian Bowl	I	Wet	Griffin	Berrien Spr; St. Joseph River.
Ann Arbor	AA	Wet	Griffin	Ann Arbor. E. edge-Huron River.
Jackson	J	Wet	Brookston	Jackson(S.W.) Park St. at RR.
Windsor[a]	W	Wet-mesic	Granby	2 mi. S. of Windsor, Canada.
Otter Creek[b]	O	Wet-mesic	Selfridge	4 mi. S. of Monroe, betw. RR line.
Algonac	A	Wet-mesic	Gilford-Berrien	Algonac St. Pk., St. Clair River.
Sturgis[b]	S	Mesic	Fox	4 mi. W. of Sturgis,betw. US-12 & RR.
Fairfax[b]	F	Mesic	Conover	W. edge Fairfax;betw. Hwy 86 & RR.
Bertrand[b]	B	Dry-mesic	Spinks	RR at Betrand; 3 mi. S. of Niles.
Newaygo	N	Dry	Sparta	Appr. 5 mi. east of Newaygo.

a. Canadian prairie just east of Detroit, Michigan; included for comparison with other Michigan prairies in this area.

b. Strip prairie stand bordering railroad.

c. Symbols used for identification of prairie stands on map and for column headings in Table 3.

Table 2: Distribution of Groups In Prairie Flora

Family Group	No. of spp.
Composites	98
Grasses	39
Legumes	34
Sedges; etc.	23
Roses	18
Figworts	18
Mints	17
Umbels	14
Milkweeds	13
Lilies	11
Pinks	10
Crowfoots	10
Orchids	9

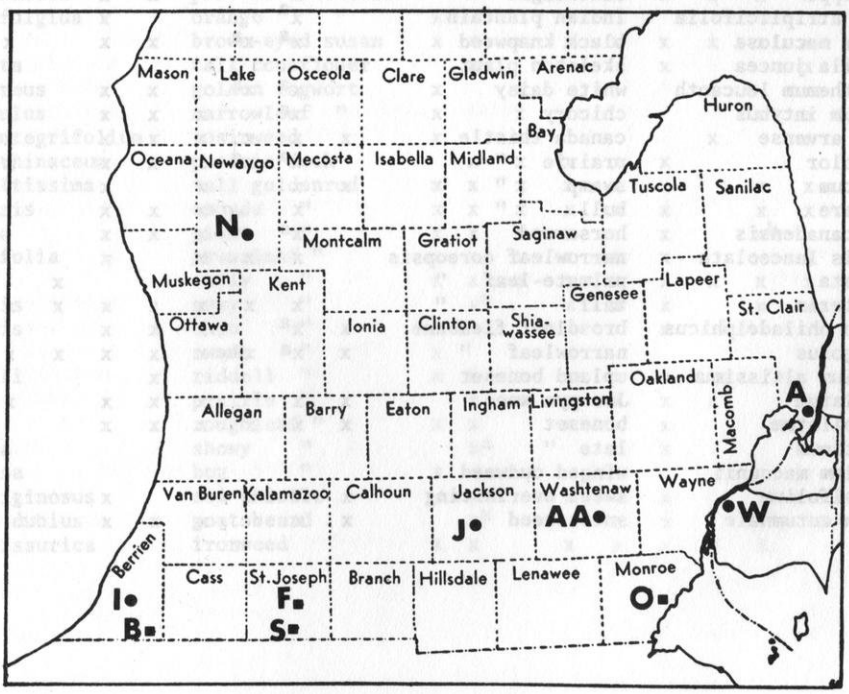

Fig. 1. Sites studied in Michigan.

Table 3: Floristic Composition of Michigan Prairies

Composites	Prairie Stands:[c]	I	AA	J	W	O	A	S	F	B	N
Achillea millefolium	yarrow	x	x[a]	x[a]	x	x	x	x	x	x	x
Actinomeris alternifolia	wingstem	x									
Ambrosia artemisiifolia	c. ragweed		x[a]	x	x	x	x	x			x
A. psilostachya	western "										x
Antennaria neglecta	1-vein pussytoes						x		x	x	x
A. plantaginifolia	3-vein "			x		x		x			x
Artemisia caudata	cancer root									x	x
Aster azureus	azure aster				x		x		x	x	x
A. dumosus	strict "	x									
A. ericoides	heath "		x[a]		x	x	x				x
A. junciformis	bog "	x									
A. laevis	smooth "	x	x	x	x	x	x	x	x	x	
A. lateriflorus	calico "	x	x		x						
A. lucidulus	glossyleaf "	x	x				x				
A. macrophyllus	largeleaf "		x[a]				x				
A. novae-angliae	new england "	x	x	x	x	x[b]	x		x[b]		
A. pilosus	hairy "	x	x	x	x	x	x	x	x	x	x
A. prealtus	willow "	x									
A. ptarmicoides	stiff "										x
A. puniceus	redstem "	x	x				x				
A. sagittifolius	arrowleaf "	x	x		x		x		x	x	
A. sericeus	silky "										x
A. simplex	panicle "	x	x		x	x	x				x[b]
A. umbellatus	flat-top "	x	x	x	x	x	x		x		
Bidens spp.	sticktight		x			x	x				
Cacalia atriplicifolia	Indian plantain		x[a]				x			x	x
Centauea maculosa	black knapweed		x[a]	x[a]		x	x		x		x
Chondrilla juncea	skeleton plant										x
Chrysanthemum leucanth	white daisy		x[a]	x[a]		x	x			x	
Cichorium intybus	chicory		x[a]		x	x	x				
Cirsium arvense	canada thistle	x	x	x	x	x	x		x		
C. discolor	prairie "		x[a]	x[a]	x	x	x		x	x	
C. muticum	swamp "	x	x		x		x				
C. vulgare	bull "		x		x	x	x			x	
Conyza canadensis	horseweed		x[a]		x	x	x			x	x
Coreopsis lanceolata	narrowleaf coreopsis		x	x	x		x			x	x
C. palmata	palmate-leaf "							x		x	
C. tripteris	tall "		x	x	x	x	x	x	x	x	
Erigeron philadelphicus	broadleaf fleabane	x	x[a]		x	x	x				
E. strigosus	narrowleaf "	x	x[a]	x[a]	x	x	x	x	x	x	x
Eupatorium altissimum	upland boneset					x					
E. maculatum	Joe pye weed	x	x		x	x	x		x		
E. perfoliatum	boneset	x	x	x	x	x	x				
E. serotinum	late "									x	
Gnaphalium macounii	winged cudweed										x
G. obtusifolium	sweet everlasting	x		x			x				x
Helenium autumnale	sneezeweed	x	x		x	x	x				

	Prairie Stands:	I	AA	J	W	O	A	S	F	B	N
Helianthus decapetalus	thinleaf sunflower			x		x					
H. divaricatus	woodland "		x[a]		x		x			x	x
H. giganteus	giant "	x	x	x	x	x	x				
H. grosseserratus	largetooth "	x	x	x	x	x	x				
H. laetiflorus	showy "							x			x
H. maximiliani	maximilian "	x	x			x	x				
H. mollis	hairy "			x[a]							
H. occidentalis	nakedstem "							x	x	x	x
H. strumosus	paleleaf "		x				x				
H. tuberosus	Jerusalem artichoke		x				x				
Heliopsis helianthoides	ox-eye	x	x				x				
Hieracium aurantiacum	tawny hawkweed						x				x
H. canadense	canada "						x		x		
H. florentinum	yellow "									x	x
H. longipilum	longhair "								x		x
H. scabrum	rough "						x				
H. venosum	smooth "			x			x				
Inula helenium	elecampane						x				
Krigia sp.	dwarf dandelion				x						x
Kuhnia eupatorioides	false boneset									x	x
Lactuca biennis	blue lettuce	x	x		x		x			x	
L. canadensis	yellow "	x	x	x	x	x	x	x	x	x	x
Liatris aspera	stiff blazing star		x[a]			x	x			x	x
L. cylindacea	cylindric " "										x
L. spicata	spiked " "	x			x		x				
Prenanthes alba	lion paw		x		x		x				
P. racemosa	hairy lion paw	x	x	x	x		x				
Ratibida pinnata	prairie coneflower		x	x	x	x	x	x	x	x	
Rudbeckia fulgida	orange "	x									
R. hirta	brown-eyed susan	x	x	x	x	x	x	x	x	x	x
R. laciniata	tall coneflower		x				x			x	
Senecio aureus	golden ragwort	x		x							
S. pauperculus	narrowleaf "	x		x					x	x	x
Silphium integrifolium	rosinweed	x		x				x		x	
S. terebinthinaceum	prairie dock		x	x	x	x	x				
Solidago altissima	tall goldenrod	x	x	x	x	x	x		x	x	
S. canadensis	canada "	x	x	x	x	x	x		x	x	x
S. gigantea	giant "	x	x	x	x		x		x[b]		
S. graminifolia	grassleaf "	x	x	x	x	x	x				
S. juncea	early "	x	x	x	x	x	x	x	x	x	x
S. nemoralis	gray "		x[a]		x	x	x		x	x	x
S. ohioensis	ohio "						x				
S. patula	swamp "	x									
S. riddellii	riddell "	x	x	x	x	x	x				
S. rigida	prairie "		x	x	x	x	x	x		x	x
S. rugosa	roughleaf "	x	x		x		x				
S. speciosa	showy "		x[a]				x				x
S. uliginosa	bog "	x									
Sonchus uliginosus	sow thistle		x		x		x				
Tragopogon dubius	goatsbeard		x[a]			x	x				x
Vernonia missurica	ironweed	x	x		x	x	x	x	x		

	Prairie Stands:	I	AA	J	W	O	A	S	F	B	N
Legumes											
Amorpha canescens	leadplant							x		x	
A. fruticosa	false indigo		x[a]								
Amphicarpa bracteata	hog peanut	x	x		x	x	x			x	
Apios americana	wild bean	x	x	x	x	x	x			x	
Baptisia leucantha	white indigo								x		
B. tinctoria	yellow "				x		x				
Cassia hebecarpa	partridge pea	x									
Crotalaria sagittalis	rattlebox										x
Desmodium canadense	canada ticktrefoil	x	x	x	x	x	x		x	x	x
D. ciliare	obtuse "						x				
D. cuspidatum	sharpleaf "		x				x				
D. dillenii	dillen "				x		x			x	
D. glutinosum	branched "		x[a]				x				x
D. illinoense	illinois "		x[a]				x	x	x	x	
D. marilandicum	small-leaf "								x	x	
D. paniculatum	panicle "	x	x				x				x
Lathyrus ochroleucus	cream pea						x		x		
L. palustris	marsh "	x			x	x	x				
Lespedeza capitata	narrowleaf bush clover		x[a]		x	x	x		x	x	x
L. hirta	roundleaf " "						x		x		x
L. procumbens	creeping " "		x[a]				x			x	
Lupinus perennis	lupine						x	x		x	x
Medicago sativa	alfalfa		x[a]	x[a]	x	x		x		x	
Melilotus albus	white sweet clover	x	x[a]	x[a]	x	x	x	x	x	x	x
M. officinalis	yellow " "		x	x		x	x				
Strophostyles helvola	trailing bean				x	x					
Tephrosia virginiana	goatrue										x
Trifolium agrarium	yellow hop clover						x				
T. hybridum	pink clover		x	x	x	x	x				
T. pratense	red "		x[a]	x[a]	x	x	x			x	
T. repens	white "		x[a]		x		x				
Vicia cracca	carolina vetch		x				x				
V. villosa	hairy "					x					x
V. sativa	vetch					x					
Lilies											
Aletris farinosa	colic root				x		x				
Allium canadense	canada onion	x				x					
A. cernuum	nodding "	x					x				
Asparagus officinalis	asparagus				x	x	x			x	
Lilium michiganense	michigan lily	x			x		x	x			
Polygonatum pubescens	solomon seal		x		x	x				x	
P. canaliculatum	giant" "	x				x		x		x	
Smilacina racemosa	false " "	x			x			x		x	
S. stellata	starry" "	x						x	x	x	
Smilax ecirrata	carrion flower				x	x	x			x	
Zygadenus glaucus	white camass	x			x						

	Prairie Stands:	I	AA	J	W	O	A	S	F	B	N
Orchids											
Cypripedium calceolus	yellow ladyslipper	x		x							
C. candidum	white "	x									
C. reginae	showy "	x									
Habenaria hyperborea	green bog orchid	x									
H. lacera	ragged fringed "					x					
H. psycodes	purple fringed "	x									
Spiranthes cernua	nodding ladies tresses	x				x	x				
S. lacera	slender " "										x
S. romanzoffiana	bog " "	x									
Pinks											
Arenaria stricta	stiff sandwort										x
Cerastium arvense	large chickweed										x
Dianthus armeria	deptford pink					x	x			x	
Lychnis alba	evening lychnis			x[a]			x			x	x
L. coronaria	mullein pink									x	
Saponaria officinalis	bouncing bet			x[b]		x			x	x	x
Silene antirrhina	sleepy catchfly					x		x		x	x
S. cucubalus	bladder campion			x[a]		x					
S. noctiflora	night catchfly							x			
Stellaria longifolia	longleaf chickweed	x		x							
Crowfoots											
Anemone canadensis	canada anemone	x	x	x	x	x	x				x
A. cylindrica	longfruit "				x		x	x	x	x	x
A. virginiana	thimbleweed	x		x	x		x				
Caltha palustris	marsh marigold	x	x				x				
Clematis virginiana	virgin bower		x			x					x
Ranunculus abortivus	smallfruit crowfoot	x					x				
R. fascicularis	prairie crowfoot									x	x
R. hispidus	hairy buttercup	x		x							
R. septentrionalis	swamp "					x					
Thalictrum dasycarpum	tall meadowrue	x	x	x	x	x	x	x		x	
Roses											
Agrimonia gryposepala	agrimony	x			x	x	x				
Amelanchier spicata	small shadbush										x
Filipendula rubra	queen-of-the-prairie	x									
Fragaria virginiana	wild strawberry	x	x	x	x	x	x	x	x	x	x
Geum alleppicum	yellow avens						x				x
G. canadensis	canada "						x				
G. laciniatum	rough "					x					
G. triflorum	prairie "										x
G. virginianum	swamp "					x					
Potentilla anserina	silverweed				x	x	x				
P. argentea	silvery cinquefoil						x				
P. arguta	prairie "			x[a]	x						x
P. canadensis	canada "	x		x		x	x			x	x
P. recta	meadow "			x[a]		x	x		x	x	x
Rosa carolina	field rose			x[a]		x	x		x	x	x
R. palustris	swamp "	x				x	x		x		
Spiraea alba	meadowsweet	x			x	x	x				x
S. tomentosa	hardhack				x		x				

	Prairie Stands:	I	AA	J	W	O	A	S	F	B	N
Umbels											
Angelica atropurpurea	giant angelica	x	x	x							
Berula pusilla	cutleaf water parsnip	x									
Cicuta bulbifera	bulblet hemlock	x	x				x				
C. maculata	water "	x	x		x	x	x				
Conium maculatum	poison "	x				x					
Daucus carota	wild carrot	x	x[a]	x[a]	x	x	x	x	x	x	x
Eryngium yuccifolium	false yucca							x			
Heracleum lanatum	cow parsnip	x	x				x	x			
Oxypolis rigidior	cowbane	x	x	x	x		x[b]				
Pastinacea sativa	wild parsnip	x	x	x	x		x			x	
Sium suave	water "		x		x						
Taenidia integerrima	bank "				x		x	x			
Thaspium barbinode	meadow "	x						x	x	x	
Zizia aurea	golden alexander	x	x	x				x		x	
Milkweeds											
Acerates hirtella	florida milkweed				x						
A. viridiflora	green "				x						x
Asclepias amplexicaulis	prairie "							x			x
A. exaltata	polkleaf "	x					x				
A. incarnata	swamp "	x	x	x	x	x[b]	x[b]				
A. purpurascens	purple "						x	x			
A. sullivantii	sullivant "				x	x[b]	x[b]				
A. syriaca	common "	x	x	x	x	x	x	x	x	x	x
A. tuberosa	orange "	x	x[a]		x	x	x	x	x	x	x
A. verticillata	whorled "			x[a]				x		x	x
Apocynum androsaeifolium	dogbane		x		x	x	x	x			
A. cannabinum	stemmed Ind. plantain	x	x	x	x	x	x	x			x
A. sibiricum	sessile " "	x	x		x		x			x	
Mints											
Blephilia ciliata	downy blephilia										x
Lycopus americana	cutleaf horehound	x			x	x	x				
L. uniflorus	tuber "				x						
Mentha arvensis	field mint	x			x		x				
M. piperata	peppermint	x									
M. spicata	spearmint	x									
Monarda fistulosa	wild bergamot	x	x	x	x	x	x	x	x	x	x
M. punctata	horsemint										x
Prunella vulgaris	self heal	x	x	x	x	x	x				
Pycnanthemum virg.	mt. mint	x	x	x	x	x	x				
Satureja vulgaris	wild basil									x	
Scutellaria galericulata	skullcap	x			x		x				
S. lateriflora	mad dog skullcap	x					x				
Stachys hyssopifolia	narrowleaf hedge nettle										x
S. palustris	marsh " "	x			x						
S. tenuifolia	smooth " "	x									x
Teucrium canadense	wood sage				x		x				x

		Prairie Stands:	I	AA	J	W	O	A	S	F	B	N
	Sedges, Rushes, etc.											
Sagittaria latifolia	arrowhead		x									
Carex pensylvanica[d]	pennsylvania sedge								x	x	x	x
Scleria triglomerata	nut rush											x
Cyperus filiculmis	slender cyperus											x
Eleocharis erythropoda	spike rush		x		x							
Bulbostylis capillaris	hair sedge											x
Scirpus atrovirens	green rush		x		x		x	x				
S. cyperinus	woolgrass				x		x	x				
S. validus	great bulrush		x				x					
Juncus dudleyi	dudley rush				x							
J. greenei	greene "											x
J. torreyi	torry "			x								
Luzulu multiflora	woodrush		x		x					x		x
	Grasses											
Agrostis gigantea	redtop		x		x	x	x	x	x			x
A. hyemalis	ticklegrass											x
Andropogon gerardi	big bluestem		x	x	x	x	x	x	x	x	x	x
A. scoparius	little "			x[a]	x[a]	x	x	x	x	x	x	x
Aristida purpurascens	3-awn grass											x
Bromus inermis	smooth brome		x		x[a]		x	x	x	x		
B. secalinus	chess											x
B. tectorum	downy chess									x		
Calamagrostis canadensis	blue joint		x	x	x	x	x	x				
Dactylis glomerata	orchard grass					x	x					
Danthonia spicata	poverty grass											x
Elymus canadensis	canada rye		x					x				
E. virginicus	virginia rye		x		x		x					
Eragrostis pectinecea	tufted love grass											x
E. spectabilis	purple " "					x	x				x	
Festuca ovina	sheep fescue											x
Glyceria striata	manna grass											x[b]
Hierochloe odorata	sweetgrass					x						
Koeleria cristata	junegrass											x
Leptoloma cognatum	witchgrass						x					x
Muhlenbergia spp.	muhlygrass		x	x			x					
Panicum capillare	tumblegrass											x
P. commonsianum	panic grass											x
P. depauperatum	starved panic grass											x
P. implicatum	tenn. " "				x[a]		x				x	x
P. oligosanthes	scribner " "											x
P. virgatum	switchgrass				x[a]	x	x			x		x
Phalaris arundinacea	reed canary grass		x									
Phleum pratense	timothy						x				x	
Phragmites australis	giantreed		x				x	x				
Poa compressa	canada blue grass		x		x		x	x	x	x	x	x
Puccinellia distans	alkali grass					x						
Sorghastrum nutans	Indian grass		x	x	x	x	x	x	x	x	x	x
Spartina pectinata	prairie cordgrass		x	x		x		x		x[b]		x[b]
Sporobolus cryptandrus	sand dropseed					x						x
S. vaginiflorus	sheathed dropseed						x					
Stipa spartea	needle grass											x
Tridens flavus	purpletop						x				x	
Triodia flavus	tall redtop						x					

	Prairie Stands:	I	AA	J	W	O	A	S	F	B	N
Violets											
Viola affinis	LeConte violet	x							x		
V. cucullata	bog "	x									
V. papilionacea	butterfly "	x									
V. pedata	birdfoot "										x
V. sagittata	arrowleaf "				x				x		x
V. septentrionalis	bearded blue violet							x	x		
V. sororia	hairy wood "									x	
Figworts											
Antirrhinum majus	sm. snapdragon		x[a]	x[a]		x		x			
Aureolaria flava	downy f. foxglove				x						x
A. pedicularia	clammy " "										x
A. virginica	smooth " "		x		x						
Castilleja coccinea	paintbrush	x									
Chelone glabra	turtlehead	x	x		x		x				
Gerardia purpurea	purple gerardia	x			x	x	x				
G. tenuifolia	slenderleaf "				x		x				
Linaria canadensis	blue toadflax										x
L. vulgaris	butter & eggs		x[a]	x[a]	x	x				x	x[b]
Mimulus ringens	monkeyflower				x		x				
Pedicularis lanceolata	swamp betony	x	x	x	x		x				x[b]
Pentstemon digitalis	foxglove beard tongue					x					x
P. hirsutus	hairy " "			x	x					x	x
Scrophularia lanceolata	narrowleaf figwort					x				x	
S. marilandica	broadleaf "		x								
Verbascum thapsus	c. mullein			x[a]		x		x	x	x	x
Veronicastrum virg.	culver root	x	x	x	x	x	x	x	x	x[b]	x[b]
Other Species[e]											
Equisetum arvense	field horsetail	x	x		x	x					
E. fluviatile	water "	x									
E. hiemale	tall scouring rush						x				
E. laevigatum	smooth " "	x				x	x				
Onoclea sensibilis	sensitive fern	x		x	x					x	
Osmunda regalis	royal "	x									
Pteridium aquilinum	bracken "				x		x		x	x	x
Thelypteris palustris	marsh "	x	x		x	x	x				
Typha latifolia	broadleaf cattail	x	x	x		x	x				
T. angustifolia	narrowleaf "	x				x					
Alisma plantago-aq.	water plantain					x	x				
Tradescantia ohioensis	spiderwort	x		x	x	x	x	x		x	
Dioscorea villosa	wild yam	x		x			x				
Hypoxis hirsuta	yellow stargrass	x		x	x	x	x				
Iris virginica	blue iris	x	x			x	x				
Sisyrinchium albidum	pale blue-eyed grass	x		x		x					
A. angustifolium	stout " " "			x							
Boehmeria cylindrica	false nettle	x				x					
Comandra richardsiana	false toadflax				x			x	x	x	x
Rumex crispus	curly dock					x	x				
R. acetosella	sour grass					x	x				
Polygonella articulata	jointweed										x
Polygonum convolvulus	black bindweed					x	x			x	
P. douglasii	douglas knotgrass										x

	Prairie Stands:	I	AA	J	W	O	A	S	F	B	N
Oxybaphus nyctagineus	umbrellawort			x		x	x			x	x
Arabis lyrata	lyreleaf mustard										x
Barbarea vulgaris	yellow rocket			x		x		x	x	x	
Berteroa incana	hoary alyssum										x
Cardamine bulbosa	bitter cress	x	x								
Lepedium campestre	field cress	x		x				x	x		
Penthorum sedoides	ditch stonecrop				x	x					
Heuchera hirsuticaulis	alumroot	x		x		x	x	x			x[b]
Parnassus glauca	grass-of-parnassus	x	x				x				
Saxifraga pensylvanica	swamp saxifrage	x	x								x[b]
Oxalis europaea	yellow wood sorrel				x	x					
Geranium maculatum	wild geranium	x	x	x	x		x	x	x	x	x
Linum sulcatum	prairie flax										x
Polygala polygama	purple milkwort										x
P. sanguinea	common "				x		x				
P. seneca	seneca snakeroot	x									
P. verticillata	whorled milkwort				x	x	x				
Croton glandulosus	croton									x	
Euphorbia corollata	flowering spurge	x	x	x	x	x	x	x	x	x	x
E. cyparissias	cypress spurge									x	x
E. dentata	toothed "				x	x				x	
E. preslii	nodding "			x		x				x	
Celastrus scandens	bittersweet		x[a]			x				x	
Impatiens biflora	jewelweed	x	x		x		x				
Vitis riparia	wild grape	x	x	x	x	x	x			x	
Hypericum majus	large St. Johnswort		x				x				
H. mutilum	smallflower " "	x									
H. perforatum	common " "	x	x	x	x	x	x	x	x		x
Helianthemum canadense	rockrose		x				x		x		x
Lechea villosa	pinweed				x						x
Opuntia compressa	prickly pear cactus										x
Lythrum alatum	prairie loosestrife	x	x	x	x	x	x				
L. salicaria	large "		x				x				
Ludwigia alternifolia	seedbox				x						
L. polycarpa	false loosestrife					x					
Epilobium adenocaulon	n. willowherb	x	x								
Oenothera spp.	evening primrose	x			x	x	x		x	x	x
Gaura biennis	gaura				x	x					
Lysimachia terrestris	swamp candle					x					
Steironema ciliatum	fringed loosestrife	x	x		x		x			x	
S. lanceolatum	lanceleaf "									x	x
S. quadriflorum	whorled "	x	x		x		x				
Naumburgia thyrsiflora	tufted "				x						
Gentiana andrewsii	bottle gentian	x			x	x	x				x[b]
G. crinita	fringed "	x			x						
Centaurium pulchellum	centaury				x						
Convolvulus arvensis	field bindweed	x				x					x
C. sepium	hedge "	x	x		x	x	x	x			
Phlox pilosa	prairie phlox		x	x	x		x	x		x	x[b]
Polemonium reptans	greek valerian	x									
Lithospermum canescens	hoary puccoon				x			x	x	x	x
Verbena bracteata	bracted vervain										x
V. hastata	common "	x		x	x		x				
V. stricta	hoary "				x						x
V. urticifolia	white "	x			x	x	x		x		

	Prairie Stands:	I	AA	J	W	O	A	S	F	B	N
Physalis heterophylla	hairy groundcherry				x	x				x	x
Solanum dulcamara	bittersweet nightshade	x	x		x		x			x	
Houstonia longifolia	longleaf bluet										x
Galium aparine	early bedstraw					x				x	
G. asprellum	rough "	x	x			x	x				
G. boreale	northern "		x		x		x			x	
G. circaezans	wild licorice									x	
G. pilosum	hairy bedstraw									x	x
G. triflorum	sweetscent "	x			x		x				
Valeriana ciliata	valerian	x									
Dipsacus sylvestris	teasel					x					
Echinocystis lobata	w. cucumber		x				x				
Campanula aparinoides	marsh bellflower	x	x								
Spectularia perfoliata	venus looking glass									x	x
Lobelia cardinalis	cardinal flower	x			x						
L. inflata	Indian tobacco						x				
L. kalmii	Kalm lobelia	x									
L. siphilitica	giant "	x									
L. spicata	pale "			x	x	x	x				x
Grand Total: 409 spp.	Column Total:	178	141	110	164	161	201	67	73	117	152

a. Found on higher ground.
b. Growing in low habitat.
c. For locations represented by symbols at head of columns, see Table 1.
d. Sedges found at Indian Bowl prairie (I) as follows: Carex bebbii, C. granularis, C. hystricina, C. interior, C. leptalea, C. prairea (also at S), C. sterilis, C. stipata, C. stricta, and C. tetanica (also at S).
e. Interesting species also found at Otter Creek prairie stand (O) are: Ammania teres, Epilobium hirsutum, Hibiscus trionum, Ludwigia palustris and Proserpinacea palustris.

Ann Arbor Wet Prairie

An excellent wet prairie exists along the floodplain of the Huron River on the eastern outskirts of Ann Arbor. The tract of relatively flat land lies between the river and the Penn Central Railroad. Mesic prairie species also exist on the borders of the tract along the higher ground adjacent to the railroad and the adjoining woods. The vegetation of the area has been described earlier (Thompson, 1968).

Jackson Prairie

Located in the southwestern part of Jackson, Michigan, this stand occupies the low ground, between Park Street and the railroad, where it surrounds a small marshy pond. Although only several acres in size, it possesses an interesting assortment of prairie species. A number of mesic species extend along the higher ground bordering the railroad.

Windsor Prairie

This prairie (Rogers, 1966), located a short distance south of Windsor, Ontario, in Canada, is centered around Ojibway Park close to the Detroit River. It is located on a portion of the old lake plain, is relatively flat, and shows quite a range in vegetational patterns.

It is one of the best remaining prairie stands, covering over 1.6 km^2, and represents the type of prairie existing along the Detroit River locality at the time of the early settlers. Although located in Canada, it is included in the study areas for comparison with less extensive prairie stands found along the Detroit and St. Clair Rivers.

Algonac Prairie

Covering a portion of the old, sandy, glacial lake plain about 1.6 km north of Algonac, Michigan, this prairie lies along the St. Clair River in Algonac State Park. The study area consists of four separate tracts totaling 14.2 ha under preservation by the Park (Thompson, 1972). Changes in elevation are slight but the water table is high.

Newaygo Dry Prairie

This dry prairie area consists of a number of local tracts confined to Sparta loam where open prairie stands occur. Known to the earliest settlers in this region, the vegetation has been described by Veatch (1928) and by Hauser (1953). It is the most northern of Michigan prairies, located a few km east of Newaygo.

Of particular interest is the occurrence of the prairie avens (*Geum triflorum*) which is very rare in the state. Of the study areas, this is the only prairie which contains the prickly pear cactus (*Opuntia compressa*). A large portion of the area is essentially flat but in a few low local depressions moister habitats occur.

Strip Prairies

Scharrer's studies (1972) in southwestern Michigan revealed a number of prairie remnants that exist in this part of the state along railroad right-of-ways. The best of these usually occurred where roadways paralleled the railroad so that larger areas of undisturbed vegetation existed. Several of these strip prairies were included in this study as follows:

Fairfax -

Situated just west of Fairfax, this tract extends between the railroad and Hwy. 86 for a distance of 2 km. Of interest are false yucca (*Eryngium yuccifolium*) and white wild indigo (*Baptisia leucantha*).

Bertrand -

This tract extends along the north-south railroad running through the town of Bertrand. The best portion of this very sandy stand starts at the Indiana state line and runs north for a distance of 2 km. The historical Portage Prairie extended into this area.

Otter Creek -

A broad strip of land, 30 m wide, separates two sets of tracks along the Penn Central Railroad (1.5 km west of I-75) south of South Otter Creek Road, several km south of Monroe, Michigan. This narrow strip, and a second 15 m strip, extending about 3 km south to Cousino Road, contain an excellent assortment of plants. With a range of approximately 3 m in elevation, the terrain is quite variable with a number of low wet areas and higher ground. There are several excellent stands of litle bluestem (*Andropogon scoparius*), big bluestem (*A. gerardi*) and prairie cordgrass (*Spartina pectinata*) existing respectively at high, intermediate and low levels of terrain. Several excellent stands of *Asclepias sullivantii* are also found here.

Sturgis Prairie -

Located 5 km west of Sturgis, this tract lies between the railroad and Hwy. US-12 just east of the point where the highway crosses the railroad. Of the various strip prairies, this tract exhibits the densest vegetative cover.

FLORISTIC COMPOSITION OF MICHIGAN PRAIRIE STANDS

The species found in the 10 study tracts were compiled (Table 3) to illustrate the floristic composition of these prairie stands. Nomenclarure follows Voss (1972) for the monocots, and Gleason (1952) for the dicots. This listing includes a total of 409 species of which nearly 40% (161 species) occur in at least four of the prairies studied; 112 species (25%) occur in five or more stands and 75 species are found in six or more of the 10 prairies. Fortyseven of these 75 species are included by Curtis (1959) as species prevalent in Wisconsin prairies showing that the more common prairie species in Michigan are similar to those of the prairies farther west. Further similarity to other prairie areas is indicated by 250 species of prairie plants included in Swink's (1969) *Plants of the Chicago Region.* Over 200 of these species are represented in the above floristic listing.

The greatest number of species are the composites with 98 species, followed by the grass family with 39 species, legumes (34 species) and sedges (23 species). The mints, roses and figworts have 17 to 18 species each (Table 2). The greatest number of species (201) is found at the Algonac Prairie; 178 species were cataloged at the Indian Bowl Prairie. Between 141-164 species occur individually at the Ann Arbor, Windsor, Otter Creek, and Newaygo sites with lower numbers at the Bertrand (117 species) and the Jackson (110 species) stands. The smallest number of species (67 and 73 respectively) is found at the Sturgis and Fairfax sites. Both of these tracts are strip prairies, the number of species reflect both the smaller size of the areas involved and the lack of terrain variety.

An examination of the floristic data on the Algonac, Ann Arbor and Otter Creek Prairies shows these areas to be very similar to the Windsor Prairie, suggesting that these represent a typical composition for stands in southeastern Michigan.

A few scattered shrubs were found in the above study areas. Only a few of these in the rose family were included in the listing. Shrubs encountered in low areas included red-osier dogwood (*Cornus stolonifera*), silky dogwood (*Cornus purpursi*), bog birch (*Betula pumila*), poison sumac (*Rhus vernix*), nannyberry (*Viburnum lentago*) and willows (*Salix* sp.). In drier tracts prairie willow (*Salix humilis*), hazel (*Corylus americana*), dwarf oak (*Quercus prinoides*), gray dogwood (*Cornus racemosa*), New Jersey tea (*Ceanothus americanus*) and smooth sumac (*Rhus glabra*) were among those found.

The Newaygo Prairie is the most distinctive in that it contains 29 species not found in any of the other study areas. It's dry character is indicated by all of the six possible indicator species for dry sites listed by Curtis. Also, out of 31 prevalent dry prairie species which Curtis lists, 28 species are found at Newaygo; 20 such species occur at Bertrand (other sites have 13 or less). In contrast, the Indian Bowl Prairie, containing all of Curtis' 10 wet prairie indicator species and 34 of the 39 species listed as prevalent in Wisconsin wet prairies, exhibits its wet prairie character. For this classification the Windsor and Algonac Prairies show 33 species indicating that they possess excellent wet prairie habitats.

This study shows that the prairie stands in Michigan contain a large and an interesting assortment of plant species including many typical prairie species which would be worth preservation.

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ABSTRACT

Studies during the period 1971-74 were made of nine prairie stands in southern Michigan (one stand at Windsor, Ontario, Canada), selected to represent a range of ecological conditions. Based on data collected at different phases of the growing season, the floristic composition of these stands was determined in relation to site conditions such as location, soil series, and moisture conditions.

These data show that the common species of plants in these tracts are prairie species, many of which occur in Chicago area prairie stands and in Wisconsin prairies farther west. The character of the prairie stands varies with the habitat conditions of the different sites.

KEY WORDS

Floristics, prairie stands, Michigan, Ontario.

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VASCULAR FLORA OF BARNES AND STUTSMAN COUNTIES, NORTH DAKOTA

Carolyn S. Godfread and William T. Barker

INTRODUCTION

Barnes and Stutsman counties comprise an area of approximately six thousand square kilometers in east-central North Dakota. The western part of Stutsman County is within the Missouri Plateau. Eastern Stutsman County and Barnes County are within the Drift Prairie. The Missouri Escarpment trends south through the center of Stutsman County and forms the boundary between these two areas (see Fig. 1).

The Drift Prairie is a gently undulating plain laid down by glacial action. The resulting deposition, referred to as till, or drift, is composed of an unsorted mixture of clay, silt, pebbles and cobbles. Soils of the Drift Prairie are suitable for agriculture, as a result, most of the land is farmed. Within Barnes County, alone, 87% of the land is under cultivation according to the 1969 Census of Agriculture.

Major landforms in the Drift Prairie are the result of glacial processes. Occasional hills, or kames, rise above the surrounding plain. In addition to kames, several end moraines provide topographic relief. Throughout the Drift Prairie there are many small lakes and marshes.

In places the change from the Drift Prairie to the Missouri Coteau is abrupt (the coteau being the eastern edge of the Missouri Plateau). The coteau occupies most of western Stutsman County. This belt of hills marks the terminus of the Wisconsin ice sheet. The ice advanced up and over the pre-existing Missouri Escarpment and then underwent extensive stagnation. Melting of buried ice blocks produced closed depressions separated by moranic hills consisting mainly of till. Due to the rough topography, much of the land within the coteau remains in native vegetation.

Most of the depressions of the Coteau and Drift Prairie lack external drainage. The region is so young, geologically speaking, that stream drainage has not had time to develop. Water collects in depressions forming lakes and ponds.

The major streams that have developed occupy the channels formed by glacial meltwater. This is particularly evident when one considers the size of the Sheyenne River Valley in relation to the size of the small river that presently occupies it. The Sheyenne is in Barnes County while the James River flows through eastern Stutsman County.

Except for the gallery forests of the two rivers, the prevalent vegetation is grassland of a transitional type occupying a broad ecotone between the True Prairie of the Red River Valley and the Mixed Prairie of the Missouri Plateau (Whitman, 1963). In the transition zone, the species of the Mixed-Grass Prairie occupy the more mesic situations (Carpenter, 1940).

RELATION OF TOPOGRAPHY TO PLANT COMMUNITIES

The landscape of this transitional zone is characterized by rolling topography. The slopes form a drainage gradient from the well drained hilltops to standing water in depressions. Dix and Smeins (1966) in their study of the vegetation of Nelson County, North Dakota, found this drainage regime to be the most important environmental factor determining plant distribu-

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tion. In our study we have recognized their vegetational units as a basis for habitat description (see Fig. 2).

Steep slopes and hilltops lose much of their precipitation through run off. Such areas are designated as high prairie. Mid-prairie includes mid slopes and level areas where the available moisture approximates that received from precipitation. Low prairie is constituted by sites that receive more run off than they, in turn, loose. Meadows have relatively poor drainage and thus may have gravitational water remaining in the upper soil horizons for several weeks in the spring. Marshes have permanent water remaining throughout most summers but they may dry by August or September.

Each vegetation zone, from high prairie to marsh, is characterized by indicator species, which are simply those species most commonly found at that level.

HIGH PRAIRIE

High prairie is notable for the fact that relatively few forbs are numerous. The grasses are primarily those that characterize the mixed prairie to the west. *Calamovilfa longifolia* is found on sandy high prairie. *Agropyron smithii* and *Stipa comata* are also characteristic. Under these midheight grasses shorter grasses and carices develop such as *Bouteloua gracilis, Koeleria cristata, Carex eleocharis*, and *Carex filifolia*.

All but one of the forbs that seem limited to high prairie are species whose distributions lie within the plains region. Four reach their eastern limit in Stutsman County. *Potentilla concinna* and *Phlox hoodii* have not been found east of the coteau. *Astragalus gilviflorus* has been found as far east as the bluffs of the James River of Stutsman County. *Polygala alba* is present in eastern Stutsman County but has not been found in Barnes County. *Lomatium foeniculaceum* extends its distribution eastward to the Red River Valley. Others extend into Minnesota. Examples of that group are *Mammalaria vivipara, Lygodesmia juncea* and *Castilleja sessiliflora*.

MID-PRAIRIE

Other forbs, along with the grasses of the high prairie, are not restricted to that zone but are found on mid-slopes as well. In addition, the mid-prairie supports grasses not present on the high prairie such as *Bouteloua curtipendula* and *Andropogon scoparius*. Little bluestem forms conspicuous reddish colored patches on hillsides in late summer.

The mid-prairie supports many forbs. In early spring, north-facing slopes may appear covered with *Anemone patens. Draba nemorosa* is small, but abundant, as is the diminutive *Androsace occidentalis.*

In late May and early June *Viola pedatifida* appears here and there on high and mid-prairies. At the same time *Astragalus agrestis*, though one of the smaller legumes, is common and conspicuous. Other prominant forbs of late spring are *Geum triflorum, Senecio integerrimus* and *Penstemon albidus.*

Campanula rotundifolia is common in early summer, but occasional plants continue to flower until August. *Potentilla arguta* and *Anemone cylindrica* are less conspicuous but nevertheless characteristic of mid-prairie in early summer. *Lilium philadelphicum* provides the brightest touches of color and, while common on mid-prairie, it does range down into the low prairie. Among the other forbs of late June and early July are *Gaillardia aristata, Delphinium virescens, Echinacea angustifolia, Achillea millifolium* and *Ratibida columnifera.*

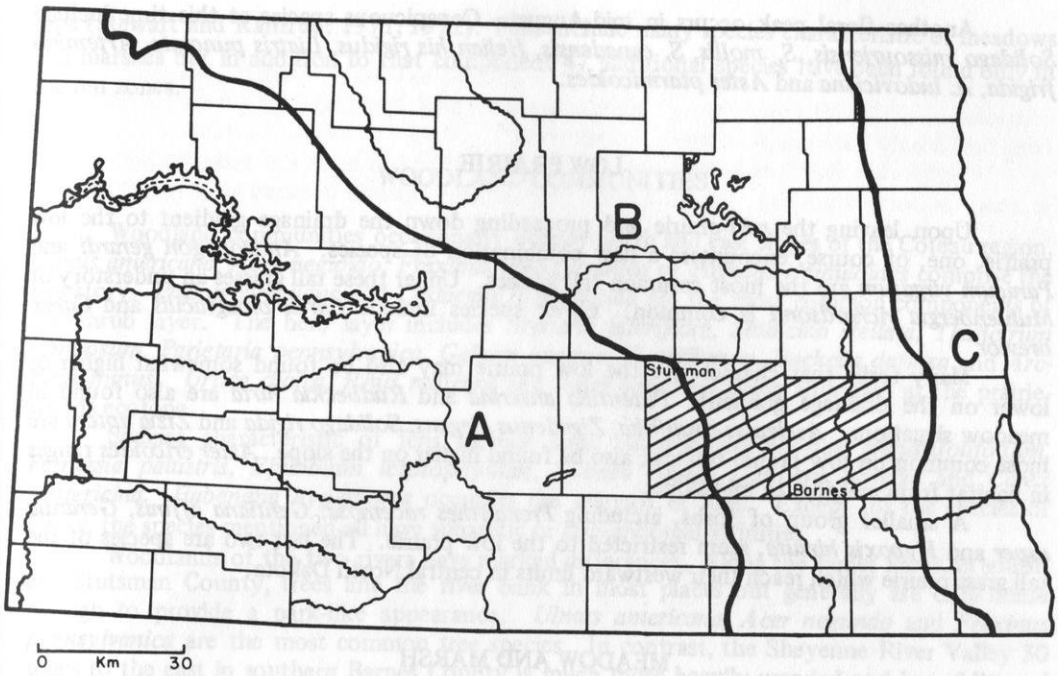

Fig. 1. Principal physiographic areas of North Dakota (modified from Omodt et al., 1968) A. Missouri Plateau, B. Drift Prairie, and C. Red River Valley.

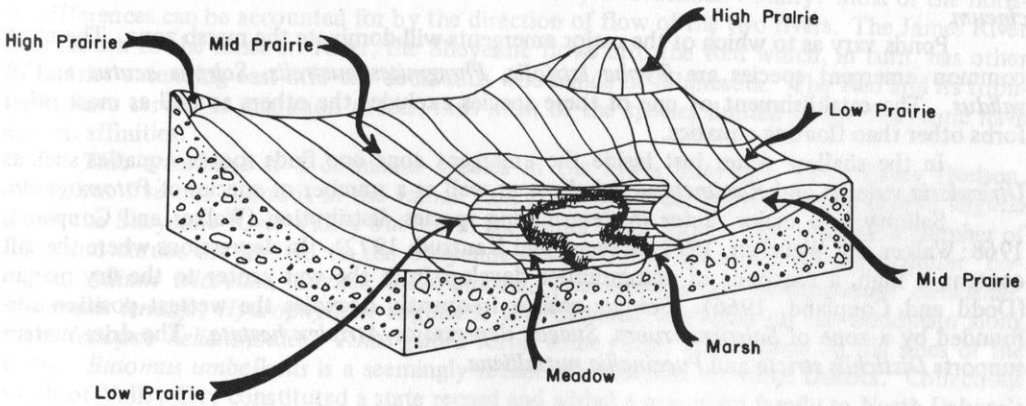

Fig. 2. Relief diagram of Missouri Coteau with associated plant communities.

Another floral peak occurs in mid-August. Conspicuous species at this time include *Solidago missouriensis, S. mollis, S. canadensis, Helianthis rigidus, Liatris punctata, Artemisia frigida, A. ludoviciana* and *Aster ptarmicoides.*

LOW PRAIRIE

Upon leaving the mid-prairie and proceeding down the drainage gradient to the low prairie, one, of course, encounters a new combination of species. *Andropogon gerardi* and *Panicum virgatum* are the most common tall grasses. Under these tall grasses an understory of *Muhlenbergia richardsonii* is common. *Carex* species include *Carex praegracilis* and *Carex brevior.*

Many forbs that characterize the low prairie may also be found somewhat higher or lower on the drainage gradient. *Potentilla anserina* and *Rudbeckia hirta* are also found in meadow situations. *Asclepias ovalifolia, Zigadenus elegans, Solidago rigida* and *Zizia aptera* are most common on low prairie but can also be found higher on the slope. *Aster ericoides* ranges in habitat from meadow to mid-slope.

A smaller group of forbs, including *Prenanthes racemosa, Gentiana affinis, Gerardia asper* and *Hypoxis hirsuta*, seem restricted to the low prairie. The last two are species of the tall grass prairie which reach their westward limits in central North Dakota.

MEADOW AND MARSH

Meadow situations are also characterized by a distinctive complement of grass and Carex species. *Calamagrostis inexpansa* is one of the most common. *Scolochloa festucea* often forms nearly pure stands in areas that are mowed. Other important grass species are *Glyceria grandis, Beckmannia syzigachne* and *Spartina pectinata. Juncus balticus* often extends up into the low prairie. *Carex lanuginosa* is also very common.

From July on, a number of forbs become conspicuous including *Mentha arvensis, Apocynum sibiricum, Stachys palustris, Lycopus asper, Verbena hastata* and *Polygonum coccineum.*

Ponds vary as to which of the major emergents will dominate the marsh zone. The most common emergent species are *Typha latifolia, Phragmites australis, Scirpus acutus* and *S. validus*. The establishment of one of these species excludes the others as well as most other forbs other than floating aquatics.

In the shallow water just inside the emergent zone one finds rooted aquatics such as *Utricularia vulgaris* and *Ranunculus flabellaris* as well as a number of species of *Potomogeton.*

Salinity is a major factor in determining species distribution (Walker and Coupland, 1968; Walker and Wehrhan, 1971; Stewart and Kantrud, 1972). In depressions where the salt content is high, a sequence of communities develop from the wet center to the dry margin (Dodd and Coupland, 1966). *Scirpus validus* frequently occupies the wettest position surrounded by a zone of *Salcornia rubra, Suaeda depressa* or *Atriplex hastata.* The drier margin supports *Distichlis stricta* and *Puccinellia nuttalliana.*

FEN

Occasional spring seepage areas occur on the hillsides bordering the river valleys and along the margins of ponds and lakes. The waters are alkaline so these areas can best be termed

fens (Stewart and Kantrud, 1971, 1972). Fens include many species characteristic of meadows and marshes but in addition to that component 47 additional species have been found only in the fen zones.

WOODLAND COMMUNITIES

Woodland communities occasionally occupy north and east slopes of the Coteau region. *Ulmus americana, Acer negundo, Fraxinus pennsylvanica* or *Populus tremuloides* comprise the overstory. *Prunus virginiana* and *Crataegus rotundifolia* are the most common components of the shrub layer. The herb layer includes *Arenaria lateriflora, Smilicina stellata, Thalictrum venulosum, Parietaria pennsylvanica, Galium aparine, G. triflorum, Hackelia deflexa* and *Arctium minus. Urtica dioica, Rhus radicans* and *Aster laevis* are often abundant at the prairie-woods ecotone.

Species characteristic of fens include *Salix candida, Eriophorum angustifolifolium, Parnassia palustris, Epilobium letptophyllum, Lobelia kalmii, Gentiana procera* and *Carex hystericina. Habenaria hyperborea* occupies the margins of fens. Except for the species of *Carex,* the species mentioned all have subarctic or circumboreal affinities.

Woodlands of the two rivers have marked differences. Along the James River, in southern Stutsman County, trees line the river bank in most places but generally are only dense enough to provide a park-like appearance. *Ulmus americana, Acer negundo* and *Fraxinus pennsylvanica* are the most common tree species. In contrast, the Sheyenne River Valley 30 miles to the east in southern Barnes County is much more heavily wooded and has additional tree species.

FLORISTIC COMPARISON OF RIVER VALLEYS

An interesting contrast between the James and the Sheyenne River Valleys can be found in a floristic comparison. Sixty species have been found in the Sheyenne River Valley of Barnes County that are not present in the James River Valley of Stutsman County. Most of the floristic differences can be accounted for by the direction of flow of the two rivers. The James River flows south to the Missouri River, the Sheyenne flows into the Red which, in turn, has other tributaries extending east into the deciduous woodlands of Minnesota. The Red and its tributaries have served as migration routes, thus most of the species limited to the Sheyenne have eastern affinities.

Tilia americana is a dominant species in the lower Sheyenne River Valley (Nelson, 1964) but I've not found it in the James Valley. Both *Betula papyrifera* and *Ostrya virginia* are in the Sheyenne River Valley but not in the James River Valley. A considerable number of forbs and shrubs are limited to the Sheyenne River Valley. Among these are *Trillium cernuum, Allium tricocum, Circaea quadrisulcata, Prenanthes alba, Menispermum canadense, Viburnum lentago, Hydrophyllum virginiana* and *Clematis virginiana* on the floodplain along with *Heliopsis helianthoides. Rhus glabra* forms some rather large stands on the sides of the valley. *Butomus umbellatus* is a seemingly recent introduction to North Dakota. Collections south of Valley City constituted a state record and added a new plant family to North Dakota's flora.

A smaller element limited to the Sheyenne River Valley is basically western but for some reason is not present in Stutsman County. *Astragalus racemosa* and *Iva axillaris* both grow on exposed clay. Collections of *I. axillaris* along the Sheyenne River Valley represent the plant's easternmost extension in North Dakota. It's not found in Minnesota.

DISTURBED AREAS

In both counties a number of species are limited to or make their best development on disturbed areas. Occasionally weeds are introduced along railroads. *Cenchrus longispinus* has been found only in the railroad yards at Jamestown.

Temporary field ponds have their own unique flora. Species that make their best development in such situations include *Alisma gramineum, Gratiola neglecta* and *Veronica peregrina*.

SPECIES DIVERSITY

A consideration of species diversity adds an additional parameter to community descriptions of the Coteau and Drift Prairies of Barnes and Stutsman Counties. A total of about 450 species have been found associated with the previously mentioned communities after excluding species most typical of wooded and disturbed areas. High, mid and low prairies together have 244 associated species. About 100 species occur in meadows. Of this 100, about 20 also occur in the low prairie. Eighty species are typical of the marsh and open water zones. Approximately 30 of these occasionally appear in the meadow also. Woody communities of the river valleys with their associated understory add about 240 species. Woody communities of the Coteau have only about 60 species, all of which may be found in the river valleys. Species not accounted for by the previously listed communities are components of disturbed areas.

COMPARISON OF THE PRESENT WITH PREVIOUS STUDIES

The present study of Barnes County has been the first opportunity in North Dakota to repeat an earlier floristic survey. In 1912 Dr. H. F. Bergman published a county checklist (Bergman, 1912). The list includes 454 species after being brought into agreement with currently accepted nomenclature. Recent collections resulting from this study and from the work of Dr. O. A. Stevens have added 233 species to the checklist of vascular flora of Barnes County. No doubt many of these species were present during Dr. Bergman's time, however, some, notably *Typha angustifolia, Lotus corniculatus* and *Butomus umbellatus*, have surely been introduced since that time.

CONCLUSION

Combining the species from all habitats together into a statistical summary gives a total of 780 species for the two counties (see Table 1).

Table I: Statistical Summary of Vascular Plants from Barnes and Stutsman Counties, North Dakota.

	Families	Genera	Species
Pteridophytes:	3	3	7
Conifers:	1	1	1
Monocots:	17	82	223
Dicots:	72	263	549
	93	349	780

ABSTRACT

Field and herbarium studies carried out over the period 1971 to 1974 have resulted in a checklist of 780 vascular species for Barnes and Stutsman Counties. The topography of these counties is a result of glacial processes. The dominant features are the gently rolling Drift Prairie, the moranic region of the Missouri Coteau, and two small rivers, the James and the Sheyenne, which occupy large glacial drainage channels.

The characteristic undulating topographic features and associated drainage gradient of the Drift Prairie and the Missouri Coteau allow for the development of five recognizable plant communities. These plant communities are: High Prairie, Mid-prairie, Low Prairie, Meadow and Marsh. Approximately 450 species were found to be associated with these five plant communities. An additional 60 or more species are associated with woodland communities that occasionally occupy the north and east slopes of the Coteau region. The woody communities of the river valleys with their associated understory are more diverse, having about 240 species. A comparison of the flora of the two river valleys within the counties studied shows that the Sheyenne Valley has 60 species not encountered in the James Valley. Most of the species restricted to the Sheyenne Valley have eastern affinities. The species not accounted for by the previously listed communities are components of disturbed areas such as roadsides, cultivated fields, railroad grades and gravel pits.

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Section IV: MANAGEMENT, RESTORATION AND USES

Practitioners, users, and those who have a concern for the prairie at heart share this section. Papers range from involving the prairie species in landscaping and erosion control, to the management, restoration and use of many prairie tracts that have escaped destruction. Several people behind these papers were without formalized training in ecological disciplines, but were some of the most enthusiastic contributors. Their membership in this Conference makes it unique and more worthwhile.

PRAIRIE ECOSYSTEMS ARE ESSENTIAL FOR ENVIRONMENTAL MONITORING

Paul C. Lemon

As recounted on the stage, in song and often thru radio "... O bury me not, on the lone prairie" appears to imply that there is one prairie ecosystem or biome. In the broad sense this is true, but for buffs and serious prairie ecologists there are many subdivisions or types. Shelford (1963) treats fourteen grassland communities. Küchler's map (1964) of potential vegetation includes 25 types of grassland although some of us might call the coastal types "brackish marsh." At the xeric extreme, of course, grasslands may tend to merge with various desert or shrub types. The humid end of the spectrum constitutes the contact with deciduous trees and is referred to as savanna or grassland-forest mosaic. Thus, grassland and the mixture of prairie species with related types might give at least 50 communities capable of recognition and reasonably discreet description. If I seem anxious to retain a large number of natural areas in our prairies it can be considered partly justified by the great diversity of grass-dominated ecosystems.

Scholars of the prairie ecosystems readily visualize the reasons for this diversity. It can be quickly stated by two "truisms": (a) moisture availability decreases in an east to west continuum along the 40° parallel (Kansas-Nebraska line), and (b) length of growing season or severity of winters is another climatic continuum following the 100° meridian, or a bit to the west of it. Thus, with these two continua intersecting at roughly right angles we have a plethora of expected permutations.

Figure 1 illustrates the pertinent isohyets for the Great Plains and immediately adjoining areas. It is interesting that the 1000 mm line is nearly identical with the prairie boundary from southern Indiana southward to the Gulf. From Indiana northward the line or ecotone requires other interpretations (Lemon, 1970). In fact one influence which is very powerful in the northern half of the prairie is brought out in Figure 2. This map shows, though a little indirectly, the problem of the winter season. It is a multiple problem: limitation on plant growth caused by the short summer, seasonal moisture stresses, frost heaving and other direct temperature factors. The roughly east-west lines on Figure 2 express both the severe cold of winter and/or severe heat in summer. A mean temperature difference exceeding 15.5 C, July minus January, reflects the cold, "physiologically arid" climate of the boreal forest extending across Canada. Consequently, these effects produce the contact with coniferous forests generally along the northern boundaries of the prairie or parkland. The 7.2 C line extends diagonally across the broadest part of the grassland at middle latitudes and represents a less violent seasonal contrast.

It is hardly necessary to dwell upon the great size and dimensions of the prairie biome for it extends clear across the United States and comprises 35% of its land area (lower 48). From the southern edge of mesquite savanna (15° Lat.) to the aspen parkland in Alberta (nearly 55° Lat.) would measure about 4,000 km, while the greatest east-west dimension is 2,800 km. The grassland types and the related shrub or savanna combinations are given in Table 1, as planimetered on Küchler's (1964) map. These area figures do not include the extremely arid types (virtually semi-desert), sagebrush, nor the eastern brackish and other marshes. One soon sees (Table 1) that the Central Grasslands have the greatest number of research natural areas, with an aggregate total of 340,000 hectares or 3,400 km^2. It is striking that this area represents merely 0.2% of the gross area.

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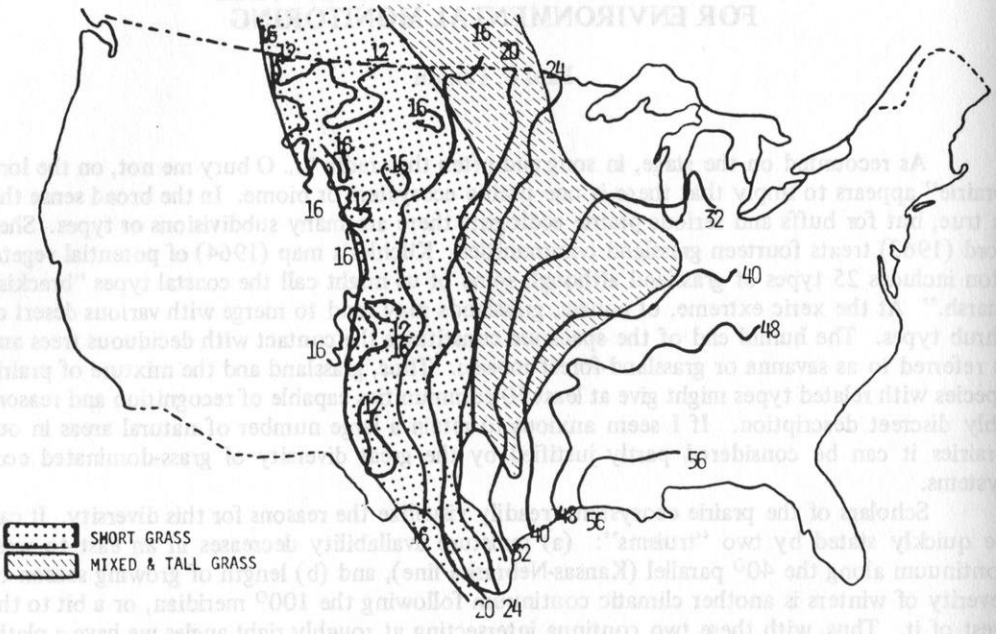

Fig. 1. Isohyets showing lines of average annual precipitation (inches).

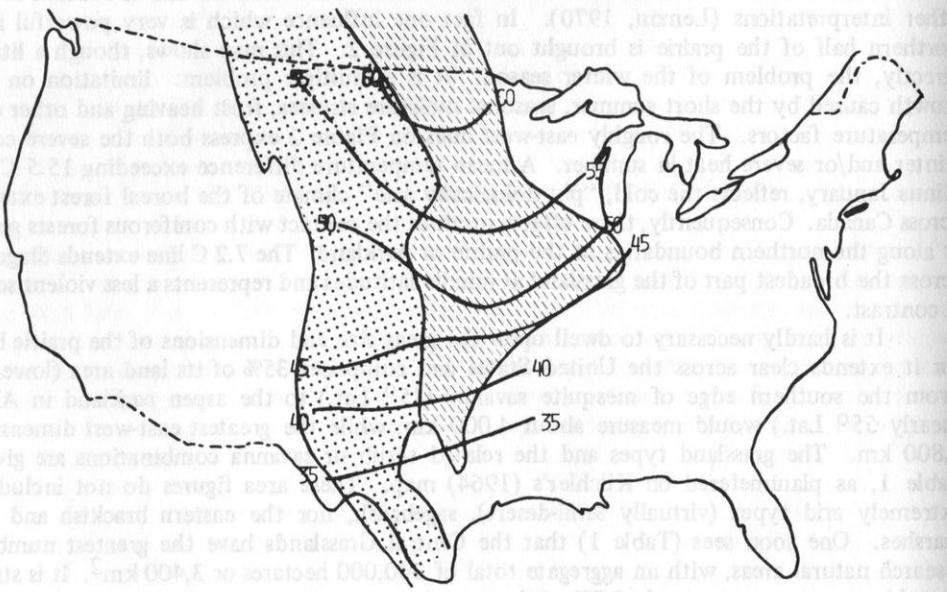

Fig. 2. Average annual temperature change, July minus January (°F).

Table 1. Summary of type areas for grasslands and combinations of grassland with western shrub types or eastern forest types. (As planimetered from Küchler's map of Potential Natural Vegetation of the U.S., 1964).

Sub-Region	Area (km^2)	Number of Natural Areas Inventoried	Total Area of Natural Areas Inventoried (Hectares)	Average Area of Research Natural Areas (Hectares)
I. Central Grasslands (K-63 to 78, excepting K-72 & 73)	1,594,000	154	340,000	2,215
II. Western Grasslands (K-47 to 54, except for K-52)	231,000	13	163,000	—*
Sub-total	1,825,000	167	503,000	
III. Western Shrub-Grassland Combinations (K-56 to 62)	290,000	28	132,100	2,040**
IV. Grassland-Forest Combinations (K-81 to 88)	565,000	86	210,500	2,450
Sub-total	855,000	114	342,600	
TOTAL	2,680,000 ($1,035,000 mi.^2$)	281	845,600	Avg. = 2,275***

* not calculated since one area was 56,000 ha
** does not include Jornada Experimental Range which has 77,000 ha
*** Does not include II. Western Grasslands

As regards current concepts on species diversity, it must be fairly admitted that our ideas are partly in a state of flux. There has been considerable discussion in the last few years, as ecologists have sought to determine the biological meaning of diversity and how best to measure it. Monk (1967) has suggested that diversity apparently increases with (a) an increased variety of niches, (b) narrower niches or greater niche overlap, (c) more stable environment, (d) less rigorous environment, (e) succession, (f) increased productivity, and (g) increased biomass. Patten (1963) has stated that high productivity in plankton is associated with high diversity. However, Whittaker (1965) pointed out that in the Great Smokey Mountains, diversity does not necessarily parallel community production. Working in California grasslands, McNaughton (1967) indicated that diversity is principally a mechanism which generates stability while dominance is a mechanism which generates community productivity. It is the relatively rare species which contribute most to diversity and yet relatively little to the energy flow through an ecosystem.

Perhaps it is well to briefly recount some of the logic and reasoning required to scientifically justify the whole idea of ecological research areas. A system of ecological preserves "... can be likened to an information storage system, or library, of enormous complexity and incomparable significance. The information stored provides research and educational opportunities for the study of natural ecosystems or any of their parts. Like a library, ... (these) ... areas are intended for use, but the user must not consume or damage the materials" (Franklin et al, 1972). Our primary goal, then, is to establish and maintain the maximum diversity of natural ecosystems that will provide services similar to those of a well-stocked library or data bank. It is becoming increasingly urgent for us to make an accounting of our ecological resources. What lands and water will we need as basic working materials for our research? Myriads of questions are being raised by land owners, land managers, politicians, and citizens. The ecologist's answers will be as useful as his research permits. It is now important that we examine our research machinery and materials. The public will clamor for the facts and guidance needed for policy formulation in environmental problems. In fact, there is now a steady expansion in public and private funding for environmental and biological research. The excellence of our product (ecological resource management) will be determined by the quality of the machine (research natural areas) and the skill of the operators (working ecologists). Examples of natural prairie provide baseline resources with which scientists must work to appraise the cause and effect of human alteration. Since certain species show the effect of environmental change before others, identification and monitoring by means of indicator species provides a desirable technique.

It goes without saying that all areas are not equally useful for ecological research. Consequently, great care must go into the initial selection of an area proposed for preservation. Although no one person has a corner on the ultimate wisdom of this process, the following suggestions are offered:

a) The area must be a valid sample of a natural ecosystem,
b) The area might also contain rare or endangered plants or animals or rare examples of botanic, zoologic or geologic phenomena,
c) The area should be suitable for research activities which involve non-consumptive investigation of ecologic processes,
d) The area may represent an ecosystem, already modified by man, that provides opportunities to study responses and recovery from such modification,
e) An area may have a potential for environmental education programs for students and others interested.

Protection of natural areas is not a new concept. About 2,400 years ago, the Roman government established a natural area out of devotion to the God Jupiter. The Vallombrosa

Forest, now a part of the Florence Faculty of Forestry, began as a monastery forest. The common denominator for these two religious-education areas is that the human mind, while being in a basically natural environment, is said to be stimulated to development of original ideas (Zinke, 1970). A number of countries have more recent histories of protecting natural areas including the USSR, Finland, and the western Canadian provinces of British Columbia and the Yukon Territory.

The absence of an adequate system of grassland preserves in the United States, and in many other countries, is due in the main to the rapidity of the development process. Establishment of a system of preserves now, as opposed to some time (say, 25 years in the future) will result in lower costs of acquisition and at the same time provide assurance that our future needs will be met. On the other hand, delay will bring appreciating values and greater cost of acquisition. Further delay may result in complete loss of some needful areas. When a "higher use" is found for lands in the natural preserves one of two conditions exist: (1) if the newly discovered use is marginal, there is no substantial cost consideration, (2) if the new use offers an extremely high profit margin, and appears to be intrinsically important to the economy, it would be well to relocate the proposed enterprise in a different ecosystem, keeping the grassland preserve as an essential monitoring area.

It is important that a system of ecological preserves is assured continuity and protection far into the future. We know relatively little about the genetic stability of highly productive mono-cultures of plants and animals used for food and fiber, and the need occasionally arises for the reintroduction of genetic characteristics lost in the past from domestic strains. The sustained protection of research natural areas gives multiple yields in scientific research. Although many of the intended results of research are accomplished, the serendipity (loosely called "spin-off") value of scientific research is probably equally as great. Fleming, for instance, accidentally contaminated a *Staphylococcus* colony in 1928 and the result of the accident was the discovery of penicillin. The public is as yet only vaguely aware of some of the important needs to be met by research natural areas. A system of ecological preserves can provide a key function by maintaining indicator species for environmental monitoring as well as the protection of endangered plants and animals.

In spite of rapid progress in development of sensors and modern electronic devices, a natural community remains the most precise and cheapest indicator of either local or cosmic changes. Adequate samples of the various prairie ecosystem sub-types can provide information on either man-caused or natural events. In the classic days of early plant ecology it was thought that selected individual plant species were the most useful for gauging responses to climatic or resource management practices. More recently it has been recognized by many researchers that the entire community, including measurements on the animal life, is a more accurate method of assessing changes over time. Ecosystem sample areas are especially valuable near climatic or physiographic boundaries or along some type of gradient. It is vital, therefore, to take all measures in our power to obtain and maintain adequate prairie research areas.

Ecological preserves will provide basic information essential for the integration of biological and technological decisions. There is definitely a need to determine a "speed limit" for the technological race we are presently engaged in. We recognize the need to use controls for those manufactured creations (automobiles, aircraft, weapons, etc.) that are capable of injury to man. We are doing ourselves a disservice by not recognizing the need to impose limitations on destructive capacity that may degrade the environment. Other potential benefits range from very intangible items (ethics, survival value, germ plasm pools, etc.) to the more classic research that provides guidance in management of the nation's essential natural resources.

Although it may first seem that use of ecological preserves is limited to a minority (the scientific and educational communities), the benefits derived affect everyone from very local to international levels. There is a growing body of opinion that man must develop and

maintain an environmental awareness if he wishes to solve his problems of adaptation and permanence. Ecologists seek to investigate grasslands to better understand climate and the land productivity of semi-arid situations. Much of the west has been strongly modified since the days of abundant antelope, bison, and plains bighorn. It is urgent to preserve or reconstitute working examples of prairie for ecological reserach. In view of the complexity and wide variability of the prairie biome we must expect to retain a large number of study sites, surely in the hundreds or possibly over a thousand.

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THE AMERICAN PRAIRIE INVENTORY A PRELIMINARY REPORT

Richard H. Wagner

The American grassland once extended in a virtually unbroken sweep from the bluestem prairie of Illinois to the wheatgrass of the Cascade foothills with major outlyers in Alabama, Mississippi, and Florida. Over these millions of hectares, countless combinations of species sorted themselves out along gradients of moisture, temperature, and soil types into six major grasslands: the tallgrass prairie of the midwest; a transitional mixed grass prairie; the shortgrass prairie of the Great Plains; the bunch grass prairie of the Pacific Northwest; the California bunchgrass prairie; and the desert grassland of the Southwest.

Today, most of the grasslands have been plowed into cornfields, covered by subdivisions, improved by the introduction of pasture grasses, or simply overgrazed which has encouraged the invasion of undesirable annual grasses and Eurasian weeds. So while much of the United States west of the Mississippi is still covered with grass, there are few tracts of the original grassland that have not been altered by man in the last 120 years. As the frontier recedes into history, more and more people are becoming convinced that representative samples of the original grasslands be preserved as living links with a landscape that profoundly shaped human history on this continent.

But there are more compelling reasons than nostalgia for preserving representative samples of the American grasslands. A virgin grassland contains species of grasses, forbs, insects, birds, and mammals that have evolved together over thousands of years and have become well adapted to their environment. Virgin grasslands can, therefore, be considered reservoirs of genetic information of great potential usefulness to man. With energy costs increasing, it is the plants and animals that have adapted naturally to their environments which can teach us most about productivity and can provide guidelines for the development of food and forage plants better adapted to their environments and less demanding of man-supplied energy.

In February, 1974 the American Prairie Inventory was set up under an initial grant from the Nature Conservancy to locate and list all formally preserved examples of grassland types in the United States, and to seek out further unpreserved examples of grassland types that haven't been plowed, seeded, or severely overgrazed; tracts whose scientific value as grassland remnants may not be widely recognized. Grassland is defined for the purposes of the study as any vegetation that is dominated by native species of grasses and forbs excluding only marshes and alpine-subalpine meadows. A few types where grassland species intergrade with adjoining woody types are also included. Because of its national scope, the grassland classification scheme used was that of Küchler (1965). All grassland areas reported were assigned to the most appropriate or likely type.

Time and financial limitations made it impossible to inventory grasslands directly in the field. Consequently the Inventory has depended entirely on published lists and the recommendations of informed collaborators across the country. To make this pool of contributors as large as possible, the following categories of potential sources were contacted: National Forest Supervisors; National Grassland Supervisors; National Wildlife Refuge Managers; National Park and Monument Supervisors; Army, Navy, and Air Force base Information Officers; Indian Reservation area offices; State Park Directors; State Fish/Game/Wildlife officials; major conservation organizations such as the Wildlife Federation, Sierra Club, Isaac Walton League; ornitho-

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logical groups; TNC chapter heads; private foundations; county agents in all counties which might contain grassland; academicians in all two and four year colleges in or near grassland areas; attendees at previous Midwest Prairie Conferences; and a lengthy miscellaneous list recommended by these primary sources. Altogether close to 3500 people were contacted and supplied with inventory forms. As in the biblical parable of the mustard seed, the results were variable.

As might be expected, some individuals and groups were extremely generous with their time and data, others less so. But to all who were able to contribute, this brief preliminary report is gratefully dedicated.

Because of the limitation on space the detailed results of the Inventory cannot be presented here. However, some brief comparisons and conclusions can be made.

1. Although there is an upper limit on the area of any grassland type remaining in any state, the number of reported remnants is closely related to the density of remnant seekers and their industry.

2. All K-types but K-87 (mesquite-oak savanna) are represented in some preserve somewhere although not necessarily in every state in which they occur, or in many critical areas.

3. Only four states with grassland types have no preserves; Alabama, Arkansas, Louisiana, and Nevada.

4. The two states with the greatest diversity of grassland types, Oklahoma and Texas, have the fewest number of grassland preserves.

5. There should be a nationally coordinated effort to assure that representative as well as unusual examples of each grassland type -- not necessarily Professor Kuchler's system, but some commonly accepted kind of grassland classification -- be preserved as reference points, genetic pools, outdoor classrooms, aesthetic/historic sites -- as many uses for as many people as can be mutually accommodated congruent with preservation of the maximum species diversity of the area.

6. Statewide grassland inventories, especially of the larger western states, should be begun as soon as possible so that prospective sites can be located and put into some kind of protected status before they are lost. With the advent of greater demand and higher prices for fossil fuels, and the widespread distribution in the grassland states of oil shale, oil sands, oil fields, soft coal, and natural gas, few areas can be considered safe without specific preserve status. Also the increasing worldwide shortage of protein with the rising prices that accompany shortage will place any tillable, irrigatable grassland in jeopardy.

Within five to ten years the present opportunity for preservation will have passed and grasslands if preserved will have to depend on restoration techniques that hopefully will have emerged by then. Fortunately many states have become and are becoming aware of the necessity and desirability of some kind of state preserve or natural area system. However, many states sleep on, lulled perhaps by the vastness of their grasslands or the acreage already in federal ownership. If your state falls in this category a statewide workshop of interested parties is certainly in order to get the ball rolling. If this is done in all states with important grassland types there is no reason why a national system of grassland and other vegetation types as well cannot evolve to assure future generations of a glimpse of the natural diversity of a continent we today take for granted.

While the initial phase of The American Prairie Inventory has been completed, the files remain open for further additions, deletions, corrections, and comments. To accommodate this an inventory sheet is included in this report which can be duplicated and mailed in to the TAPI office. Since this is only a first approximation there is ample opportunity for continuing contribution to the Inventory.

It is hoped that the full, detailed report including state spot maps showing remnant grassland locations, reproduction of the complete data cards themselves, and a thorough data

analysis, will be published and made available at cost. When the report is available, an announcement will be sent to each contributor.

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THE AMERICAN PRAIRIE INVENTORY

Inventory of Existing and Potential Grassland Natural Areas

This form is intended as an aid in assembling the necessary information for each area recommended. If you know of any such areas in your region, please fill out this form and mail it back to TAPI. Additional forms are available from TAPI, 3753 Seventeenth Street, San Francisco, California 94114

Local name of area:

Location: State_____ County_____ Range_____ Township_____

Section_____ Quartersection_____ Nearest City_____

Distance and compass bearing to nearest city_____

Ownership: (Federal agency, state agency, private, etc.)

Acreage:

Küchler type: (or dominant species)

Current management:

Condition:

Threat: (Most likely mode of future destruction)

(Imminence of threat)

Local name of area:

Location: State_____ County_____Range_____Township_____

Section_____ Quartersection_____ Nearest City_____

Distance and compass bearing to nearest city_____

Ownership: (Federal agency, state agency, private, etc.)

Acreage:

Küchler type: (or dominant species)

Current management:

Condition:

Threat: (Most likely mode of future destruction)

(Imminence of threat)

Reported by: Name_____ Title_____

Phone_____Address_____

PRAIRIE WETLANDS SINCE NEPA

Alan L. Smith

INTRODUCTION

Prairie wetlands (marshes) form an intermediate plant community which has characteristics of both terrestrial and aquatic or marine ecosystems. Wetlands, historically, have been regarded as liabilities rather than assets; engineers and farmers have viewed them as obstacles to industrial or agricultural development. Thus, widespread drainage of wetlands has occurred. However, public attitude has shifted over the past two or three decades and was manifested with the inception of the National Environmental Policy Act (NEPA) of 1970.

While NEPA has initiated important federal regulations regarding the protection and utilization of coastal wetlands, policy-making decisions regarding wetlands of the interior continental United States have been lacking. Two states have enacted inland wetland legislation compared with 30 states which are under the auspices of the Coastal Zone Management Act. The objectives of this paper are to summarize:

1) characteristics and importance of our wetlands
2) the current status of national policy regarding protection and utilization of wetlands
3) future needs regarding national policy of our wetlands

PRAIRIE WETLANDS DEFINED

A general definition of wetlands will be used throughout this paper to include those land areas which are inundated part of the year due to a high water table, thereby supporting a vegetation different from the adjacent uplands. A recent wetland classification system can be found in Haueisen (1973). Wetlands are characterized by plant species which exhibit a wide variety of adaptation and wide tolerance ranges for survival in an environment with alternating wet and dry periods.

ECOLOGICAL ROLE OF WETLANDS

Agricultural and industrial development has placed undue impacts on the nation's wetlands, especially along the coast. The origin of the coastal marsh problem goes as deep as the basic settlement patterns of the United States. The single greatest pressure currently impinging on the coastal marsh is sheer population pressure. The United States has a population of approximately 212 million; 168 million live in the thirty coastal states. Moreover, the majority of coastal state residents lives within fifty miles of the shore or major inlets.

Increased population also has increased the use of wetlands for recreation; hunting and fishing being the major activity bringing people to the wetlands. If sound natural resource management policies are to be formulated for inland wetlands, it will be necessary for policy makers to understand the ecological role of these wetlands.

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Hydrologic Role

Wetlands play a major role in the hydrologic cycle by storing groundwater essential to agricultural, domestic, and industrial needs. Wetlands also stabilize surface waters to alleviate drought and flood damage.

Productivity

Wetlands are among the most productive biological systems. Oxygen is produced at a net increase of twenty tons per day through photosynthesis and reduction reactions involving compounds of nitrogen and sulfur (Grant and Patrick, 1970). Tidal marshes and estuaries are among the most fertile areas in the world in terms of energy, calories, proteins, carbohydrates and vitamins. The only other areas which can be compared with them in productivity are fluvial plains and rice paddies (Dow, 1972). Coastal marshes are fertile because of efficient nutrient exchange, flowing water, accessibility to sunlight, and nearly continuous production. Less is known of the productivity of cold water wetlands in the north than of the warm water areas of the south. Northern inland wetlands also lack the continuous flow of water through the system which is so characteristic of coastal wetlands. Odum (1960) reported an annual production of approximately 79 million calories per hectare (32 million per acre). Dow (1966) estimates the productivity of wetlands in Maine to be at least three-fourths that of southern marshes or approximately 59 million calories per hectare (24 million per acre) per year.

Dry, green herbage production values from studies conducted in western Minnesota (Smeins and Olsen, 1970) and North Dakota (Smith, 1973) provide rough estimates of production of northern wetlands compared with adjacent field crops and natural prairie. Applying the average caloric value of 4 kcal/g presented by Kormondy (1969), the potential energy produced by the vegetation is calculated (Table 1). Unpublished data collected by Smith for the Texas Gulf Coast prairies and marshes also are presented (Table 1).

Fisheries and Wildlife Production

Wetlands are valuable for producing wildlife, particularly fish, waterfowl, and fur bearers, that contribute both aesthetically and economically to the nation's well-being. Dow (1966) has provided an excellent breakdown of the commercial value of fishes and shellfish produced by marshes and estuaries along the Maine coast.

The prairie pothole region of the northern plains has long been recognized as the nation's "duck factory," producing about 50 percent of the ducks on the North American continent. These wetlands are more important as breeding areas while southern wetlands are essential as wintering grounds. These wetlands represent about 10 percent of our nation's total wetlands.

Other Roles

Goodwin and Niering (1974) identified wetlands as performing a significant role in the filtration of pollutants as well as identifying their usefulness for educational and recreational purposes. The desirability of wetlands performing a filtration process is questionable since we do not fully understand the final consequence of these wetlands serving as a sink for pollutants. It also is doubtful that inland wetlands, which are essentially enclosed systems, can play the same role in pollution filtration as the open swamps and coastal marshes.

NATIONAL POLICY REGARDING WETLANDS

According to Haueisen (1973), the federal government has focused on two major areas in regard to wetland protection; pollution control and preservation of migratory bird nesting

Table 1. Estimated potential energy (kcals)[a] of wetland vegetation compared with other selected habitat types.

Study	Habitat	Production kg/ha	Production lb/a	Kcal/ha (millions)
Hadley & Buccos 1967	Salicornia-Suaeda	1,090	971	4.36
	Poa-Melilotus (burned)	2,536	2,260	9.42
	Distichlis-Hordeum-Poa	3,535	3,150	14.14
Smeins & Olsen 1970	Stipa prairie	3,424	3,050	13.70
	Andropogon prairie	3,816	3,400	15.26
	Scolochloa marsh	7,840	6,985	31.36
	Hordeum (Barley)	10,988	9,790	42.95
Smith 1973	Scolochloa (unburned)	8,000	7,128	32.00
	Scolochloa (burned)	10,720	9,552	42.88
Smith 1973 (unpublished data)	Texas Gulf Coast Prairie	7,000	6,237	28.00
	Texas Gulf Coast Marsh	10,075	8,977	40.30

[a] kcals estimated from production values reported for each study using estimate of 4 kcal/g dried plant material (Kormandy, 1969), except for Smith, 1973, (unpublished data) which are based on actual values generated from bomb calorimetry.

and feeding areas. He provides a chronological history of federal legislation regarding the government's role in pollution control. The Clean Water Restoration Act of 1966 was probably one of the most important acts and the most significant segment of this act was the transfer of responsibility of the Oil Pollution Act of 1924 to the Secretary of Interior and changed that Act to include inland waters.

The second focus of federal programs pertains to migratory waterfowl. The Migratory Bird Treaty Act of 1918 gave jurisdiction of protection of migratory birds to the federal government. The Migratory Bird Conservation Act of 1929 provided establishment of migratory bird refuges. Financial assistance by the Migratory Bird Hunting Stamp Act of 1934 helped procure these lands.

Wetlands acquisition and development by states was made possible by enactment of the Federal Aid and Wildlife Restoration Act of 1937 and was assisted by an amendment to the Hunting Stamp Act in 1949 with a raise in cost of the "duck stamp" to $2.00. Another in 1958 increased it to $3.00 (Haueisen, 1973).

While these amendments provided for wetland acquisition for the waterfowl production areas and suitable areas for migratory bird refuges, wetland conversion continues to be lost at an alarming rate. The Accelerated Wetlands Acquisition Act of 1961 allowed for the purchase of essential wetlands while they still existed.

While we discussed the value of inland wetlands in terms of their productivity, it may be appropriate to report specific monetary value when communicating with those responsible for policy decisions regarding wetlands. The environmental movement has generated a public awareness of the need to regulate and manage the uses of natural resources to insure their continued availability and use for the greatest public benefit. NEPA passed in 1970 has two purposes. First, the law declares protection of man's environment to be a continuing policy of the nation; secondly, it requires that the effects on the human environment of any major federal action, including licensing, be fully disclosed to public scrutiny. Many biological reports have been prepared as a result of NEPA but are ignored because frequently they are concerned with intangibles, such as the importance of wildlife habitat. Dow advanced the idea as early as 1966, "that the only effective method of insuring protection and intelligent utilization of estuaries and associated wetlands is to use the same techniques that exploiters of these areas have been employing for years – the appeal of economic return." Dow (1966) provides comparative estimates of growth income for best garden farms in Maine as $2,000 per acre per year, while major marshlands of Maine produced $4,000 worth of nutrients per acre per year. Goodwin and Niering (1973) provide data which indicate that swamps in the southeastern United States have a value of $3,000 annually as a sediment accretor, and other wetlands in the southeast have a value estimated at $7,000 per year on a multiple-use basis.

Environmental Protection Agency Policy

The administrator's decision statement on policy to protect the nation's wetlands released February 21, 1973, established EPA policy to protect wetland ecosystems from destruction. This policy "shall give particular cognizance and consideration to any proposal that has the potential to damage the wetlands, to recognize the irreplacement value and man's dependence on them, to maintain an environment acceptable to society and to protect them from damaging misuses..."

"It shall be the agency's policy to minimize alterations in the quantity or quality of the natural flow of water that nourishes wetlands and to protect wetlands from adverse practices..."

"The agency will not grant federal funds for the construction of municipal wastewater treatment facilities or other waste-treatment associated appurtenances which may interfere with the existing wetland ecosystems..."

"The Department of the Interior will be consulted to aid in the determination of the probable impact of the pollution abatement program on the pertinent fish and wildlife resources of wetlands..." (Ruckelshaus, 1973).

Coastal Zone Management

The forces of NEPA have resulted in an unprecedented surge in coastal area scientific research, establishment of coastal planning and management organizations in many states, and in passage of the Coastal Zone Management Act of 1972. This act specifically asserts, "The key to more effective protection and use of land and water resources of the coastal zone is to encourage the states to exercise their full authority over the lands and waters in the coastal zone." (Ludwigson, 1974). Thirty states are eligible for federal funds through the Coastal Zone

Management Act of 1972. This includes all states whose boundaries are on the Pacific and Atlantic Oceans, the Gulf Coast, and the Great Lakes.

Current Status

The availability of federal funds through the Coastal Zone Management Act of 1972 has resulted in a number of the thirty coastal zone states, including Alaska and Hawaii, to initiate coastal zone management plans. Since no funds are available through this Act for the management of prairie wetlands, states in the interior are still operating under antiquated policies. United States Department of Agriculture census (1969) figures show approximately 6.15 million hectares (15.23 million acres) of wetlands have been drained in the northern plains (Table 2). Goodwin and Niering (1974) have estimated the original total of wetlands at 5.1 million hectares (12.7 million acres). Dredging, filling, and pollution have reduced the original area to almost half or 2.8 million hectares (7 million acres). This represents approximately 3.5 percent of the total land area of the continental United States. While coastal wetlands are protected by law, those of the interior are still drained for primarily agricultural purposes.

The Starkweather Project proposed in North Dakota called for the drainage of 20,250 hectares (50,000 acres) of prairie pothole wetlands in North Dakota (Houck, 1973). Drainage of these wetlands will benefit 91 farm units while, in the process, irreplaceable wildlife habitat will be lost to the nation. Objectives of this program are to increase agricultural production of corn and wheat. Houck points out that these are the same crops we also pay farmers not to grow at a cost of additional millions of dollars. For example, in 1971, farmers were paid more than 2.75 billion dollars to idle 14.9 million hectares (37 million acres) of surplus cropland, in 1972 more than 25 million hectares (62 million acres) were idle. It would seem proper to restore production of all previous cultivated land before draining existing wetlands.

A recent protest to the United States Atomic Energy Commission regarding the sacrifice of 4,050 hectares (10,000 acres) of valuable farmland for an atomic energy electrical generating plant, requested that the plant site be shifted to "nonproductive marshland." A spokesman for the power company concerned stated, "Marshland is not necessarily unproductive land ...it may be highly productive for marine life." (Hill, 1974). This attitude on the part of company officials is encouraging.

What is currently being done to protect the wetlands of the inland prairie region? Apparently, very little since existing laws do not identify the inland prairie wetlands nor do they provide for their protection and utilization. It is encouraging that Connecticut and Massachusetts now have inland wetland legislation.

Previous research on wetlands includes work by Walker (1965, 1969), Dix and Smeins (1967) and Walker and Coupland (1968, 1970). All performed studies to determine overall phytosociological relationships. Dodd and Coupland (1966) evaluated phytosociological relationships of saline wetlands in Canada. Millar (1969) expressed the necessity for autecological studies as the next step toward more complete understanding of inland wetland ecology. Smeins and Olsen (1970) compared species composition and production of one wetland with that of surrounding prairie and agricultural land. Sloan (1970) described the hydrological cycle of prairie potholes in North Dakota with emphasis on salinity. Smith (1971, 1973) described plant species relationship in relation to land use and management.

While each of the preceding publications represents an increase in our understanding of the ecology of inland wetlands, a considerable amount of basic information still is required. Information necessary for decision making regarding national policy on wetland utilization includes:

1) more detailed estimates of wetland productivity
2) distribution of energy flow through these wetlands
3) patterns of nutrient cycling through wetlands
4) economic return realized from wetlands by current land use

5) potential future utilization of these wetlands
6) possible impacts to these wetlands by changes in utilization
7) cost-benefit analyses of these changed utilization patterns versus current cost benefits.

In summary, I would like to quote Dow (1972), "The lack of utilization is the main problem in marshes and estuaries. The potential is there, but man has not yet learned how to utilize the marsh efficiently. When he does - and that day is not far removed - the coastal marsh will become one of our major sources of food." We also must learn to use our inland wetlands more efficiently in their current form or lose them.

Table 2. Land drained for agricultural purposes in six states of the northern Great Plains region.[a]

State	Land in Farms[b]		Drained Land[b,c]		
	Hectares	Acres	Hectares	Acres	Percent Drained
Minnesota	10.7	26.42	2.43	6.01	22.7
Iowa	13.15	32.47	2.78	6.87	21.2
South Dakota	16.03	39.59	.14	.35	2.2
North Dakota	16.35	40.38	.51	1.26	3.1
Nebraska	18.09	44.66	.19	.48	.01
Montana	23.38	57.73	.10	.26	.44
TOTAL	97.70	241.25	6.15	15.23	49.65

[a] United States Census of Agriculture 1969.

[b] Units in millions of hectares (acres).

[c] Drained land refers only to agricultural land drained by man-made facilities.

ABSTRACT

Prairie wetlands (marshes) form an ecotone between the terrestrial and aquatic or marine ecosystems. Vegetative production of these marshes is usually greater than the surrounding or adjacent prairie. Marshes of the northern and southern Great Plains states are of two types: inland and coastal. Salinity, an important environmental parameter influencing species distribution, ranges from fresh to saline. Requirements of NEPA call for detailed environmental impact statements on all federal activities that have a significant effect on their surroundings. The Coastal Zone Management Act of 1972 provides more effective protection and use of the land and water resources of the coastal zone and encourages states to exercise

full authority over the lands and waters in the coastal zone. Environmental Protection Agency policy is to minimize alteration in the quantity and quality of water that nourishes wetlands. Thus, measures are being taken to protect coastal wetlands but few, if any, safeguards are being enacted to protect our inland wetlands.

KEY WORDS

Prairie wetlands, marshes, NEPA, coastal zone management, water resources.

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THE BLACKLAND PRAIRIE OF TEXAS: CONSERVATION OF REPRESENTATIVE CLIMAX REMNANTS

David H. Riskind and O. Brown Collins

INTRODUCTION

The Blackland Prairie, a major land resource area of Texas, extends from the Red River in the northeastern portion of the State to the San Antonio River in the southwest and encompasses approximately 4,260,000 ha (Godfrey, Carter and McKee, 1969). The Prairie varies in width from 70 km along the Red River to 12 km along the San Antonio River. Climatic gradients as well as variation in edaphic factors combine to form a vegetationally diverse plant formation composed of seven distinctive community types. Community dynamics, floristics, climatic and edaphic factors have been discussed by Collins, Smeins and Riskind (1975) at this conference and need not be repeated here.

In order to preserve the biotic diversity so characteristic of the Blackland Prairie it is incumbent upon us to preserve selected remnants of each of the seven community types which together constitute the Blackland Prairie of Texas.

HISTORICAL BACKGROUND AND CONTEMPORARY TRENDS

During the middle portion of the 19th century the Blackland Prairie was considered prime rangeland. By 1880, however, most of the productivity of the Blacklands was insufficient for the purposes of self-sustained cattle production (Nimmo, 1885). Conversion from grazing to farming economy profoundly influenced the Blacklands. Improved tillage equipment and methodology soon made possible widespread and intensive cultivation of agricultural products, primarily cotton (Bolton, 1914). Efficient, mechanized farm implements and large scale agri-business merely accelerated the decline of the Blacklands. By 1910, the region supported a higher population density than any other area of comparable size west of the Mississippi River (Goldenweiser, 1919). The Blackland Prairie continued to sustain a large rural population through the early 1900's (Bonnen and Thidobeaux, 1937), but the great drought of the 1930's forced many people to move into urban areas. This migration spawned a trend in urban growth that continues today. In all, slightly over 10% of the Blackland resource area is classified as urban (Texas Soil and Water Conservation Needs Committee, 1970a). Current figures indicate 1,725,000 ha or 68% of the land is cultivated with an additional 850,000 ha or 22% in tame pasture (Texas Soil and Water Conservation Needs Committee, 1970b). As a result of cultivation, overgrazing, and other often imprudent landuse practices, there are few, if any, remnants of climax vegetation of the Blackland Prairie. A speculative but liberal estimate as to the remaining remnant Blackland tracts would be 1% or 43,000 ha. Included within this 1% are remnant grasslands which have been managed, some intensively so, for hay meadows and pasturelands; therefore, there remains a pitifully small percentage of what ecologists would consider prime Blackland Prairie.

Today, all remaining plots are small with the largest, a commercial hay meadow, about 810 ha in extent. *The majority of the remaining prairielands are in Lamar County of northeast Texas.* These northeast Texas grasslands have remained unplowed due to their high productiv-

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ity (the result of climate, rich soils and lengthy growing seasons) which has led to their "conservation" in the form of hay meadows. Most of the hay meadows were commercialized by the 1850's and several have remained productive to this day; however, not without ecological sacrifices. Production has been maintained through heavy application of fertilizers and herbicides. The ecological consequences are obvious and need not be detailed herein.

Yet another center of remnant prairies is the area around Temple and Waco in Bell and McLennan Counties respectively. Virtually nothing remains in the southwestern region of the Blacklands between the Colorado and San Antonio Rivers in the vicinity of Austin and San Antonio.

Today as municipalities grow and expand and as land increases in value, more and more remnant plots are being replaced by suburban developments, trailer parks, industrial districts, retirement ranchettes, urban sprawl, feed lots, or cropland. Such biological travesties are proceeding at an unprecedented rate, tragically enough in spite of today's so-called "environmental enlightenment."

REMNANT BLACKLANDS: AN OVERVIEW

A brief review of the remaining categories of Blackland Prairie reveals that the need for prairie conservation in Texas is imperative if we are to conserve even the most meager representative Blacklands remnants.

Remnant Blacklands include life estates and similar legal trusts which have somehow maintained the land in its natural character. Also there are parcels which have been maintained through long term ownership by single families. Unfortunately, most of the Blacklands in such categories are held by elderly individuals with few, if any, provisions made for the custody of the resource upon their deaths. Although no figures are readily available on the quantity of Blacklands held in such a manner, it is strongly suspected to be relatively high. But the elderly owners of Blacklands constitute one of the most significant factors responsible for the preservation of parcels of grasslands not only in Texas but also elsewhere. Perhaps because the elderly are tied to a traditional life on the prairie or to the yearly practice of harvesting the variety of forbs, grasses and legumes from a hay meadow they seem to venerate the unbroken prairie sod. Once the land resource is inherited by younger generations, however, the prairie is invariably "plowed under" for a seemingly more profitable endeavor.

A miniscule portion of the Blacklands has been preserved through direct private action or indirectly by conservationists who have shown an owner the value and merits of prairie conservation.

Unfortunately, lands held in the abovementioned categories are destined to be short term holdings, at least under our present laws governing taxes and land value assessments. Without tax incentives and tax laws which recognize the value of the conservation of significant natural resources there can be little hope for privately financed conservation endeavors.

Municipalities and industrial interests have within their jurisdiction some excellent remnants of the Blacklands, but these plots are destined to be consumed. Such land is owned purely for expansion or for speculative purposes and unless there is a remarkable turn of events all prairielands in this category will invariably be destroyed. Today we know of remnant Blacklands within the corporate limits of Temple, Waco, and Dallas, Texas, but their destiny appears to be all too clear.

The State of Texas apparently owns no remnant parcels of the Blackland Prairie, not even within the State Park System. There are, however, plans by the Texas Parks and Wildlife Department for prairie management and restoration within the State Park System.

Parenthetically, we should acknowledge the restorative measures which have been

initiated by a few dedicated Texas conservationists. Although these individuals are few in number, their contribution is particularly significant because they have demonstrated that prairie restoration in the Blacklands is indeed feasible, given dedication, perseverance, and time. We must not, however, be deluded into accepting prairie restoration as the ultimate solution to the conservation of our irreplaceable prairie resources, for restoration is merely a single, although important, aspect of prairie conservation. Meaningful prairie conservation must concentrate upon the acquisition of ecologically and biologically sound tracts of remnant grasslands.

None of the State owned universities own any preserves or natural areas in which there remain significant portions of Prairie. However, the Texas Research Foundation at Renner, Texas was recently deeded to the Texas A&M University system as a research station and contains a small Blacklands plot.

Because of the special nature of a land grant university system an assessment should be made of lands over which the State universities may exercise some control. The result of such an assessment could conceivably reveal that the State does indeed have a great deal of influence over some valuable Blackland Prairie remnants.

Private academic institutions neither control nor own any parcels of Blacklands; however, such institutions *may* be able to exercise significant influence over the disposition of prairielands. It is possible that within the public school lands of Texas there are extant remnant Blacklands; at this time, however, we are unable to verify this contention.

The most significant remaining tracts of Blackland Prairie are the private, commercial plots managed for native hay production. In fact, the largest single remaining tract is an 810 ha hay meadow in Lamar County in northeast Texas. Although Blacklands managed as hay meadows still maintain the character of a prairie whose sod has not been broken, they are far from prime examples of pristine Blackland community types. Mowing and the arbitrary use of herbicides and fertilizers to increase production have greatly diluted the native biota which was once a part of these prairies. Yet these very hay meadows may form the backbone of an extensive Blacklands preserve, for through management they can be restored and in time they will recover completely.

Aside from the very minor contribution made to the remnant inventory of Blacklands by "defacto plots" and others which are usually inaccessible for exploitation, such as corner plots, rights-of-way, and rough inaccessible terrain, the two remaining categories of remnant prairie are lands owned either by the Federal Government or by private non-profit foundations.

The United States Department of Agriculture controls 202±ha within its Blacklands Research Station at Riesel and Temple. Some of the remaining plots have been studied extensively, particularly with regard to the effects of fire and mowing (see Smeins, 1972). One of the Station's plots was among the first stand of Blackland Prairie to be quantitatively analyzed. Dr. E. J. Dyksterhuis studied the Blacklands here in 1946 (unpublished manuscript). Unfortunately, as in all large agencies, there is frequently a lack of purpose, sensitivity, or well defined goals; at the Blackland Prairie Research Station this had led to the arbitrary destruction of significant parcels of prairielands to be replaced by the ubiquitous sorghum and cottom fields. Too, watershed research has led to the disturbance of other fine remnant plots. Had the Federal Government understood the plight of prairielands in Texas it is doubtful that the pristine prairie would have been destroyed for such short term gains.

Other Federal Agencies, such as the Corps of Engineers, United States Department of Agriculture, or the Department of Defense may own additional small prairie remnants but unless a comprehensive survey is initiated we will most likely never be able to determine the exact status of the remaining portions of the Blackland Prairie in Texas.

As in all situations there is always a ray of hope. The Texas Chapter of the Nature Conservancy now owns a 40 ha prairie in Lamar County, now known as Tridens Prairie. Formerly a hay meadow, this parcel is now recovering nicely and represents one of the singularly most

unique community types of the Blackland Prairie, the *Sporobolus-Tridens-Paspalum* type (see Collins, Smeins and Riskind, this volume, for a detailed description of this community type). Tridens Prairie represents the only tract of Blacklands which is now held in perpetuity by any method--it is therefore a milestone for Blackland Prairie conservation in Texas. All remaining plots are vulnerable and subject to destruction and it is altogether too clear that an entire ecosystem with its concomitant communities is threatened in Texas.

CONSERVATION STRATEGIES

Thus far we have presented a rather pessimistic summary of the plight of the remnant parcels of Blackland Prairie in Texas. That grasslands over the world are threatened is no new revelation, but until now few conservationists have attempted to focus attention upon the Blackland Prairie of Texas. As we shall see, conservation of grassland resources has much in common the world over.

Delineation of conservation problems is often easy, but the issue of paramount importance is one of delineating a vehicle for action.

As has been mentioned earlier in this conference, we know of approximately 360 remnant tracts of Blacklands as of 1970. Eighty-three of these have been quantitatively sampled. All were prime candidates for natural preserves. Today, however, about half of these prime 83 tracts have been destroyed. Some are now cultivated fields of milo or cotton; others are suburban developments. Although the 1970 survey was effective, it was not comprehensive. There was no subjective appraisal of the resources, nor were any provisions made for monitoring the resources.

In order to create a viable, dynamic program for Blacklands preservation we must first establish a Blacklands inventory and survey. At present a similar project called "The American Prairie Inventory" is being conducted by the Nature Conservancy. This project is indeed ambitious, but we are more chauvinistic and, without detracting from such a comprehensive survey, we would like to focus attention on the Blackland Prairie of Texas--a truly remarkable and seldom appreciated grassland resource of North America.

Our proposed survey would appraise the resources as well as locate them and provide the all-important ownership and historical data. The community types described by Collins, Smeins and Riskind (this volume) would serve as the basic descriptive tool for the Blacklands survey.

Obviously, an organization is needed which can serve to direct, fund, and coordinate the requisite guidance. Such an organization is now in the incipient stages of formation in Texas and is to be called the Texas Prairie Foundation. This organization will act as a clearing house for all information pertinent to the Blackland Prairie in Texas (other types of grasslands in Texas will as well be included). The Texas Prairie Foundation will also fund, buy, sell, trade, accept as gifts and/or administer life estates for the purposes of conserving prairielands within Texas. In addition, it will direct research, provide for educational materials and information relevant to prairie resources, management, and restoration and will offer consultation services for those in need of advice on the conservation or management of prairielands. A governing board will administer and manage all such grasslands as become the property of the Foundation. In essence, the Texas Prairie Foundation will act as a forum and clearing house for all matters pertinent to grasslands in Texas, with special emphasis on the Blackland Prairie.

Although the formation of a Prairie Foundation in Texas would do much to further the conservation of grasslands within the State, we must recognize that the Foundation is only a means to an end and certainly not an end in itself. It is only through well organized, highly

vocal interest groups, both public and private, that conservation efforts become fulfilled; to be successful we must utilize and affect the numbers of *existing* conservation entities whether they be local or national, public or private.

Basic to all conservation endeavors is a comprehensive program of sound landuse planning which, unfortunately, has yet to be adopted either statewide or nationally. The various Councils of Government throughout Texas may eventually succeed in promoting a semblance of sound landuse planning but all too often the "COG's" are mouthpieces for growth-and-development motivated organizations. Nevertheless, several Councils have been paying particular attention to the conservation needs of their areas. It remains our public duty, however frustrating, to try to influence the institutions which can potentially be of assistance in attaining grasslands conservation as well as sound programs of landuse planning.

The institutions of higher learning must be drafted into action for, as has been eloquently stated by Hugh Iltis (1969, 1972a, 1972b, 1974), if the universities as repositories of knowledge and influence are not interested in conserving our natural heritage, then we are indeed lost.

Texas is unique among most states in that its universities do not maintain a system of natural area research stations. Certainly the larger more prosperous range and agricultural oriented universities such as Texas A&M and Texas Tech would do well to begin a program for acquisition of ecologically significant lands upon which to conduct research and monitoring of native grasslands. Oregon, Washington, Illinois, Wisconsin, Indiana and California have excellent systems of this kind which we would do well to emulate. Since most of Texas was historically grassland any system of natural research areas should reflect this biological fact. Other State institutions must acquire significant natural areas with particular emphasis on grasslands, for the grasslands are disappearing at an unprecedented rate. The Texas Parks and Wildlife Department has enactments which provide for the acquisition of natural areas, but funds must be appropriated by the State legislature for each proposed acquisition. Necessarily, therefore, the public must again lobby for specific conservation measures.

The State Highway Department would do well to emulate Iowa's program for maintaining native grasslands within the highway rights-of-way. The area within rights-of-way in the Blackland Prairie makes the conservation potential impressive. But initiative on the part of the Texas Highway Department must be cultivated. Such is the public's never-ending task.

Conservation of a large, significant natural area is often enormously difficult; e.g. Tall Grass Prairie National Park, but what of the difficulties encountered in attempting to protect a patchwork of small plots scattered over a vast area. The drawbacks appear to be insurmountable, but there is nothing unique about such an approach. Many of our National Parks and State Parks contain several distinct subdivisions as do our National Forests. The Big Thicket Biological Preserve contains a number of ecological units spread over several hundred thousand acres in southeast Texas. The precedent has been established and fortunately so, for in order to preserve the diverse community types which constitute the Blackland Prairie we must acquire small unconnected plots. Some parcels would be remote, but nevertheless any preservation of the Blacklands should include each major community type. At present there is only a small hope that we will be able to preserve the biota of these prairie communities but we certainly must attempt to preserve a representative portion of the plant communities. Hopefully, the remainder of the biota will follow. Unless action is taken in the very near future it is doubtful whether there will remain examples of each of the Blacklands community types. International concern for the loss of individual species is, at present, profound; how shall we demonstrate our concern for the inevitable loss of a biotic community?

CONCLUSIONS

The Blackland Prairie of Texas represents one of the nation's outstanding grassland resources, yet it has been exploited nearly to the point of oblivion. Small, widely scattered plots are all that remain. Of the seven major community types within the Blackland Prairie, only one is thus far preserved in perpetuity--the 40 ha Tridens Prairie in Lamar County, northeast Texas. If the remaining six community types of the Blacklands are to be preserved, as well they should be, conservation measures will have to be taken decisively and deliberately and in the very near future, for the prairie resources are being consumed by the relentless purveyors of "progress."

It has been intimated that the soon to be formed Texas Prairie Foundation will shortly assume an active role in prairie conservation in Texas; yet, it is only through active and vocal public participation that conservation can be successful. It is the public who must solicit and demand conservation programs of our State and Federal agencies. The public must lobby for landuse planning and tax relief for conservation lands in public and private ownership. Moreover, authorities and academicians must continue to give unselfishly of their expertise on ecological matters or management practices so that the lay public can translate this sound advice into demands and/or action. Such cooperation has worked in the past, but we must not relent if it is to work in the future.

Finally, we feel it necessary to emphasize land acquisition of ecologically sound remnant Blacklands as the most significant conservation measure. Although merely acquiring land, either through State or Federal agencies or through private foundations, is but a simplistic conservation beginning, it is nevertheless a step in the right direction. Management policies and guidelines can be integrated into a comprehensive conservation program in due time; but if we fail to acquire representative remnant tracts of Blacklands today, there is every likelihood that they will not be available tomorrow--we are all too painfully aware of the consequences of delay in the conservation movement.

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ABSTRACT

The threat to the biological integrity of the Blackland Prairie of Texas is discussed. Historical events as well as recent and current landuse practices which pertain to the continued existence of the few remaining climax remnants of the Blacklands are outlined. The status of the Blacklands communities as viable biological resources as well as the mechanisms for prairie conservation in Texas are elucidated.

KEY WORDS

Blackland Prairie, conservation, natural areas, grasslands, prairie, Texas, Blacklands.

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PRAIRIE MANAGEMENT AND RESTORATION IN THE STATE PARKS OF TEXAS

David H. Riskind and Arnold G. Davis

An awareness of the potential for using native plants and for synthesizing, restoring and managing plant and animal communities is increasing in the Southern Plains. New applications, better propagation techniques, and the tremendous potential for selecting the most desirable ecotypes (varieties) is stimulating this increased awareness in the utilization of native plant species. Consequently, demand for using native seeds and vegetative materials in a wide variety of programs is growing.

Livestockmen now want adapted native grasses and forbs for rangeland seedings and pasture plantings. They realize that most of the plant varieties on the market are not adapted to wide areas of Texas. Most commercial varieties originated farther north and when they are moved south of their adapted range vigor is greatly diminished, forage production is reduced, seed set is generally poor, and longevity of the stand is decreased.

Many legumes and forbs once common in the prairie communities of Texas are now only infrequently encountered. Overgrazing by livestock and excessive browsing by wildlife has all but eliminated many of the desirable plants. Some will increase with proper grazing management where adequate remnants are found, but many can be re-introduced only by seeding followed by prudent management techniques.

In Texas parks and on limited acreages of private lands a movement to restore or synthesize the native plant communities is gaining momentum. An increased awareness of our environmental deterioration, concern for and interest in natural vs. "artificial" biotic communities, and the splendid color and textural contrasts offered by native plant communities has apparently stimulated an increased desire to restore and/or preserve increasing portions of our natural environment.

In many of our state parks or, for that matter, most of Texas, the true prairies are gone or greatly modified from "climax" conditions. However, prairies can be re-created or synthesized by seeding complex mixtures and through the re-introduction of native vegetative materials, although such a program requires that quantities of adapted native plant materials must be available.

Part of these needs can be supplied by harvesting stands of native plants, but very limited demand can be filled in this manner. Seed production in native stands is not reliable in the South. Weather extremes, insects, soil conditions, previous management practices and other factors affect the seed yield from season to season. Often yields (in PLS/#) are disappointingly low and the quantity is not large enough to satisfy even meager demands. For these reasons, it is important that a strong program of native plant selection, evaluation and subsequent "variety" release is maintained. Such a program helps to insure that known plants of proven capabilities will be grown and eventually offered on the commercial market.

In 1973, the Texas Parks and Wildlife Department entered into an agreement with the Soil Conservation Service, USDA, to cooperatively study adapted native plant selections under controlled conditions in state parks.

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This arrangement mutually benefits both agencies. The Texas Parks and Wildlife Department's vegetation management and restoration program is strengthened by being able to obtain sufficient quantities of *adapted* native plants for use in revegetation programs within the State parks. The SCS benefits by getting information on adaptation and production of selected plant materials under "controlled" conditions. Techniques of establishment, comparisons of promising strains and potential value of candidate varieties are cooperatively studied and evaluated.

Initial studies are conducted at the SCS' James E. "Bud" Smith Plant Materials Center, Knox City, Texas. Over one thousand collections of native grasses, legumes, forbs and woody plants have been established there for study and potential increase. All native plant collections are quantitatively and qualitatively compared to each other and to a standard commercial variety if available. Only the most promising are selected for increase and further testing under field conntions. Seed and vegetative material from over fifty selections of the most promising species are currently being produced in quantity.

From information collected at the Knox City Plant Materials Center, field studies in Texas parks and on the farms and ranches of Soil and Water Conservation District cooperators new plants are selected for release as named varieties. They are released into the market only after information on adaptation and superior characteristics are adequately known and documented in field trials.

Use of plant materials developed and selected jointly by the Soil Conservation Service and the Texas Parks and Wildlife Department within the State parks of Texas is diverse and multifaceted. Due to the relative youth of the cooperative effort (slightly less than two years) it has yet to develop into a tightly structured program. What follows then is largely an outline for prairie management and restoration within the state parks of Texas.

The first phase of the program was to determine the condition of the grassland resources within the state parks. Within a short time and after considerable field work a reasonable concept of the existing resources within the state park system was obtained. Resource management plans in selected parks were developed accordingly.

Although the ideal type of management program would seem to involve community rejuvenation through management and/or restoration, due to pragmatic considerations this has not always been our objective. However, we might add that such a goal is something that we would like to someday attain throughout the state park system. Instead we are dealing with only carefully selected small plots usually less than 5 ha in extent. At the present time we have developed several significantly different levels of management and restoration programs for biotic assemblages within Texas' state parks but for the purposes of this Conference we will confine our comments to grassland or prairie restoration.

For clarity as well as for the purpose of establishing a reference point to which we can all relate, let us briefly outline the various types of grasslands with which we are dealing in the Texas state park system. Although the western two-thirds of Texas has been characterized as grassland of one type or another, we will refer only to those categories of grassland which can be accurately described as prairie.

In the interest of brevity we have also excluded the more complex issue of Texas' savannahs from this discussion, but mention should be made that others have included savannahs within discussions of mixed as well as true prairie (Dyksterhuis, 1946, 1948; Allred and Mitchell, 1955; Launchbaugh, 1955; Weaver and Albertson, 1956). Each of the following categories of prairie are found within the Texas park system: short grass prairie, mixed prairie and true prairie, including some tall grass prairie. Detailed descriptions of each of these grasslands can be obtained from a rapidly growing body of literature (Dyksterhuis, 1946, 1948; Tharp, 1952; Allred and Mitchell, 1955; Allred, 1956; Collins, Smeins and Riskind, 1975) and we will

therefore not describe them herein.

Of the categories of prairielands, mixed prairie is best represented in the state park system, followed by short grass prairie with the true prairie being most poorly represented. In terms of physiographic place names the representation of grasslands in order of decreasing occurrence in the Texas state parks are: Rolling Plains, Llano Estacado or High Plains, Grand Prairie (including Fort Worth Prairie), Coastal Prairie, and Blackland Prairie (including Fayette and San Antonio Prairies).

Unfortunately, the quality of prairielands within the Texas park system is uniformly poor, or in the parlance of SCS range conservationists, in fair to good condition. Admittedly, there had not been a concerted effort in the past to acquire excellent examples of grassland resources but also to be considered is the simple truth that there is a paucity of climax grassland available for acquisition in Texas. Then, too, it is only in recent times that an appreciable segment of the public has become interested in the acquisition of grasslands for conservation purposes. Nonetheless, most of the prairielands within the Texas park system can be categorized as *restorable* although some tracts should be considered restorable only with the understanding that the restorer is exceedingly patient.

Parenthetically, we should interject a brief note in reference to our management and restoration philosophy. Our ultimate objective is to restore the natural processes to the natural areas within our state parks. Of course our management and restoration work interferes, at least temporarily, with natural phenomenon but our activities are designed to accelerate the process of natural succession and thereby speed the recovery of the communities toward their climax potential.

In the case of the very best portions of remnant prairie in Texas parks we are talking about a relatively simple, uncomplicated management program; a program including controlled grazing, burning, mechanical or hand shredding, limited chemical control (spot application), seasonal mowing, etc. Also within the category of simple management would be the introduction of limited quantities of selected native plant materials.

Grassland restorative measures in the state parks are by contrast the most elaborate, time consuming, costly, and procedurally complex. It should be understood that management is also inherent in all restoration projects just as it should be understood that all good management is restorative in nature. Grasslands falling within the "restorable" category are usually characterized as grazing disclimaxes (zootic disclimax) and without exception the vast majority of grasslands within Texas' state parks have in the past been severely overgrazed. Translated into ecological terms, the starting point for grasslands restoration in Texas parks is invariably somewhere within the very early stages of secondary succession and frequently there are no nearby seed sources of the desirable climax species to facilitate natural revegetation.

In such cases the SCS Plant Materials Center at Knox City, Texas provides the TP&WD with the necessary plant materials. It should be clearly understood, however, that detailed grassland restoration projects normally require several years of advance preparation, planning and seed production.

A comprehensive restoration program would include a detailed site description, land use history, biological surveys, soil surveys, and collection and production of the necessary plant materials (in certain parts of the state selected adapted native plant materials are available commercially). Previous to any ground work, all the various parameters of the restoration plan are organized into a formal resource management plan which is then looked upon as a procedural handbook specifically tailored for each particular restoration project.

Site preparation for restoration plantings seem to span the range of possibilities, and rightly so, for our projects deal with different types of prairielands throughout the diverse regions of Texas. We have seeded into dead litter crops in north Texas and have seeded directly into Johnson grass stubble in central and south Texas. We have fallow plowed and seeded into

clean, weed-free seed beds or have seeded into recently burned plots. We have seeded complex mixtures simultaneously or have applied plant materials in the more traditional two season (fall, late winter) method. Most of our seeding has been with a Nisbet range seed drill, but we have also seeded by hand broadcast or by spreading hay. We have transplanted prairie sod and have achieved a reasonable degree of success. Our restoration projects have varied in size from small interpretive plots to 100 ha fields.

We feel that we have tried a reasonable spectrum of restorative measures--all using native adapted species. It is unfortunate that we have yet to experience sufficient time "in the field" so that we could present glowing results at this conference. We have carefully directed our restorative programs toward state parks for which we have both sufficient natural resource data and sufficient adapted native plant material and thus we would hope to insure a greater degree of success in our endeavors.

Most of the more conventional restoration methodologies have long been applied in the Midwest and Plains States and it is because of the previous experimentation that we have been able to proceed with such confidence and apparent success. We are indeed indebted to our precursors.

Long range goals to be included in TP&WD grassland restoration projects include detailed monitoring programs (which in turn provide feedback to our SCS-TP&WD cooperative native plant materials development program and to the improvement and refinement of management techniques) as well as accompanying interpretive programs directed toward increasing public interest in and awareness of our dwindling grassland resources. In fact, we have routinely involved the public on a volunteer basis in management practices, e.g., selected removal of woody invaders, fire control and hand collection and broadcast of desirable grass and forb seeds. Such involvement, we find, is an excellent method for stimulating public interest in grasslands or indeed, conservation and restoration in general. We need not remind this audience that all conservation and restorative endeavors profit from public interest, awareness, and involvement.

Our ultimate long range goal is the creation of sufficient governmental and public interest in the acquisition of remnant prairielands of superior quality. We can think of no better way to demonstrate the value of a natural prairie than by involving others in the agonizing, time consuming trials and tribulations of prairie restoration! Truthfully, however, we believe that there is no substitute for the preservation of natural prairielands. Restoration, in the final analysis, should be considered as only a valuable tool and not an end in itself.

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ABSTRACT

The Soil Conservation Service and the Texas Parks and Wildlife Department are cooperatively involved in the production of native, adapted plant materials for use in prairie restoration projects in the State parks of Texas. Basic methods for the evaluation, selection, and production of adapted native plant materials are discussed. Prairie resources, as represented in the state parks of Texas, are briefly reviewed and assessed. Management and restoration philosophy and methodology for prairie resources within the Texas state parks are elucidated.

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SENSING OUR PRAIRIE HERITAGE: ENVIRONMENTAL EDUCATION AND COMMUNITY VISIONS

Gary Paul Nabhan

Carl Sandburg has a yarn describing the arrival of newcomers to the Great Plains. As wagon after covered wagon of peoples of different temperments ask, "What kind of folks live around here?" the Early Sodbuster of Kansas has a dry reply. "Well, stranger, what kinds of folks was there in the country you come from? ... that's about the kind of folks you'll find around here."[1]

That tale helps us realize the prejudices with which most of us approach a place and its life. Without the perceptual, historical and ecological roots of their assumptions being recognized, variations of simple cliches still organize the way many people treat the grasslands. The ideas that the Central Grasslands are plain and monocultural and that they are the mainstay or heartland of America are functioning cliches.

In *The Great Plains in Transition*, Carl Kraenzel notes that inappropriate assumptions, traditions and institutions sooner or later lead to failure in the plains:

> They blamed their misfortunes on the climate (drought, hail, blizzards, dust) and its attendant rigors (leaf rust and grasshoppers). Inexperienced in the conditions that make for the uniqueness of a semi-arid land, they did not look for an explanation of their hardships in the inappropriateness of their forest way of living. They failed to see the need for fitting their institutions and their philosophy to the facts of the semi-aridity of the plains.[2]

This presentation describes three efforts in grasslands-oriented environmental education which work with the region, the biome. Part One presents a special field study by three Prescott College students, "The Literature, Natural and Cultural History of the Great Plains and Prairies." It is tempered with Part Two, regarding Pleasant Valley Farm, Illinois, a year round environmental education center of the Community Renewal Society. Part Three mentions the Wright-Ingraham Institute in Colorado, an evolving environmental university of the Plains, while projecting into the future of learning and living within the Central Grasslands of North America.

PART ONE: A GRASSLANDS TREK

Prescott College in Arizona is a young, innovative institution most noticeably active in multi-disciplinary environmental studies, especially relating to the West and its future. Students may assume a good part of the responsibility for designing their own curriculum; my friends and I planned our own grasslands course under the supervision of a handful of professors. Cathy Preus has noted that during pre-course preparation,

[1]Carl Sandburg, *From the People, Yes! Collected Poems of Carl Sandburg.* (New York: Harcourt, Brace and Jovanovich).

[2]Carl Kraenzel, *The Great Plains in Transition*. (Norman: University of Oklahoma Press).

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> ...this study changed in conception as my reading progressed and as I began to grasp some of the profound meaning and depth and variety of the people and history of this land. It began to dawn on me that what I and my two friends ... were attempting to do was in effect – seek out and try to understand our own American Heritage. I began to realize that there is some real, solid history to America, the continent, and to epic America from the 1500's until today. And most important, I began to discover my roots.[3]

I would like to emphasize two aspects of our grasslands studies:

1. Consideration of "prairie ecology" as the study of both natural and cultural phenomena.
2. The circular feedback we developed between readings and interviews, and field activities.

To get a sense of regional life, our studies often took focus on the relationships between natural and cultural elements. Prairie ecology includes human ecology. We were interested in the Scandinavian immigrants to the Northern Plains, as well as in the grasses and forbs and land uses which came along with them. We learned about the bison through the eyes of the Plains Indians, geographers, ethologists, ethno-zoologists and artists, and with our own eyes.

That other emphasis, field experiences in the context of background studies, was also essential. The sociologist's concept of "Plain yonland" did not ring home until we spent time on farms outside of Pilger, Nebraska. Neither were the complexities of prairie restoration respected until we visited the Wilson Prairie Seed Farm, and Dr. David Lyon's roadside prairies in Linn County, Iowa.

Howard Lyon summarizes the course in this way:

> It was the American West and Mid-West, the spirit of history, literature, creation as reflected in the people and the land. There is a region that is part of us now as we are part of it ... We've been there. We'll keep returning for the rest of our lives.[4]

PART TWO: PEOPLES IN RESIDENCE AT THE PRAIRIE'S EDGE

Environmental education should gear itself to giving students a chance to "make a terrain their own" through active participation. The "terrain" or "subject matter" may be the mastery of a skill, or awareness of environmental processes. Yet it should develop a link with the student's own background. This link, through experience, can give the student the capability of extending a skill or awareness long after a class is over. Education then is not a lesson or exercise which we perform. Instead, it is the integrating of an awareness or skill or discipline as a continuing part of ourselves. We simply begin to feel at home in an activity. In regional (environmental) education, we each begin to read the landscape we're in with our own personal visions, as members of the ecological communities existing there.

[3]Cathy Preus, Literature, Natural and Cultural History of the Plains and Prairies. Unpublished journal and essays.

[4]Howard Lyon, Literature and Cultural History of the Great Plains. Unpublished essays.

Too often, "outdoor education," especially for urban minorities in this country, is irrelevant to any of the pressing needs or conditions which young people experience in their home. Until a person feels a link between his own livelihood and the ecological conditions, the critical environmental problems within which he lives, "environmental education" remains superficial and myopic.

Dealing with these problems, Pleasant Valley Farm in Woodstock, Illinois has designed a number of programs which relate natural communities and human communities, minorities and environmental issues, ethics with resource uses. Serving over 10,000 Midwesterners a year, the 460 acre site includes a demonstration farm, tent camps, gardens, natural areas, a prairie reseeding project, pioneer crafts workshops, plus meeting and recreation facilities.

Beyond facilities, the people at the Farm have a concern for relating "the natural and cultural" in ways relevant to the present needs and desires of the regional community. Through "survival" programs, food growing and processing workshops, students enter into the energy web of the farm, and more fully participate in functions essential to their own sustenance. Regional explorations allow students to visit unique features and ethnic settlements, discuss land uses with residents, and travel by various modes of transportation. People thus become aware of other social and physical components of the region, in terms of historic trends and current issues.

Through developing an environmental quality plan for the site and facilities operations, re-diversified habitats, and a culturally sensitive community, the Farm has begun to implement new fitnesses of human elements within the total environment. A staff statement in 1972 voiced this purpose:

> As a residential center for environmental learning, Pleasant Valley's evolving, continually changing intent is the exploration of new relationships of people with one another and with the earth, in order to assist people and their institutions in the renewal and rebuilding of purposes and tasks needed for a new society.[5]

PART THREE: IMAGINED FUTURES FOR PRAIRIE ENVIRONMENTAL LEARNING

By speaking for a new society, the Farm staff, among others (vanDresser, 1972), recognize a need for new expressions and syntheses of durable life - ways and forms, along with an acceptance of our regional limits to growth, as keys to a healthier future. Yet, where will the insights for a more resourceful human existence in the prairies develop from? Can there be a low energy-consuming, stabilized economy based on the intrinsic values of the grassland ecosystem? Are such ideals possible, or will environmental education always include new elegies to extirpated species, mined shale lands, channelized rivers and wasted fertilities?

The Prairie Conferences have always discussed the fitting uses of prairies and their elements. Can future work include the design of human living systems to be more fully synergized with the natural features and native organisms of grassland ecosystems?

In other ecosystems, a research group called the New Alchemy Institute has been working with ecological food production and human life support, doing much with locally available resources (Todd, 1971). A cooperating institution, the Wright-Ingraham Institute in Colorado, has begun designing an "ecologically-adapted, place-rooted" Running Creek Field Station on the Plains (Holmes, 1974). Dealing with ecology and design related to semi-arid lands, the field station now maintains grass and wildflower reseeding projects, solar and wind monitoring, plus architecture and land use experimentation. Their Architects on the Plains workshop and Grasslands Seminar in the summer of 1974 are two educational programs for residents in the surrounding vicinity.

If more environmental education can focus on our basic, cultural relationships with the life-support system (energy, food, shelter), students in the future may begin to explore functional designs adapted to the regional system, the biome.

Imagine a resident environmental education program for teenagers in which they work to maintain a mini life-support system, which includes many native growth forms for their sustenance. They live in lodgings which are partially underground, with prairie grasses (Wik, 1973) and solar collectors instead of tin rooves, plus rammed earth walls for insulation. The lodgings are almost entirely visually and audially absorbed by their semi-subterranean nature and the tall grasses above them. Apiaries and low density herbivore grazing sectors allow selected animals to participate in the management of vegetation in exchange for food. Partially edible weedy plants associated with grazed lands are harvested for human foods until a seeding/grazing balance begins to take effect. Small garden plots, orchard spots and pothole fishponds include native species used by prehistoric prairie cultures (Weidel, 1961), while using wastes from living quarters as nutrient and energy inputs (Anon., 1972). Edible berries, legumes and composites are remixed into the grasslands. Burrowing animals are the only "plows" accepted for soil conditioning after initial site preparation (Phillips and Young, 1973). "Gamebirds" are reintroduced and perennial herbage provides protection for beginning coveys. Biological control of pests is undertaken in the vicinity of food production (Swan, 1964). Windmills geared to local weather conditions assist with water-pumping and part-time energy production.

In such an idealized environment, the components of which are already designed, environmental education could form a bond between the natural environment and the "work environment" needed for human survival. Kids could mature knowing that their economic well-being not only includes ecological considerations, but that it ultimately depends on them.

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CERA: AN OUTDOOR BIOLOGICAL LABORATORY

B. F. Graham

INTRODUCTION

Given the exciting challenge of writing a set of specifications for an ideal natural area for teaching purposes, one would almost certainly include the following characteristics:

1) ACCESSIBILITY, not only for organized class trips, but, possibly more important, for individual students pursuing the answers to questions which have aroused their curiosity.

2) VARIETY. There should be something there for everyone. Just as diversity in nature determines the potential success of an ecosystem, a variety of natural communities and physical characteristics increases the chance that a natural area will satisfy the demands upon it.

3) ADEQUATE SIZE. An outdoor area must be large enough to tolerate the disturbances incident to its educational and recreational role. Trampling, collecting, trapping, seining, and vehicular use, all possibly justifiable disturbance factors, must be anticipated and regulated in terms of their potential long-range effects. A teaching area, on the other hand, must provide for "hands on" experience. If students cannot bring all five senses into use in experiencing field biology, the full potential impact of the experience is being missed.

Accessibility, variety and adequate size – guided by these criteria the Department of Biology, at Grinnell College, searched and, in 1968, acquired the Henry S. Conard Environmental Research Area. The 365 acre (148 ha) tract, in Richland Township of Jasper County, Iowa was purchased with funds made available by the Alfred P. Sloan Foundation. Dr. Henry Conard, in whose honor the facility has been named, was Professor of Botany at Grinnell for 38 years, and was an internationally known authority on the mosses and the waterlilies. His documentation of the natural history of Iowa, and of Long Island, is classic; and his little paperbacked key, "Plants of Iowa," has accompanied generations of botanists in the field in Iowa and adjacent states.

THE CONARD ENVIRONMENTAL RESEARCH AREA

The Conard Environmental Research Area, known to its friends by the acronym CERA, is, indeed, readily accessible. Eleven miles (17.7 km) southwest of the campus, it can be approached by the strongly motivated hiker, or the moderately enthusiastic bicyclist. In addition, our Department of Biology maintains three vehicles, two of which, when not in use for class field trips, are available to individual students or small groups who have data or specimens to collect, or observations to make. A good gravel county road constitutes our mile-long northern boundary, and all vehicular access to the area is from this road -- a real advantage in traffic control.

It is in its truly wonderful diversity, however, that the CERA really stands out as a superb natural laboratory! On its strongly rolling terrain, derived from Kansan glacial drift and subsequent aeolian deposits, one can work with an infinite variety of soil parameters. The topographic relief embraces 125 feet (38 m), and there are soils which have evolved under prairie, forest and floodplain. Aquatic habitats include several intermittent streams in deep wooded draws, a 1,500-foot (458 m) segment of the North Skunk River with its associated floodplain, and a 14 acre (5.7 ha) lake, constructed in 1972.

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At the time of purchase, approximately 150 acres (60.7 ha) of the 365 acre (148 ha) farm were cropped, the rest having been in woodland and horse pasture. Beginning in the spring of 1969, we have made several plantings of prairie grass mixtures, and they now occupy approximately one-half of the previously cropped land. It is our hope, eventually, to restore the remaining half, but at this time it remains our sole source of operating funds, and must continue to produce corn and soybeans.

In the prairie grass plantings at CERA, the mixtures of native species have been varied from one site to another according primarily to soil and drainage characteristics. Several planting techniques have been tried, with success ranging from good to excellent, but they must be detailed at another time. Species which have been included in the plantings include big bluestem, little bluestem, Indiangrass, switchgrass, Reed's canarygrass, sideoats grama and green needlegrass. Complementing these plantings, and equally exciting, is an area of some 60 acres (24.3 ha) along the south edge of the property which appears to have survived two centuries of man's use and misuse as pasture. Here the native grasses are in their rightful association with an abundant assortment of prairie forbs. It is our hope, of course, that the forbs, given the opportunity to recover, will find their way to our grass plantations and speed their return to the natural condition. The management problem with which we are faced here is the removal of aggressive, mostly thorny, woody invasives which are the result of overgrazing and protection from burning.

In addition to the planted and native prairie at CERA, we enjoy approximately 100 acres (40.5 ha) of planted and old growth woodland. White pine, red pine, Norway spruce, European larch and black walnut are represented among the 10,000 trees planted in 1969 and 1970. These are of interest to our small, but consistent group of students, both male and female, whose sights are set on graduate study in forestry or some related field. The trees, planted along our northern boundary, adjacent to the road, will one day, we hope, play an additional role in screening the grasslands from the many bird hunters who cruise past the area in season.

Among the older woods is a 10 acre (4.0 ha) grove near the main entrance. It is an impressively handsome stand of bur oak, apparently left from a selective cut of hickory and other species of oak. The American elms were also left, but they have now succumbed to the Dutch elm disease and become a happy hunting ground for the red-headed woodpeckers. Development plans call for a dual role to be played by this area. First, it is to be an arboretum for woody species not naturally present at the CERA. To this end, some 400 woody plants have been set out and are now locked in mortal combat with the abundant, and very discriminating white-tailed deer. Second, although we do not encourage picnics in the area, we are resigned to the fact that there will be a certain amount of picnic-type activity there. We are, therefore, hoping to confine it to a limited area near the main entrance, by providing a few picnic sites in the arboretum.

Of several other wooded areas at CERA, one, in particular, deserves special mention. This is a 60 acre (24.3 ha) forest which extends along the west bank of the North Skunk River, and occupies a deeply dissected slope rising steeply, some 120 feet (37 m), from floodplain to our Hillcrest Prairie plantation. In May the rich humus floor of this deeply shaded woodland is carpeted with a spring floral display without equal! Nowhere is the beauty of nature, nor its ephemeral quality, more dramatically illustrated than in the glorious annual splash of color which occurs here! It is an ideal place for the Taxonomy class to be introduced to a key to the spring flowers, or for the Ecology class to see, and thus believe, the orderly transition from floodplain and bottomland with its cottonwood, willow and silver maple associates to the rich upland mixture of oak and hickory species. The animals, too, abound in this luxuriant habitat. Deer, squirrel, raccoon, opossum, fox, coyote, rabbits -- all are present and have been studied by our students. Also present are dozens of species of birds ranging in size from the raucous

wren to the stately great-horned owl, and in color from the drab catbird to the flashy red-headed woodpecker. The soil is teeming with life, and each organism plays host to many others. Even the least imaginative student, in a laboratory like this, can find questions to pique his curiosity and start him on the quest that is the science of life.

In conclusion, a word seems appropriate about the kinds of uses which, after five years, characterize CERA. None of us in the department is surprised at the fast-growing popularity of the lab in the obvious academic areas. Advanced courses in Plant Taxonomy, Mycology, Limnology and Plant and Animal Ecology draw heavily on the variety of resources there; and, as mentioned earlier, Independent Student Research, a course for junior and senior majors, provides for most participants a first exposure to the thrills as well as the frustrations of investigating the structure and function of nature. Other colleges, within a hundred-mile radius of Grinnell, are beginning to find it a worthwhile experience for their students to travel to the CERA for exposure to its rich diversity of habitat types. At the professional level, on the other hand, Iowa State University soil scientists have found that the CERA offers an opportunity for long-range study of the effects of various cultivation techniques on soil erosion in corn. Reasonable assurance of minimal disturbance in long-term studies is, of course, one of the most valuable assets of a facility like this. Another such study, initiated by one of our faculty members, is evaluating the effect on prairie succession of small rodent exclosure. Recently, a degree of immortality has been imparted to the Conard Environmental Research Area with the naming of a new species of springtail first observed in the forest litter there. The scholarly description of *Friesea cera* reads, in part, "...with larger lamella simple, small lamella with three very small teeth; mandible with seven or eight teeth; tibiotarsus without clavate tenent hairs; unguis untoothed; tenaculum bidentate; mucrodens one and one-half to two times length of the longest anal spine..." (Christiansen and Bellinger 1973).

As impressive and gratifying as this kind of feedback from the research area is, I must confess that I derive an equal amount of satisfaction from the enthusiasm and perceptive appreciation frequently demonstrated by the growing numbers of public school students who come to see, at CERA, some of the things they have read and talked about in class. One of my second grade friends, for example, wrote, "Dear Mr. Graham. Thank you for taking us through the woods. I found three pretty rocks in the field, and during the next day we found a tick in my eyelid. Your friend, Jay." Jay's classmate, Kurt, wrote, "Thank you for showing us around the CERA. And what I liked is the deer tracks and the birds." And always helpful in encouraging a teacher like me to temper his enthusiasm with objective reality are incisive notes like the one from Annette, whose enthusiasm at this time has, I hope, outstripped her ability to spell. Her note read, simply, "Dear Mr. Graham. Thanks a million for the tripe."

ABSTRACT

Purchased by Grinnell College in 1968, the 365 acre (148 ha) Conard Environmental Research Area (CERA) has become an educational facility of increasing popularity for a variety of groups and individuals. It is a highly diversified area, in central Iowa, dedicated to the study of the structure and function of tallgrass prairie and associated ecosystems. It is being developed to satisfy the many demands of class study, individual research and the kinds of nature oriented recreation for which it is uniquely suited.

KEY WORDS

Iowa, grassland, prairie, Conard, Grinnell College, field station.

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THE USAGE OF GOOSE LAKE PRAIRIE STATE PARK

Joseph J. Nyhoff

Goose Lake Prairie State Park is located in northeastern Illinois, 95.6 km southwest of Chicago. It is situated just between Interstate 55-66, a major North-South artery and Interstate 80, a major East-West artery. It is within two hours driving time of eight million people, the population of Chicago and surrounding suburbs.

Goose Lake Prairie State Park is the largest prairie remnant in Illinois. It has dry, mesic and wet prairie, marshes and pot-hole ponds. The park is predominantly tall grasses: Big bluestem (*Andropogon gerardi*), Indian grass (*Sorghastum nutans*), Little bluestem (*Andropogon scoparius*), Switchgrass (*Panicum virgatum*), Prairie Cordgrass (*Spartina pectinata*) and blue joint (*Calamagrostis canadensis*). The total park acreage is 954 ha, almost 2/3 of which is nature preserve. The nature preserve varies from a small area of virgin prairie to grazed dry areas that have huge numbers of hawthorns, to wet prairie predominantly covered by blue joint grass, to several small severely disturbed areas of Kentucky Blue (*Poa pratensis*) formed when the area was farmed, homesteaded or heavily grazed. The Nature Preserve originally was the site for 1/3 of a 809 ha lake called Goose Lake. In the 1890's drainage began and by 1910 the lake was reduced in size to 297 ha. In 1973 there were less than 40 ha of open, shallow water scattered throughout a large marsh. The prairie was and is even today too wet and too rocky for any farming operation.

The remaining 342 ha lying to the south and west of the Nature Preserve are approximately 3.04 m higher in elevation and therefore drier. This area was farmed and pastured from the early 1860's until purchased by the State of Illinois in 1969 and 1970. It is this surrounding buffer zone that is being used for the placement of support facilities.

Goose Lake Prairie was set aside in order to preserve prairie vegetation and keep alive the heritage of the Prairie State. Its second and third primary functions are to serve as an area for research and education. But being a state park it belongs to the people of the state and as such should be accessible to them. To serve all three purposes requires some rules and regulations restricting activities in this environmentally unique park.

Due to the park's location and the publicity it has already received, it draws a wide range of visitors. There are basically five groups of people who use Goose Lake Prairie State Park. They are the prairie researchers, students, environmentally active groups, the general public, and volunteers. Each group has special needs and interests. Researchers are the smallest group and probably the easiest to accommodate. Anyone wishing to do research at Goose Lake Prairie State Park has first to obtain a permit from the Nature Preserve Commission stating the purpose of their research and when they will be doing their work. They are then allowed to enter special areas of the park and bring along certain specified equipment. Copies of their results are submitted to the Department of Conservation. In 1974 there were ten projects underway. Individuals are studying such subjects as bees, and the short-billed marsh wrens and, surveying the mammals, plants and insects.

Students visiting the park range in age from college ecology classes to first and second graders. There are obviously fewer college classes and they are generally smaller in size than the grammar school classes. Graduate and undergraduate classes are given much more latitude to observe the prairie. But the professor is still required to sign a ledger in the office stating which area he wishes to enter and the number in his group. At this time he is advised as to which areas are too wet to allow usage and about any other factors limiting traffic on the prairie.

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High school and grammar school classes almost by sheer weight of numbers must be restricted to a trail system.

The activist groups such as the Audubon Society, Sierra Club, Chicago Academy of Science, and the Morton Arboretum field trips are small enough in numbers and advanced enough in knowledge to be restricted only as far as are college field trips. Groups such as these sometimes bring in their own tour leaders or ask the park for assistance. Due to a limited staff these were the only groups that until last June we were able to provide with a field trip leader. This summer was the first summer that we had a summer interpreter. His job is to lead field trips as well as plan a trail guide and establish signing on the new trail. The park does need a full-time interpreter and one is anticipated for fiscal year 1976.

The fourth group, the general public, makes up the bulk of our visitation. They are the most difficult group to handle. In general they expect a state park to have at the very least a campground and picnic area. Any park named Goose Lake should have fishing, or boating or swimming! John Q. comes expecting to find an area whose sole existence is for the pleasurable use of his leisure time. This doesn't show a lack of intelligence on his part. It shows the enormity of our job in educating him to the value of a prairie park. He comes from a plastic, urban world. He may come from any level, from blue collar to corporation executive. In his environment he has developed some specialized skills such as truck driving, T.V. repair, machine operator, lawyer or accountant and made other adjustments necessary for survival. Anyone who can succeed in today's complicated world is not dumb. But he sees Goose Lake Prairie State Park as an area devoid of shade, full of harmful insects and set aside for the preservation of grasses which he associated with weeds and the grass in his lawn that he keeps manicured and would never dream of letting go to seed. The link between fertile prairie soil and the steak he ate last night is so remote for him that he could never make the connection on his own. To him the prairie is foreign and therefore hostile. The prairie must be interpreted for him. In order to do this two basic problems must be overcome. First is the prejudice against being taught. He has survived all this time without knowing about the prairie, and, learning is work! He is supposed to be enjoying himself. Second is the fact that in his daily life he is so bombarded with sights and sounds from T.V., radio, billboards, newspapers and all the other ploys of the sophisticated advertising world that his senses are numbed and it is hard to get his attention. Interpreting the prairie for him requires trained personnel and certain basic facilities.

The first facility necessary is parking. America drives, at least now. Parking should be controlled. That is, a definite number of spaces in a certain place, not haphazard along a peripheral road. It must be located in an area close to the prairie but somewhere in the surrounding buffer zone. By having a single entrance to the prairie the field staff can monitor the number of people using the park and determine for what purpose they have come. There is a 285 car, 30 bus parking lot. A .8 km entrance road to the parking lot serves to bring the public closer to the prairie before leaving their car and serves as the main entrance to the park.

The next facility necessary is some form of orientation building or nature center. This building serves as a transition zone between the air conditioned car and the walk on the prairie. Displays, audio-visual equipment and an information booth will all serve to familiarize the public with the prairie and to prepare them better for their walk. Goose Lake Prairie State Park has planned a two phase orientation building. Phase one would house offices, information booth, sales counter (for such things as bird check lists, field guides, binoculars, etc.), an audio-visual and display room, drinking fountains and restrooms. It is designed to create a traffic flow that goes from the parking lot through the building up on to the roof and then down a ramp onto the nature trail: Which brings us to the next facility necessary, a network of trails. To foster the activities and attitudes which we desire, a nature trail into the prairie is necessary. There are basically two types of trail used for nature trails; native and surfaced. At Goose Lake Prairie State Park our main heavy use interpretative trail will be raised by gravel 38.1 cm

because the area is wet in the spring and fall. We are going to use CA6 for the base, a brown river gravel with a 7.62 cm cap CA 10. This is a relatively chemically inert substance. Construction of this trail was to be done during the winter months while the ground was frozen so as not to damage the native vegetation, but in 1974 there was a major thaw on January 8th and the ground never froze again. A mowed trail was rejected because the area is too wet during most of the year and a mowed trail is almost impossible to put in and maintain due to the clumps of native grasses. These clumps also make walking very difficult. We felt that wood chips would not be an acceptable trail surface for aesthetic reasons and they are not chemically inert. White gravel was ruled out on the same grounds. For the past three years we have used an old road as a trail into the park. The public has not ventured off the road into the tall grass. This old trail, having been a road through, is rather straight. They have not cut corners on the curves as they do on wooded trails so no fencing is felt needed. It is customary in trail building to go no more than 30.48 cm before curving the trail because we wish to keep an element of surprise and also hide the fact that there are groups of people ahead and behind on the trail. I wonder if this is a viable concept on a prairie trail because after burning in the spring and when the standing dead is all matted and the new grasses aren't full height there is an open view. This view does not close until the grasses reach 1.82 m.

There are several limitations on the length of the trail (chiggers, mosquitoes, ticks, flies, no shade, etc.). Therefore, it is believed that a 1.6 km trail with a 1.8 km loop will suffice for the general public's desire for walking. A section of this trail will cross a marsh area and floating bridges will be used. Additional trails may be planned but the particulars have not been determined yet.

A fourth facility necessary would be a picnic area. It would not be used to entice people into the area just for a picnic but to provide an opportunity for visitors to relax, eat and then either go back home or back out onto the prairie again. In 1973 a .8 ha temporary picnic facility was established in an old farm pasture. This area was chosen because it was the only place with trees that was dry enough to use and it was adjacent to a peripheral road. Eventually a master management plan will lay out an interior road system with two or three fully developed picnic areas, with water, toilets, picnic tables, grills and some form of playground equipment. The temporary facility doesn't have the water or playground equipment.

One facility not seen by the public but necessary to keep all the others functioning properly is a maintenance facility. This will be set outside the Nature Preserve in the buffer area. A fairly extensive area is necessary. It will be used for vehicles, equipment, gravel and storage. Here will also be the shop building used for sign and display construction, general repair and maintenance of equipment. The area should also include space for the employees to eat, change and get cleaned.

One function of the staff is control. The park boundaries must be marked and kept inviolate. Unauthorized vehicles must be kept out, hunters must be kept out (a major problem at certain times during the year) and people must be prevented from disturbing the vegetation by indiscriminate picnicking, etc. Every effort will be made to allow any viable use of Goose Lake State Park. The criterion for what is acceptable and what is not is whether it destroys the prairie and the animals that live there. If it promotes an attitude that is not in accord with the object of the park it is not acceptable. Any type of driven vehicle (motorcycle, four-wheel drive truck, All Terrain vehicle, or snowmobile), horseback riding and indiscriminate human trampling are obviously not good. Hunting, target practice, flower collecting, wild food collecting, trapping and camping will not be acceptable on the prairie. In keeping with this theme no such recreational facilities such as a swimming pool, or baseball diamond are planned in the 846 acre buffer zone. A large part of this buffer zone is being restored to prairie so that the activities that would destroy the fragile and unique prairie yet are worthwhile activities can be conducted there. In this restored area the public can walk in intimate contact with the native

grasses. High school students may repeat classic ecological experiments. Younger students may put on burlap sacks and examine the seeds that stick to the bag and the very young students may play hide and seek and look for Indians. Here mother may collect grasses for a dried grass arrangement and children may collect bouquets of prairie forbs for their parents. I urge these and other such activities that would foster an empathy for the prairie.

The original plan for our prairie planting program called for the extensive use of commercial seed and 15 acres of old field succession was restored to native grasses. This area is now three years old and doing magnificently. A small amount of compass plant (*Silphium laciniatum*), downy sunflower (*Helianthus mollis*), yellow coneflower (*Ratibida pinnata*), and prairie dock seed (*Silphium terebinthinaceum*) were drilled in along a 6 cm foot border and after two years numerous young plants were visible. This year live plants transplanted by volunteers from a future housing site were plugged in to the same area and we hope this spot that is just off our main entrance road and parking lot will give the visitor a taste of what is to come.

Goose Lake Prairie State Park has an advisory committee that meets yearly to review programs, study any factors affecting prairie management and to advise on future action. Due to a feeling of apprehension on their part about ecotype future, restoration is being done with native seed collected within the State of Illinois.

Hand collecting seed is laborious work and gives small yields. But using an Allis Chalmers model 66, 1946, combine, 72.56 kg of seed of which 32.28 kg were grass-leaved goldenrod (*Solidago graminifolia*) were collected. We were going to build a riser this summer in order to raise the header above the level of almost anything but the native grasses.

There are two major maintenance projects being undertaken on the prairie at the present; burning and tree removal. Both these projects are outlined in a Nature Preserve Masterplan.

More than 50% of the preserve is never burned in one year. Up to 1972 only one spring burning was done. A small fall burn of 8 ha was planned in the fall of 1973 but weather conditions never permitted this plan to be carried out. Our largest burn was about 343.99 ha. Since there are no mineral soil breaks allowed on the preserve, it is easier to burn a large area, 40.46 ha plus, using existing fire breaks such as ponds, railroad tracks, exterior roads, etc. Some mowed fire breaks have been used but they have proven to be relatively ineffective. A large burn is a full days work for 25 men. A large burn in 1973 encompassed 6.4 km of fire lanes. One of the many reasons for burning at Goose Lake Prairie State Park is to try to remove the large number of hawthorn trees. Unfortunately until this spring's burn, fire has not damaged many of the large hawthorns or invaded the groves of hawthorns in the prairie. One problem is that there is no fuel under the hawthorns in the groves and therefore no fire. Why the larger hawthorns or trees on the edge of the groves don't burn could be due to a number of reasons. Maybe the fire isn't hot enough or the heat not long enough or maybe the time of burning is too early or too late or some other factor that I am not aware of. This spring's burn of 343.99 ha was the most successful and it appears that fire killed 85% of the individual hawthorns and even invaded many of the groves extensively. In fact, the fire managed to jump a railroad track this year and burnt about 80.93 ha that was to have been burnt in the spring of 1975 and also burnt about 20.23 ha of prairie outside of park property.

Because fire doesn't seem to be particularly effective against hawthorns, the park is constantly looking for volunteer groups to assist in cutting trees. This is a nasty job. Hawthorns fight back when you attempt to kill them. First they stab you when you are trying to saw them, then the dead hawthorns don't burn in the prairie fire. Dead hawthorns don't rot, in fact, the stumps of cut hawthorns come back to life and sprout suckers unless the stump has been painted with a herbicide. We have been hand painting the stumps with 24D mixed with red paint.

Much of this work is done by a fifth group that uses the park, the visitor that comes out

to the park to volunteer his or her time. Such groups as the 4-H, Girl Scouts, the Audubon Society and Conservation classes have donated many hours. They assist in activities like collecting seed used in restoring the buffer zone, cutting trees, especially hawthorns, planting and weeding forbs and assisting in the yearly program of prairie burning. Their help is greatly appreciated.

ABSTRACT

The paper gives a brief account of the nature and development of Goose Lake Prairie State Park, how it is administered, who uses it, what has been done, and what is being planned to make it more useful and attractive to researchers, schools, nature groups and other visitors.

PRELUDE TO PRAIRIE

Arthur H. Ode

The Milwaukee County, Wisconsin, Park Commission began experimenting with prairie reestablishment in 1965, at the Boerner Botanical Gardens (Ode, 1968). Several acres were planted to typical grasses and forbs, and the area has matured and been expanded to approximately eight acres. The results have been gratifying from both a scientific and horicultural standpoint. A new interpretive facility, the Wehr Nature Center, was opened in June 1974, contiguous to the prairie area, and utilizing it as one of its major interpretive resources.

Milwaukee County is fortunate in having an extensive park system, extending over 14,000 acres, approximately 10% of the total county land area. Farsighted land acquisition and planning by early park officials and the Milwaukee County Board of Supervisors has preserved environmental corridors along the flood plains of the major streams and drainage patterns of the county, as well as much Lake Michigan shoreline and native woodland. Thousands of acres of these lands do not lend themselves to traditional maintenance procedures, such as mowing. Accordingly, much thought has been given to the proper method of maintaining these areas. Over the years, we had experimented with leaving a few outlying areas unmowed, with favorable results.

In the winter of 1972-73, when gasoline supplies were becoming critical for government agencies (the public was not yet to feel the effects of the "oil embargo" for several months to come), the Park Commission decided to inventory its lands for all areas which could be suitably maintained by reduced or discontinued mowing. Plans or "mow lines" were established, which would reduce grass areas mowed by approximately 10%. The following communication was sent to all County Board Supervisors, the County Executive, and the mayors and common councils of all nineteen municipalities in Milwaukee County:

"We would like to inform you of a new maintenance policy which may affect park lands in your area of jurisdiction. The areas affected are primarily parkways of the Menomonee, Little Menomonee, Root River, and Oak Creek flood plains, and segments of large metropolitan parks. Neighborhood and community parks are generally not included.

The Milwaukee County Park System has grown to nearly 14,000 acres, and it has become increasingly apparent that the function of many park areas is primarily flood plain and open space, and that it is neither practical nor advantageous to institute high maintenance mowing practices throughout them.

After years of highly successful experimentation in the Whitnall District, we have extended a program of reduced grass mowing to other applicable areas in the park system. Accordingly, we have categorized appropriate sections of major parks and parkways as wooded areas, natural areas (unmowed), and mowed areas. Landscape architects of our Division of Development, after careful study, have mapped areas involved so that maintenance personnel have exact instructions.

Among the obvious advantages of this policy are the following:

1. Significantly reduced maintenance costs, for both labor and equipment.
2. Conservation of gasoline, which is of immediate concern and may become a mandate in the near future.

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3. Reduction of air and noise pollution created by maintenance machinery.
4. Increased wildlife habitat: particularly ground nesting birds (such as pheasants, partridge, meadowlarks) and small mammals. In certain areas an increase in hawks, owls, and deer may be experienced as well.
5. Natural reintroduction of native wildflower species, such as asters, sunflowers, black-eyed susan and others.
6. Decreased presence of lawn weeds such as dandelions, which will not grow in tall grass, resulting in decreased use of toxic and expensive herbicides.
7. The taller unmowed grass produces a deeper root system, which deters erosion.

Although the natural areas maintenance program exhibits many advantages, the layman may have some questions about it. Anticipated questions are:

1. What about mosquitoes? Mosquitoes breed in stagnant water. Whether grass is long or short is not a significant factor in the size of the mosquito population.
2. What about noxious weeds, such as ragweed? Ragweed is the primary hay fever irritant because it is wind pollinated. Our crews will mow or spot-spray ragweed colonies; also thistle and burdock.
3. What about the way it looks? Esthetics are a matter of personal taste. Properly designed, with complimenting mowed areas where necessary for picnicking and sports, the waving grasses, interspersed with colorful wildflowers and harboring abundant wildlife, have been well received by the general public.

We realize that educating the public in this matter is our responsibility, and respectfully request that you refer questions or comments by your constituents to our office, attention of Mr. Art Ode, Assistant Superintendent of Parks, at 278-4356. We also know that a few adjustments in our mow lines will have to be made to accommodate neighborhood uses of which we may not be aware.

We sincerely solicit your support and understanding, since we believe our program of unmowed natural areas is both economically and ecologically sound."

Our experience over nearly two summers of the reduced maintenance procedure indicates that the public will ultimately accept such a policy, if each individual question or complaint is handled with tact and sincerity. We have adjusted mow lines to provide buffer zones between natural areas and private residences where requested; we have developed fire breaks; we have provided additional areas for sports and picnicking where requested. Exact monetary savings are difficult to compute, but we have eliminated eleven positions of laborer-equipment operator in the last three years, and are saving several thousand gallons of gasoline annually. These two factors alone amount to approximately $170,000 annually. The new policy has survived to date.

In spite of its apparent success, the fact is that our "prelude to prairie" reduced mowing policy is in constant jeopardy, due to anachronistic Wisconsin State Statutes regarding noxious weeds, which remands to individual municipalities or county boards the authority to determine what are noxious weeds, viz:

"94.20 Noxious Weeds (1) the term 'noxious weeds' as used in this chapter includes the following: Canadian thistle, leafy spurge and field bindweed (creeping Jennie) and any other such weeds as the governing body of any municipality or the county board of any county by ordinance or resolution declares to be noxious within its respective boundaries."

Plants having been declared noxious by some of the 19 municipalities of Milwaukee County, Wisconsin, are: wild mustard, goatsbeard, sow thistle, poison ivy, Queen Anne's lace, chickory, foxtail grass, meadow grass, oxeye daisy, fleabane, evening primrose, cottonwood trees, grass more than one foot in height, grass more than six inches in height, grass more than four inches in height. It is difficult to see the logic in these ordinances, but even more perplexing is a municipal ordinance banning front yard vegetable gardens (which was enforced with

much fanfare in 1973). The bulk of these ordinances are no longer oriented towards agriculture, as originally designed, but are a conscious effort to control the esthetic tastes and self expression of the individual citizens of the community. They may be unconstitutional. They *are* environmentally tragic. There have recently been some worthy efforts to amend these "weed laws" on a local basis, but the only certain means of changing these ordinances is to change the state law. This will take citizen pressure of the first order.

Despite the legal and public relations problems, our natural area policy will survive and expand, hopefully, with the eventual blessing of more reasonable weed ordinances. The next step, from "prelude" to "prairie," will involve the active propagation of prairie and other native plant species (we feel just as strongly about woodland and wetland plant communities), and their reintroduction into park natural areas. Fortunately, we have the physical plant capacity to accomplish the task. We envision the interpretive facilities of the new Wehr Nature Center as providing the impetus for nature interpretation throughout the system, utilizing our then established natural areas as outdoor classrooms.

The end result of our "prelude to prairie" policies will hopefully be a community enriched with the diversity of wildlife and native plant communities, embodying the esthetics of people like Charles Whitnall, Jens Jensen and Aldo Leopold; a community closer to ecological balance, more in harmony with nature, and enjoying the best of both worlds, i.e., the economic and cultural advantages of urban population density, yet surrounded and permeated by beautiful country. Cities need not be places to escape from, but can, with proper environmental management, be an acceptable home for man.

ABSTRACT

In 1965, the Milwaukee County, Wisconsin, Park Commission established a prairie area several acres in size, which has proven highly successful, from both an ecological and horticultural standpoint. The usefulness and economy of prairie vegetation as replacement for mowed bluegrass in many park areas has become readily apparent.

Some of the advantages of prairie, from a maintenance and ecological standpoint, can also be derived from bluegrass and other non-native grass species if mowing is eliminated or reduced in frequency, i.e., maintenance costs are reduced, fuel is conserved, air and noise pollution are reduced, wildlife habitat is increased, native plant species are encouraged, lawn weeds are discouraged, and erosion is deterred. Accordingly, Milwaukee County adopted a reduced maintenance policy for many park areas in the spring of 1973.

This ecologically sound policy was met with considerable resistance by local citizens groups and public officials. It has, however, survived, and it can be considered a prelude to the actual broad scale introduction of native species. Many, if not all, of the objections to general reduced maintenance in natural areas are also directed at the use of native species. If these objections can be met and overcome by reducing maintenance and allowing vegetation, even if non-native, to grow naturally, the foundation is laid for extensive use of native prairie species on a broad scale in urban areas.

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THE MILWAUKEE PUBLIC MUSEUM PLANTS A WILD IDEA

Lorrie Otto

The Milwaukee Public Museum has planted a demonstration yard of native plants as an alternative to mowed lawns. All of the plants are easily and readily grown; all are lodged in the memory of any observant midwesterner; all were donated by enthusiastic citizens who placed them as the birds or the wind might have planted them.

The gently sloping 12.2 x 24.4 m (40 x 80 ft.) site with its southern exposure was as monotonous as any lawn, even to the inclusion of a locust tree. The latter's leaves provided thin shade and its roots spread up through the two inches of top soil which covered the "fill" around the Museum. These roots steal the rain water, sprout forth with vigorous shoots intent on thicketting, and form a network which is difficult to penetrate with a shovel. Fortunately all vegetative gifts came with their own soil and microorganisms. The first to arrive in June 1973 were the shade tolerant plants. Wild geraniums, columbines, creeping buttercups, glecoma and a few wild strawberries were trowel planted almost on top of the ground. They were watered and heavily mulched with old leaves collected from the city dump. This is to be continued for three years. The ground pattern for these plantings was marked off by the shadow of the tree at mid-day.

In the sun-drenched portion, lawn sods were dug out, flipped over and arranged to form a curved mound varying in height from six to thirty inches. This added a rhythm to the land, echoing its glacial history and also acting as a terrace to contain melting snow and heavy rains. Silver potentilla and strawberries were scatter-planted in the crevices between the sods. Cup plant silphium and New England asters were nestled above this crescent. Black-eyed Susans, ratibida coneflowers, stiff goldenrods, heuchera, blue baptisia, rosinweed silphium, sunflower laetiflorus, bergamont, wild pink roses and purple coneflowers were added at random. As the transplanting continued through the summer, places were found for lysimachia moneywort, tansy and yarrow. Daisy, erigeron, Queen Anne's lace and chicory were bonuses which appeared among our plantings in 1974. Columbine planted at the time of the first hard freeze failed to survive the winter. Shooting stars transplanted in full bloom flourished in the cool weather this spring.

The planners emphasized that no plants should be taken from the wild. That, after all, would be defeating the purpose and insulting to the cause. Each contributor was thinning plantings from her own wild yard. Each contributor, once in her life, had had a "run in" with the local weed commissioner – that prime destroyer of our endangered plant species. (I urge the prairie conference participants to instigate plans which would remove archaic weed laws from our lives, or make provisions which would prevent ignorant men from destroying the plants which grow around the weeds!) Most of the contributors were students in classes conducted by the Riveredge Nature Center, the organization which conceived the idea that the Museum should have this project. The MPM personnel designed, wrote and published a brochure, and constructed an indoor display to accompany the landscaping during the spring and summer of 1974. A twenty minute slide show presented by a MPM or a RNC volunteer is available for garden clubs, men's clubs, schools and nature centers during the 1974-75 season. An article in the Milwaukee Sentinel was headlined, "Hooked on Grass? Exhibit Shows How to Break Habit." Really, the wild idea is being pushed widely and wildly in our city these days. Many of us are no longer content to just "play house" with our environmental concerns. We want to begin to heal the earth.

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Once the public has been unlocked from the prison of tradition or the mindless fashion of mowed lawns, it will be limited only by seed and plant sources and the availability of instructions for the propagation of them. If sunny areas are to be returned to prairie vegetation, then the proceedings of the prairie conference should be distilled and distributed through all the media.

In a natural yard there are various strata or levels of appreciation stimulated for an expanding human experience. The Museum exhibit tries to encourage people to rejoice in the dishevelled artistry of nature, in the ephemeral charm of spring flowers and the vigorous, rambunctious beauty of tall prairie perennials. Here is an opportunity to use all of the senses including common sense. The land owner will become involved with his land and the manipulation of his immediate environment, learning to transplant, collect seeds, make cuttings. He will find himself delighted by emerging sprouts and buds - the flowers - the fruit - and finally the vestigal recepticals patterned in the winter snow; taking tactile pleasure in stiff goldenrods; revelling in the odor of prairie hyssop; listening to the hum of pollinating insects on fall asters. Senses become atrophied by mowed lawns. Here they can be stimulated to perform again. When homes are encircled in native plants, the residents are swathed in the passing seasons. Spring was once just a walk in the woods, or summer was remembered as a few Sunday car rides along a country road. Now spring is each day, each hour, each minute. It does not pass so quickly. When the plastic yard is gone, the view through the window is one of constant change, and is far more beautiful than any afternoon car drive. But there is more than the visual, sensual and intellectual pleasures in this new landscaping with old plants. There is something which might best be called three dimensional delight, which is that deeply satisfying feeling of knowing that you've cared for the earth, tended its plants, sheltered and fed its animals so that you've supported the basic structure for human life. When that last curtain falls, you can say to yourself, "I understood. I prepared and passed on beauty and choices to the next generation. I was a gracious visitor in this world, and a parent in the truest and best sense of the word." This view must be the *raison d'etre* for the SECOND NATURE EXHIBIT at the MPM.

ABSTRACT

The Milwaukee Public Museum and the Riveredge Nature Center used woodland, old field and prairie plants to demonstrate that yards can be beautiful and that the grass habit can be kicked. The forbes in this permanent display were donated from the homes of Milwaukee naturalists. Archaic weed laws and the lack of seed and plant sources are inhibiting factors in healing the earth around the city and suburban houses. A natural yard expands the human experience and results in the ultimate pleasure of being a wise and gracious visitor upon the land.

THE EVALUATION, SELECTION AND INCREASE OF PRAIRIE WILDFLOWERS FOR CONSERVATION BEAUTIFICATION

Erling T. Jacobson

INTRODUCTION

Continuing its four decades of effort on behalf of improving the environment, the Soil Conservation Service today is searching for means of preserving the prairie wildflowers for tomorrow.

The SCS Plant Materials Center located at Manhattan, Kansas maintains foundation seed stocks of eight varieties of native warm season prairie grasses that have been developed cooperatively with the Kansas State University Agricultural Experiment Station and the Agricultural Research Service.

The experience gained from working with the native prairie grasses is being challenged by the diversity in numbers and kinds of perennial wildflowers found in the three central Great Plains States served by the Center: Nebraska, Kansas and Oklahoma. Every ecological niche seems to have developed its own unique array of native plants. Extensive cultivation, drainage and development have made many of these extremely rare. Their delicate and fleeting habitats are left as remnants, along railroads, abandoned country roads, old neglected cemeteries and school yards.

PROCEDURE

Several steps make up the system used at the Center to assemble, evaluate and increase seed of selected species of prairie wildflowers and return them to their natural setting for conservation beautification (Figures 1-4).

Assembly

Personal discovery and timely harvesting of seed were used to assemble over 375 field collections of wildflowers indigenous to the geographic area served by the Center. The assembly includes 64 genera and 141 species.

The field collections are cleaned and processed for planting in the evaluation nursery. A firm seed bed is prepared and the area is covered with polyethylene and treated with the soil fumigant methyl bromide. This preplant soil fumigant treatment is the key to getting a stand as it provides excellent control of weeds, nematodes and soil-borne disease organisms.

The wildflower seeds are planted with a precision seeder with depth control and press wheel for firming the soil around the seed. Irrigation water is applied to stimulate germination. Once a stand is established, the watering is discontinued and the assemblies of wildflowers are evaluated under dryland conditions.

The dates and methods of planting are also very critical to successful stand establishment. For example, a dormant seeding (November-December) is required for germinating *Penstemon*; in contrast to spring seeding of *Helianthus, Liatris, Salvia* and *Ratibida.*

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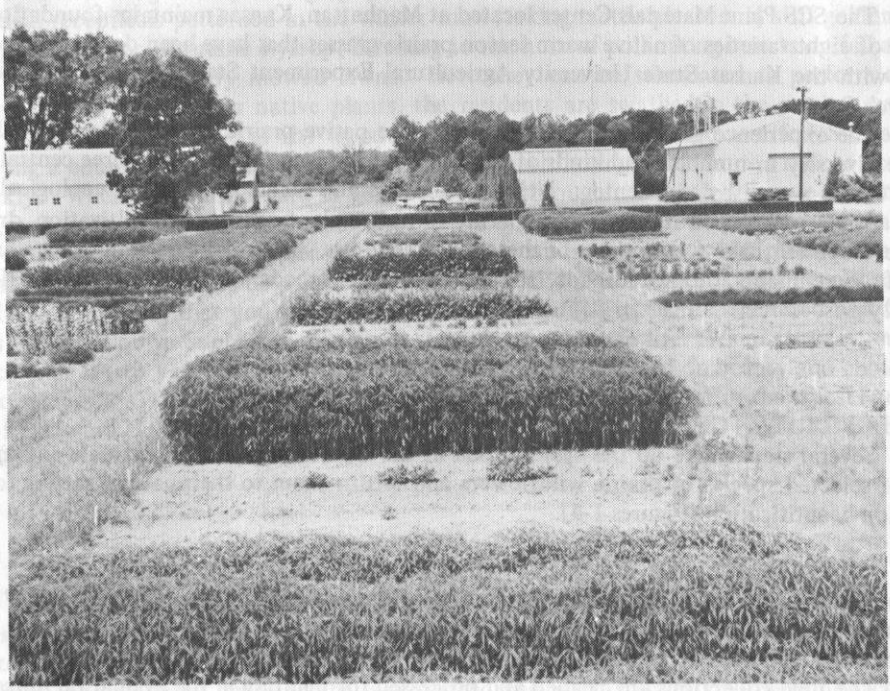

Fig. 1. The Soil Conservation Service has assembled over 375 accessions of wildflowers in the evaluation nursery. Data is recorded on performance and conservation use.

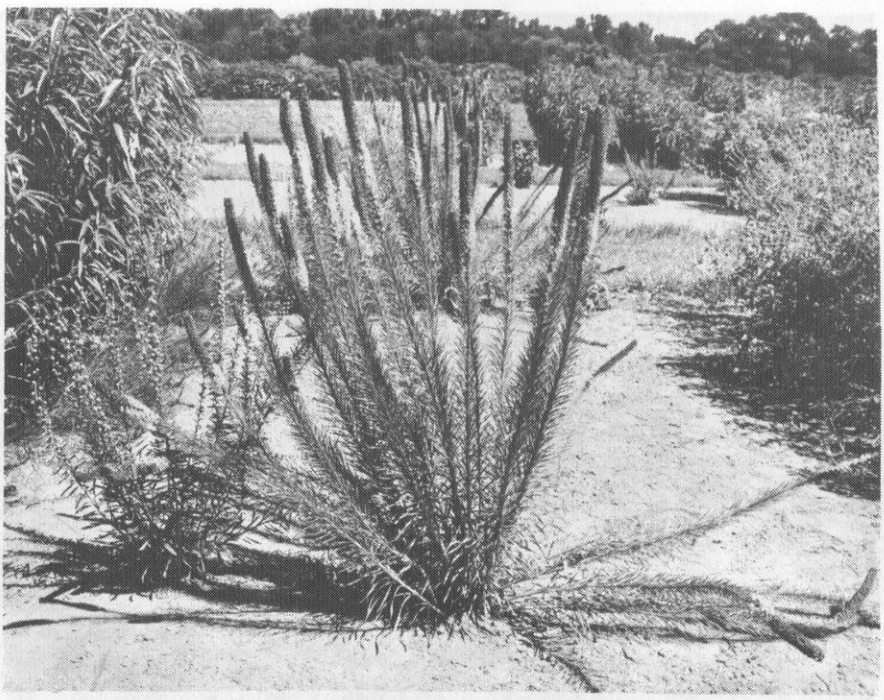

Fig. 2. Thickspike gayfeather *Liatris pycnostachya* Michx. shown in the evaluation nursery on the Center. This tall growing perennial is readily established from seed and can be planted and harvested with conventional field equipment.

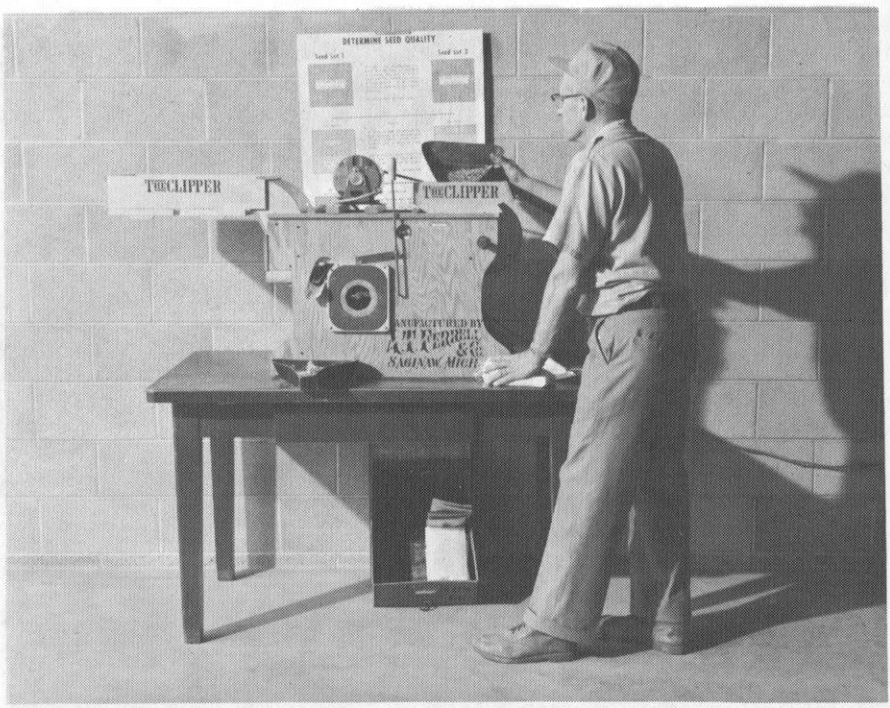

Fig. 3. A small air-screen cleaner is used to clean the seed collected in the field for planting in the evaluation nursery.

Fig. 4. A one-half acre initial increase of sawtooth sunflower being harvested on the Center with a self-propelled combine.

Evaluation

A detailed set of notes is kept on emergence, seedling vigor and rate of growth during the first year of establishment. In subsequent years spring recovery, flower color, period of bloom, height, spread, seed production and conservation use are recorded.

The performance of species selected for further evaluation is listed in Table 1. An initial seed increase of 22 species has been on the Center under field conditions. The cultural requirements for seed production being studied on the Center include: (1) field standards for isolation of insect pollinated species, (2) crop residue management, (3) weed control, (4) fertility levels, and (5) water requirements.

Seed Processing

Seed processing in its broadest sense includes all the steps involved in the preparation of harvested seed: drying, threshing, cleaning, grading, treating and packaging.

The actual seed-processing operations used on the Center vary with the stage of development of a selected species. The field collections are usually threshed on a rub-board. The material is separated using a small air-screen cleaner. The seed may be further cleaned and graded to improve seed quality. Precision seed-cleaning equipment similar to that used to process native grass seed has been used successfully on wildflowers. The sequence of machines used for processing depends on the kind of seed and the nature and kinds of contaminants, inert matter, etc. Flexibility is necessary to handle each lot in an efficient manner. The air-screencleaner separates on the basis of size and weight, and is the basic machine for all scalping and grading operations. For special problems, machines are available that separate and/or grade on the basis of length, width and surface texture. A standard seed test for purity and germination is used to evaluate seed quality. Seeding recommendations are made on a basis of pure live seed (PLS) per pound. Legumes require scarification and inoculation with special inoculants prior to planting.

Seed Certification

The Soil Conservation Service provides foundation seed to commercial seed growers and nurseries for production of certified grass and legume seed and nursery stock. The same procedures will be used for the release of wildflower seed stocks. The SCS, Plant Materials Center at Los Lunas, New Mexico officially released 'Bandera' Rocky Mountain penstemon *Penstemon strictus* Benth. in 1973. The Manhattan Plant Materials Center is cooperating with the University of Nebraska, Department of Horticulture and Forestry on the development and release of several perennial wildflower species: *Penstemon grandiflorus* Nutt., *Liatris pycnostachya* Michx., *Helianthus maximiliani* Schrad., *Liatris aspera* Michx., *Salvia azurea* Lam., *Petalostemum purpureum* (Vent.) Rydb., *Ratibida pinnata* (Vent.) Barnh., *Asclepias tuberosa* L., *Lespedeza capitata* Michx., *Liatris punctata* Hook. and *Rudbeckia hirta* L.

CONSERVATION IN ACTION

Until recently, wildflowers were used principally in horticulture and landscape gardening. Research methods were intensive and directed towards a single species.

The use of wildflowers in conservation plantings requires the production of large quantities of seed. Those species which can be established by direct seeding, managed on a broad scale and have a growth form and character that can be harvested with conventional equipment are desirable. In addition, they must have the ability to establish and compete successfully with other vegetation with a minimum of maintenance.

Table 1. The performance of selected prairie wildflowers at the Manhattan Plant Materials Center 1968-74

Species	Common Name	Vigor	Height Cm.	Spread Cm.	Bloom Start	Bloom Full	Bloom End	Color	Seed
Amorpha canescens Pursh	leadplant	3	30-60	6-9	6/7-15	6/20-30	7/25-8/25	blue	7
Asclepias tuberosa L.	butterfly milkweed	1-3	60-105	9-12	5/30-6/10	6/15-25	9/15-30	Orange	3
Baptisia australis (L.) R. BR.	blue wildindigo	1-3	30-75	6-12	5/1-10	5/15-20	5/25-30	blue	5-7
Echinacea angustifolia DC.	blacksamson echinacea	1-3	60-105	12-24	5/25-6/5	6/10-20	7/20-30	pink	3
Helianthus grosseserratus Martens	sawtooth sunflower	1	180-300	60-180	8/30-9/7	9/25-30	10/15-30	yellow	1-3
maximiliani Schrad.	maximilian sunflower	1	150-275	30-90	8/20-30	9/15-20	10/10-25	yellow	1-3
mollis Lam.	ashy sunflower	1	90-150	30-90	7/10-20	8/15-25	9/25-10/5	yellow	5
salicifolius A. Dietr.	willowleaf sunflower	1	240-370	30-45	7/15-20	9/10-15	10/15-20	yellow	1
tuberosus L.	jerusalemartichoke	1	150-210	60-120	9/20-25	10/5	10/15-20	yellow	9
Heliopsis helianthoides (L.) Sweet	sunflower heliopsis	3	120-150	30	6/20-30	8/1-10	10/5-15	yellow	1-3

Species	Common Name	Vigor	Height Cm.	Spread Cm.	Bloom Start	Bloom Full	Bloom End	Color	Seed
Lespedeza									
capitata Michx.	roundhead lespedeza	1-3	90-150	6	7/15-8/15	8/5-9/5	8/15-9/15	white	1-3
Liatris									
aspera Michx.	rough gayfeather	1-3	60-90	6-12	8/15-25	8/25-9/5	10/15-25	pink-purple	1-3
punctata Hook.	dotted gayfeather	3	45-60	6-12	8/15-25	8/25-9/5	9/15-10/15	pink-purple	3-5
pycnostachya Michx.	thickspike gayfeather	1-3	90-150	12-18	7/10-20	7/25-30	8/20-30	pink-purple	1-3
Penstemon									
cobaea Nutt.	cobaea penstemon	1	15-90	9	5/20	5/30	6/20	lav.	1
grandiflorus Nutt.	shell-leaf penstemon	1	60-105	12	5/10-20	5/20-30	6/5-10	lav.	1-3
Petalostemum									
candidum (Willd.) Michx.	white prairieclover	1	60-90	6-12	6/10-15	6/25-7/5	10/10	white	1-3
multiflorum Nutt.	roundheaded prairieclover	1	60-90	15	8/1-10	9/5-15	10/20-30	white	5
purpureum (Vent.) Rydb.	purple prairieclover	1	60-75	6-9	6/15-20	6/25-7/5	9/10-10/20	pink-purple	1-3
Ratibida									
columnifera (Nutt.) Woot. & Standl.	upright prairie-coneflower	1	60-90	6-12	6/1-10	6/20-30	10/10-20	yellow	1
pinnata (Vent.) Barnh.	grayhead prairie-coneflower	1	120-150	30-60	6/20-30	7/15-20	8/20-30	yellow	1

Species	Common Name	Vigor	Height Cm.	Spread Cm.	Bloom Start	Bloom Full	Bloom End	Color	Seed
Rudbeckia hirta L.	blackeyedsusan	1-3	30-90	30	6/1-10	6/20-30	10/1-20	yellow	1-3
Salvia azurea Lam.	pitcher sage	1-3	120-180	15	7/10-30	8/25-9/5	9/25-10/5	blue	3
Silphium integrifolium Michx.	wholeleaf rosinweed	1	150-215	15-45	6/25-7/5	7/20-30	9/20-30	yellow	1
laciniatum L.	compassplant	3	90-180	15	6/25-7/5	7/25	9/5-10	yellow	7

Legend

Vigor and seed quantity: Visual rating, 1-excellent, 3-good, 5-medium, 7-poor, 9-very poor, 0-failure.

Height: Total plant height as measured in centimeters.

Spread: Spread, row width as measured in centimeters.

Field Plantings

Plantings of wildflowers under actual field conditions have shown that they are hardy when used within the area of adaptation. In these studies, adaptation and performance are correlated with the soil and microclimate of the site.

The abundance of wildflower species make it possible to select and blend together an array of wildflowers to achieve a continuous flow of color throughout the growing season. The panorama of color begins in April in the central Great Plains States with the pink of prairie phlox and verbena. May and June bring the multi-colored penstemons, the coneflowers, primroses and wildindigos. Summer flowers make a rainbow of color with the steel blue of the leadplant, the bright blue of pitcher sage, the red-violet of gayfeathers and prairieclovers and the orange of the butterfly milkweed. By September the deep yellows of the sunflowers and goldenrods, and lavenders and purples of the asters predominate.

Landscape architects who appreciate the value of natural beauty are using native plants in their designs. Wildflowers are being included in projects that deal with restoration of land along highways and around museums, airports and factories. Educational institutions, junior colleges and high schools are developing outdoor classrooms, natural areas and arboretums. Many of the native forb and legume species provide nutritious grazing for livestock and are a food source for upland birds.

CHALLENGE OF TODAY

The Soil Conservation Service and the Conservation Committee of the Kansas Academy of Science are cooperating in compiling lists of endangered and threatened species of animals and plants in Kansas. Since the habitats of these plants are not all known there is a need to need to determine the location and status of natural populations. Information on the status of these species is solicited from scientists and other knowledgeable persons. Several of the SCS Plant Materials Centers are working on projects to protect plants in the various categories of endangered and threatened species in the geographic areas that they serve.

The challenge of today is to you that have responsibility for planning and carrying out programs which modify the environment to choose alternatives that will preserve the native prairie species for tomorrow.

ABSTRACT

The Soil Conservation Service, Plant Materials Center, Manhattan, Kansas is conducting evaluation studies on 64 genera and 141 species of wildflowers. Twenty-two species have been selected for increase and further studies are being conducted to determine the culture and management requirements for seed production. Field plantings are being made to evaluate performance under actual use conditions.

KEY WORDS

Conservation, environment, ecological niche, assembly, evaluation, seed increase, certification, pure live seed (PLS), endangered and threatened.

WINDRIFT PRAIRIE NURSERY: STORY OF A SMALL COMMERCIAL ENTERPRISE

Douglas E. Wade and Dorothy R. Wade

LOCATION AND DESCRIPTION

Windrift Prairie Nursery grows prairie forbs primarily and is a part time enterprise located in Ogle County, two miles northeast of the town of Oregon in the Rock River valley in northern Illinois.

In 1965, we purchased five acres (2.02 ha) of open and partly wooded hillside prairie pasture which had been grazed for the past fifty years. Over the past nine years we have labored to restore one and a half acres of "hillside prairie" (Fell and Fell, 1956) and two acres of woodland wildflowers and ferns. This landscaping blends with a limestone house designed by architect Verne Solberg of Sycamore, Illinois, and extends "organic" concepts developed by the late Frank Lloyd Wright.

Fire, hand-weeding, seeding, and planting of seedlings are used in restoring our hillside prairie. About one-fourth of the area, on a rotational basis, is not burned each spring. When the prairie cover thickens we have noticed a definite diminishment of *Poa pratensis* (Kentucky bluegrass) and *P. compressa* (Canada bluegrass). *Medicago lupulina* (Black medic) and *Trifolium agrarium* (Yellow hop-clover) set abundant seeds and are persistent. As of 1974 we have established 130 kinds of prairie plants.

EARLY INTEREST IN PRAIRIES

Educators should be very concerned in learning how people become oriented to prairies. The senior author's interest probably started before 1920 when he searched out areas in the vicinity of Beloit, Wisconsin for early blooms of pasque flower (*Anemone patens wolfgangiana*) for display at the public library. He also had a very unusual 7th grade teacher (trained in geography) who had located a flock of prairie chickens (*Tympanuchus cupido*) eight miles west of Beloit. Several of her students, including the senior author, bicycled to the area late April, 1922 and watched the birds on their booming ground -- a back forty of sand prairie.

In the early 1930s, the senior author was very fortunate to go on some prairie trips between Beloit and Rockford, Illinois with the late Dr. Malcolm D. Brode, Professor of Biology at Beloit College. Dr. Brode predicted correctly that most of the gravel hill prairies his classes visited would be gone within 25 years.

In the mid 1930s, the authors studied at the University of Wisconsin (Madison) under the late Professors Norman Fassett, William Longenecker, and Aldo Leopold. The junior author did some root studies of *Dodecatheon meadia* (Shooting star) and *Andropogon gerardi* (Big bluestem) at the U. W. Arboretum which was just getting started under the leadership of the above three men. During a wildlife management work assignment in 1935 near Lake Mills, Wisconsin, the senior author composed a poem dedicated to a wet mesic prairie along the Crawfish River, now identified as the Faville Scientific Area.

We gained another decade of prairie experiences while residing in Missouri, Iowa, and Saskatchewan.

The authors are at the Windrift Prairie Nursery, RD 2, Oregon, IL 61061.

In the past ten years our attention to prairies has multiplied through participation in many burns, acting unofficially as consultant to the Illinois Nature Preserves Commission, managing and studying the 59 acre Pine Rock Nature Preserve (largely sand prairie) owned by Northern Illinois University (Wade and Wade, 1970), fencing some cattle exclosures on an 80 acre prairie pasture in cooperation with the Illinois Chapter of the Nature Conservancy, being a member of the Illinois and Wisconsin Chapters of the Nature Conservancy, the Missouri Prairie Foundation, and the Flint Hills (Kansas) Prairie Association, as well as attending all of the biennial Prairie Conference meetings.

On the Lorado Taft Field Campus of Northern Illinois University we restored a small remnant hillside prairie (Wade, 1972) and created a prairie-landscape resting place on the Taft Campus for the famed Eagle's Nest Tree which, until 1972, stood below the Black Hawk statue until it fell during a fierce summer storm. Eagle's Nest Tree, a red cedar (*Juniperus virginiana*), was estimated from increment borings to be aged 650 years. Photographs of its habitat along the Rock River bluffs northeast of Oregon, Illinois taken in 1902 show a long stretch of prairie which since then has become largely treed.

From July 29 through August 3, 1974, at Taft Campus, we conducted an Interpretation of Prairies Workshop (one hour of graduate credit) with 23 teachers enrolled. The course centered on application of the principles of interpretation set forth by Freeman Tilden (Tilden, 1967).

BRINGING A PRAIRIE NURSERY INTO EXISTENCE

Our own hillside prairie, since 1965, has been increased to 130 prairie species from some three dozen which had persisted in spite of heavy grazing and competing exotics. Because we wanted an on-property supply of seeds and plants and because we had learned at various prairie meetings of a need for prairie forbs, we decided in 1970 to develop a nursery that could go "commercial."

Today, our nursery consists of 35 plots ranging in size from three by forty feet (0.9 x 12.1 m) up to eight by sixty feet (2.3 x 18.2 m). These narrow plots contoured to our hill are amenable to row planting, watering, weeding, and harvesting. A 6½ horse Troy-built rototiller has been invaluable for opening and preparing plots in heavy sod. Currently (1974) we are handling 87 species of prairie plants in our nursery, although some are low in number.

Seeds for the nursery have been gathered by hand in the Rock River valley corridor in northern Illinois, with a few obtained from generous individuals at the University of Wisconsin, the Morton Arboretum, and the Cook County Forest Preserve District. Some plants have been lifted from two areas doomed to being stripped and mined for gravel, sand, and limestone.

Increasingly our own prairie has given us a source of seeds, although we lose many seed heads to grasshoppers, larvae of butterflies and other insects. In the summer of 1974, white-tailed deer (*Odocoileus virginianus*) grazed the tops of our white prairie clover (*Petalostemum candidum*). The cottontail (*Sylvilagus floridanus*) and the mole (*Scalopus aquaticus*) are troublesome, with the latter's tunnels seemingly always following a seeded row. We even had an American toad (*Bufo americanus*) set up residence in one of our flats.

We have followed procedures of seed collection and treatment prescribed by Schulenberg (1972), Zimmerman (1972), and Schwarzmeier (1973). To insure some seeds we shall have to do more bagging.

Many of our plants are started indoors in flats under wide-spectrum grow-lights (Cherry, 1965; Elbert, 1973) with transfer to peat pots or directly into nursery plots. The flats and peat pots are moved out-of-doors into cold frames when night temperatures are above freezing.

Most of our seeding, however, goes directly into prairie plots in the spring, with a lesser

amount done in the fall. Pasque flower, prairie smoke (*Geum triflorum*), prairie phlox (*Phlox pilosa*), and lupine (*Lupinus perennis occidentalis*) are sowed as soon as seeds are matured.

One-year seedlings and some two-year transplants from thinning make up the bulk of our sales items, with buyers coming to the nursery to obtain freshly dug plants. Plants with some soil left on the roots and lightly moistened are packed in light-colored plastic bags and cardboard boxes for protection during transit. Survival has been good provided plants have been kept cool and quickly transplanted and watered for a few days.

Our advertising so far has been largely by word of mouth, but notices in landscape journals and books on wildflower cultivation would be useful. Plant and seed lists sent to known prairie workers has been most helpful.

ETHICAL CONSIDERATIONS

The licensing of prairie forbs nurseries is new, in our opinion, to most state agencies and needs to be clarified as to its significance beyond the usual efforts to moderate transmission of pests and diseases. Such licensing does not offset the kind of genetic, ecologic and evolutionary potential for injury described by Schwarzmeier in his paper, "What Are Our Responsibilities in Prairie Restoration?" (1972). Schwarzmeier raised some tough questions concerning "native prairie mechanisms" and urged the "creation of a strong national agency having charge over the transmission of organisms, especially as regards restricting any new type as long as that type appears to be a potential degradational infector of land systems." The practices followed by prairie workers in collecting and distributing plants and seeds need to be analyzed and discussed. Surely there are some prairie areas that should be off-limits to collecting or insensitive trampling.

There is need, also, to clarify the uses and distribution of "salvaged" plants from doomed areas.

If the identity and function of "corridors" (Schwarzmeier, 1972) can be clarified, nurseries could be situated or operated to serve specified corridors.

Ecotype distribution problems and development of a Code of Ethics applicable to all handlers of prairie seeds and plants is open to a concerted exploration by agencies and organizations such as the Nature Preserves Commission of Illinois, the Scientific Areas Preservation Council of Wisconsin and the Nature Conservancy.

To gain a truly ethical and monitored system of ecologically and genetically sound distribution of "commercially" handled prairie species will not be easy. Both Charles Elton (1958) and Leopold (1970) should be required reading. They reveal the propensity of human beings to mess things up in general. In the meanwhile, nursery persons dealing with wild species and so-called superior strains developed at plant materials centers are caught on the horns of a dilemma of what to distribute and where.

For those who may wish to dig more and deeply into ethical matters there are the writings of Thoreau or more recently those of Küchler (1972), Egler (1972), Potter (1971), Kozlovsky (1974), and Hardin (1972). Are certain kinds of prairie seed and plant commercial distribution another facet to add to Hardin's "The tragedy of the commons" (1972)?

SOME EDUCATIONAL IMPLICATIONS AND PROJECTIONS

In association with outdoor education programs at the Lorado Taft Field Campus, we have had many opportunities, other than those already described, to extend some elementary information about prairies to over 8,000 students and teachers in the past ten years. Our own

small hillside prairie and nursery have been starting places for many visitors to see, feel, study, record information, and photograph.

Desire to understand prairies is increasing in many ways and there is need to offer enthusiastic tyros a variety of ways to get with it. One has only to examine the attendance rosters of the four Midwest Prairie conferences to catch some of the excitement of the prairie movement. In this spirit we offer the following two "Vistas."

VISTA NO. 1 – PRAIRIE PLANTS EXHIBITION AREAS

We construe Prairie Plants Exhibition Areas as containing a series of small plots (six by six feet (1.82 x 1.82 m) separated by paths, with each plot containing a planting of a single prairie species. This small size would make it easier to get the plots established and maintained than getting a mixed species prairie restoration. An exhibition containing perhaps 100 plots should be quite impressive, especially if enhanced by tastefully landscaped borders and a carefully designed interpretive building containing explanatory audio-visuals to extend interpretation of prairies in general.

The plots in an exhibition area could serve many purposes: botanical studies (including identification), phenological studies and data accumulation, observations on associated animals, seed collection, photography, art, aesthetics, and accrual of questions and answers, etc. Visitors and chiggers could stay disassociated, provided the visitors stayed on the paths.

VISTA NO. 2 – PRAIRIE NURSERY PLANT RECORD FORM

In the course of managing a prairie nursery, there are many records and observations that should be captured more precisely and orderly. Record forms developed in arboretums and plant materials centers should be examined. A form should at least encourage the "tagging" of species being handled and the accumulation of information that otherwise could be lost.

We can only suggest some of the possible ingredients of a record form. "STATUS" on the form refers to value rating of P, PP, PPP developed by Schulenberg (1972) at the Morton Arboretum. A triple P status would indicate a plant rated as highly desirable (an indicator plant you would look for when attempting to assess the quality of a prairie). A rating system for landscape values could also be developed.

From even a cursory look at the Plant Record form, one gets the impression that running a prairie nursery requires attention to a rather imposing number of details throughout the year. Nursery persons do have many opportunities to make some original contributions to the art, especially by working with species known to be difficult to handle under nursery conditions. By cultivating working relationships with university departments of horticulture or landscaping, some problems can be shared.

At the Windrift Prairie Nursery we have been bent toward educational as well as "business" goals and expect that our efforts will serve to edify many visitors. With realization that too many visitors would become exacting on our energy and time, we are preparing a self-guided manual to our nursery and hillside prairie. Toward this we have found the University of Wisconsin Arboretum booklet, "Guide to the Arboretum Prairies" (Reich, 1971), a useful model.

PRAIRIE NURSERY PLANT RECORD

(suggested contents only)

ACCESSION NUMBER _____ STATUS _____

SCIENTIFIC NAME _____

FAMILY _____

COMMON NAME(S) _____

A. SEEDS and/or CUTTINGS and DIVISIONS

- Collection date(s)
- Collection place(s)
  - Permission needs
- Collecting methods
  - Bagging
  - Equipment used
- Cleaning method(s)
- Storage
- Stratification
- Arthropods found
- Damage by animals
- Weights by volume
- Seed counts by wt./vol.
- Refs: maps, platbook, soils, aerial photographs
- Photographs
- Time and mileage (constants for figuring costs)

B. GROWING OF PLANTS

- Planting dates
- Amts. of seed used
- Flats, peat pots & plots
- Plot(s) Number
- Germination rates and dates
- Growth rates
- Lights used
- Cold frame
- Root growth rates
- Weeding
- Soil type & tests
- Photographs
- Time involved

C. DISPOSAL OF PLANTS

- Date(s) lifted
- Method(s)
- Size of tops & roots
- Number sold & prices
- Shipping method
- Customer
  - Name & address
  - Loci of area
- Success of planting(s)
  - Years 1,2, & 3
- Photographs
- Time & Mileage

D. MISCELLANEOUS RECORDS AND INFORMATION

- Weather Records
- Phenological Records
- Damage by weather
  - by animals
- Reaction to insecticides
  - to herbicides
- Soil types
- Propagation by divisions
- Diseases
- Associated animals (in nursery)
- Use by animals
- Soil treatments
- Unanswered questions
- Patterns of composition in native prairies (21)
- Useful references
  - Literature
  - Persons & groups
- Landscape values
- Improvement in equipment &methods
- Other nurseries

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LANDSCAPE DESIGN WITH PRAIRIE PLANTS

Robert W. Dyas

INTRODUCTION

> Modern man with his great knowledge has it within his power to create on this earth a paradise beyond his fondest dreaming. But he is failing. And he will fail so long as his plans are conceived in obvious and heavyhanded violation of nature and nature's principles...
>
> For the moment, it seems, we have lost touch. Perhaps, we must look back. We must regain old instincts, relearn old truths. We must return to the fundamental planning wisdom of the gopher building his home and village and the beaver engineering his dam. We must return to the planning approach of the farmer working from day to day - fully aware of nature's forces, forms and features; respecting and responding to them; adapting them to his purposes. We must rediscover nature.
>
> John Ormsbee Simonds, "Landscape Architecture"

What might we discover in the nature of the prairie that might prove adaptable in the designing of our modern landscapes?

THE INHERENT BEAUTY OF THE PRAIRIE

> In desert places grew thorny plants and spiny creatures, in forests tree-dwellers and browsing beasts. On the great continental plains wherever grass wove her garment for the naked earth, the grazers chewed their cuds. In the primeval pastures, streams ran clear, and clean winds blew, and nomad man came to follow the herds, adapting to the prairie as it was.
>
> "Grass Land" by Jim, Alice and Steven C. Wilson

The character and quality of a prairie landscape result from many factors in addition to its unique vegetation, but it is this vegetational aspect which most clearly separates the prairie from other landscape types. Although trees and shrubs may be present, the dominant vegetation consists of grasses and other herbaceous plants commonly referred to as forbs. The heights of the various grasses and forbs may vary from a few inches to six or eight feet; since most of them are below our "eye-level", they seldom obstruct our view of distant horizons. "The Land of the Wide Skies", as Jim and Alice Wilson have referred to it, is a most appropriate way of describing it in terms of human experience.

Another aspect of the vegetation that appeals strongly to our human emotions is its great variety of species, and the infinite ways in which they are interrelated. There is variety of size, form, color, movement, and seasonal display to excite our visual and esthetic senses; vari-

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ety of fragrances, flavors, and textures to reward our senses of smell, taste and touch; the prairie sounds include unique wind-songs and countless songs and calls of the insects, birds, and mammals residing within it or migrating across it. Each plant species also expresses its own kind of beauty and identity through its foliage, flowers and fruit.

The beauty of the prairie landscape is more than grass and forbs and birds and bees. It is also hills and valleys, lakes and rivers, steep rocky bluffs and low-lying flat-lands. Some prairie landscapes appear in sharp contrast to adjacent forests or groves of trees; others are separated from forests by areas of savanna or scattered trees. Special, individual kinds of beauty result from the various combinations and juxtapositions of these different vegetational types.

A prairie occurring on rolling sand hills, is distinct from one occurring in glacial potholes, visually and esthetically as well as culturally or ecologically. A prairie opening surrounded by trees may have a kind of private or intimate appeal not found in an exposed "goat-prairie" on a rocky bluff or hill. The predominating short grasses of a dry site provide a very different kind of experience than that provided by the taller grasses of moister sites. Each possesses its own kind of beauty.

> The occupied landscape may be richer by far in all the subtle amenities of the original land if only the designs we apply...are becoming to the form as well as the complexion of the meadows, woods and slopes we presume to compliment...Landscape character should be intensified, not obliterated; and the ultimate harmony should emerge as a blend in which the native quality of the region and the spot still prevails after the inevitable mutilation of the construction undertaken to produce needed roads, buildings and other works of civility and comfort. These humanized landscapes are to us the most inviting and beloved, and we are pleased and inspired insofar as the whole structure and sentiment of the landscape can be preserved...
>
> There can be no deviation from the rule that the newly prepared landscape must be...a distillate or sublimation of the original myriad forms if it is to be a work of art in the sense of a high art form, timeless and historical.
>
> Stanley White, as quoted in "Landscape Architecture" by John Ormsbee Simons

What specific or unique landscape character or form can we expect to find or intensity in the prairie landscape?

LANDSCAPE DESIGN UNITS OR COMPONENTS OF THE PRAIRIE LANDSCAPE

Just as the prairie landscape consists of topography, water bodies, plants and other components interwoven into a harmonious whole, each landscape designed for human use is made up of various functional and topographic units. Although roads, buildings and other structures may be strongly emphasized in man-made landscapes, plant materials may be counted upon to provide strong landscape character. Scattered shade trees and lawns of mown grass are two plant-material components commonly used in landscape design. This popular, "parklike" landscape may be compared with a natural savanna, or grassland with trees.

The prairie might be adapted for use as an open meadow in a landscape design, much in the same way that lakes, ponds, and mown lawns have been used traditionally. With scattered trees it could express a savanna.

Plantings of taller prairie species could be used to express lowlands, while shorter ones could express uplands or a drier landscape. Instead of simply saying and being "grass", each could express its own unique attributes.

Just as a "woods" or grove of trees offers an intimate enclosure or shady retreat in the man-designed landscape, a broad expanse of "prairie" or a prairie opening can provide a pool of sunlight or a soothing panorama of waving grasses.

Forbs with showy flowers or fruit could be used to high-light seasonal changes through spring, summer, and fall. Certain individual species may be used as symbols to express a certain theme or place, such as the floral emblems of states and provinces.

The foliage and seed-heads of ripening grass are equally significant. An October walk through big bluestem and Indian grass up to ones ears is a memorable experience, and man's finest jewels cannot match a field of little bluestem sparkling in the autumn sun.

How can these exciting and inspiring aspects of the prairie and its plants be utilized in the design of landscapes for human use?

THE USE OF PRAIRIE PLANTS IN LANDSCAPE DESIGN

Until a few years ago, the use of prairie plants in landscape design was essentially limited to the incorporation of individual species as ornamentals in traditional garden components. Coneflowers, butterflyweed and other showy forbs were planted in perennial borders; rock cress and shooting stars were planted in rock gardens; wild roses and sumac were used in foundation plantings or shrub borders.

There were a few exceptions, the most outstanding of which was the "prairie landscape school" of Jens Jensen. Jensen's work, most of which was done in Illinois and Wisconsin, incorporated native plant materials almost exclusively and expressed much of the character of the natural landscape. His work is well documented and provides much inspiration for today's landscape architects here in the midwest.

More recently, the concern for preservation and restoration of prairie areas has stimulated the study and use of prairie plants by landscape designers. Also, there has been an increasing interest in the recreational and educational potential provided by prairie landscapes, both natural and restored. Together, these interests and activities have broadened and deepened public interest in nature; especially here in the midwest, this interest includes the prairie.

Sheyenne Grasslands in North Dakota, Konza Prairie in Kansas, and Sheeder Prairie in Iowa, are examples of natural prairies or grasslands preserved for human use. These were not designed or developed by man, although they may have been used for grazing or other agricultural purposes. They serve as examples we can study, enjoy, and appreciate.

The University of Wisconsin arboretum in Madison manages two restored prairies for public use; they have been planned and developed and are maintained for educational, recreational and esthetic purposes.

The Parkside Campus of the University of Wisconsin at Kenosha includes prairie as an integral part of its master plan. The Landscape Architect, Neil Porterfield of Helmuth, Obata and Kassalbaum, St. Louis, explains in the Master Landscape Plan for the 690 acre campus:

> The Parkside Campus Master Landscape Plan presents a unique solution for large scale landscapes by using ecological principles as a basis for design...the plan has been formulated through a great amount of original

> research in the application of ecological planning for man-made landscapes...Ecological factors influencing the selection of plant communities and species, their location, and ratio of species are the basis of design decisions in developing a plan for (this) campus ...the essential elements of the landscape, both natural and man-made, become determinants for the subsequent plan. These determinants provide a program which frees the designer from arbitrary selection of plant species, ratio of species and configuration. This eliminates the use of cultivated ornamental plants and introduced perennial and annual grasses...
>
> The composition of a natural landscape varies in accordance with continuous changes in environmental conditions of the site. The result is an esthetically pleasing, diversified landscape...
>
> Another important factor in using a natural landscape is its educational potential...The natural landscape of Parkside Campus will provide an excellent outdoor laboratory for the natural sciences.

Using J. T. Curtis' book "The Vegetation of Wisconsin" as a guide, the campus was divided into vegetational zones including Boreal Forest, Northern Forest, Southern Forest and Prairie. Each of these zones was sub-divided according to physiography and soils.

As the campus exists today, much of the prairie area has been seeded to prairie species; in close proximity of the buildings a mown bluegrass lawn is used. The mow-line has been developed as a gentle, though distinct, transition from the intensely used interior toward the open landscape. Some conflicts in the details of the proposed design and the aspects of maintenance are being resolved, and increasing the amount of prairie to replace some of the existing mown lawn is anticipated.

Of particular interest at Parkside Campus is the manner in which the buildings have been designed to afford the occupants full view of the expanses of prairie and woods surrounding and penetrating the buildings themselves. This arrangement makes the use of native prairie plants much more satisfying, esthetically, than conventional mown grass would be.

We have recently visited three privately owned commercial and industrial developments in which prairie plants are used. In two of these, the prairie elements are integral parts of the landscape design for each building complex, while in the third restored prairie is being developed for conservation, recreation and education.

The landscape plan for the Cuna Mutual Insurance Company site in Madison, Wisconsin, was prepared by Darrel Morrison, Landscape Architect. In this plan prairie grasses are used as a distinct design unit, integrated with units of mown grass and plantings of trees and shrubs. Forbs are being added to the original seeding of grass species; many trees and shrubs commonly associated with prairie, such as sumac, crabapple, plum and dogwood are included. Part of the prairie planting is over a parking garage and is growing in a special light-weight soil mixture. Because the prairie area was relatively small at Cuna Mutual, it was sown by hand; and, because of its close proximity to the building and shrubs, it will be maintained by hand rather than with use of fire.

The landscape plan for the Salsbury Laboratory site at Charles City, Iowa was done by Franz Lipp and Associates, Landscape Architects of Chicago. In this plan, prairie plants are used in extensive stands between the road and the main building, but separated from the building complex by a roadway and broad expanse of mown grass with scattered trees. Lower parts of the "prairie" were seeded with a selection of grasses taller than those used for the rest of the

area. No forbs have yet been included, but some grasses and forbs common to the area are present and greatly enhance the overall appearance of the planting. A ten foot wide strip is mown along both sides of the entrance road to help relate this expanse to that of the mown grass surrounding the building. The prairie planting was burned this spring, the roadway and mown areas serving as safety features.

The owners of Sather Cookie Company of Round Lake, Minnesota, are developing much of their land adjacent to Round Lake to serve more effectively as a scenic, educational, and recreational resource of the community. Trees and shrubs are being planted where row crops have been for many decades, and prairie is being restored on similar portions. Although only grasses were sown on the site three years ago, there are already a considerable number of milkweeds, coneflowers, anemones and other prairie forbs among the indian grass, switch grass, bluestems and other grasses.

Walden Park, in Madison, has been designed, installed and maintained by Professor Darrel Morrison and students in landscape architecture at the University of Wisconsin. In this small park, prairie plants occupy most of the central space, while trees, shrubs and herbs of other Wisconsin vegetation zones serve as enclosing and screening units. During a recent visit, we were pleasantly surprised by the effective enclosure and screening that was provided by the tall grasses and forbs! Subtle manipulation of ground form and proximity of buildings on two sides add to the spatial quality, and also increase the diversity of microclimates. Thus, the great variety of plant species in so small a space becomes ecologically as well as esthetically meaningful. The result is an enrichment of human experience.

PRESERVATION AND MANAGEMENT; PRAIRIE OF THE FUTURE

The preservation, establishment, and management of natural and man-designed prairies are challenging aspects that must be considered in their design or use. These studies and practices are continuous, and becoming more widespread. The use of fire is usually considered, and sometimes tends to discourage owners or administrators. We are encouraged by the progress being made, both in the practice and in public acceptance.

How did we learn to manage rice paddies, corn fields, and apple orchards? I am convinced that when we decide that we want to live and play and work amid prairie landscapes, we will create them and learn to manage them.

> One characteristic of animal behavior is that it is dominated by the physical presence of what the animal wants or fears...Man has freed himself from this dominance in two steps. First, he can remember what is out of sight...speech allows him to recall what is absent, and to put it beside what is present; and second, the practice of speech allows man to become familiar with the absent situation, to handle and explore it, and so at last to become agile in it and control it.
>
> J. Bronowski as quoted in "Landscape Architecture" by John Ormsbee Simonds

We cannot expect to physically experience prairie as it once was here in the Midwest, but, hopefully, through continued growth in our knowledge and understanding we may know and appreciate the essence or spirit of this great natural phenomenon.

The true idea of the prairie will live forever, but the prairie experiences of future generations will depend upon the interpretation and expression of the designers and custodians of our landscape.

ABSTRACT

Although the inherent beauty of the natural prairie landscape has been recognized and appreciated by some for many years, only recently has more than a token amount of attention been given toward utilizing its form or its plants in the design of landscapes for human use. Today, we can find many examples where prairie plants are being used to solve economic and ecological landscape design problems as well as to provide unique educational and esthetic experiences.

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INDUSTRY USES OF PRAIRIE GRASSES FOR EROSION CONTROL AND LANDSCAPING

Walter G. Brakeman

Prairie grasses, both natural restoration and introduced, are but one of the design tools we use for:

1. Erosion control and noise attenuation at our Peoria Proving Grounds.
2. Minimum maintenance plantings in future expansion areas at many of our manufacturing facilities.
3. Beauty with minimum maintenance of some of our public areas. These are the areas that separate buildings from public highways.

Until four years ago our knowledge of prairie grasses consisted of the historic tales of pioneers breaking up the "prairie sod" to grow wheat and corn. The breakthrough came with a visit to the USDA Plant Materials Center at Elsbury, Missouri, and an introduction to Billy Roundtree. Our interest in prairie grasses and the realization of their potential values as landscape design tools began. We discovered over thirty acres of remnants at our Peoria Proving Grounds and another twenty acres at our Denver, Colorado Parts Department which added to our efforts to learn and expand our knowledge of prairie so as to be able to use it as a landscape design tool.

Before we became aware of the potential of prairie grasses, most of our seeding efforts had been with highway seeding mixes: 80 pounds/acre of 56% Tall Fescue, 35% Rye Grass, 11% Red Top and overseeding of Reed Canary Grass in the draws. This mix is our standard for storage and minimum maintenance areas. Mowed and irrigated lawns are still the major effort for public and pedestrian areas. Both of these require topsoil, fertilizer, mulching or irrigation, and high maintenance costs.

Our initial effort with prairie seeding to reduce these maintenance costs was in June 1972 at our 2600 acre Peoria Proving Grounds. The most improbable ground conditions were selected for this first test. Seven acres of 3:1 and 4:1 slopes of subsoil and sediment dredged from basins used to control erosion. Topsoil had long ago disappeared because of the numerous testing exercises on these areas. 130 pounds of Jim Wilson's Prairie Mix of 20 lbs each of big and little bluestem, side-oats grama, Indiangrass, switchgrass and 30 lbs of western wheatgrass were given to a novice crew with instructions to disk the area once lightly and seed using no fertilizer or mulch. In addition, the seeding was done with a Hydro-seeder, however by the first week in July the seedings had grown 1-2 inches. The success of this first effort opened our eyes to the potential large dollar savings.

Subsequent seedings under more desirable conditions are proving the first effort was no fluke. Pre-prairie seedings, other than Crownvetch, are only responding after repeated applications of maintenance fertilizer at least once a year with 250 lbs of 10-8-6 per acre.

Our seeding efforts are being accomplished in two ways:

1. At the Proving Grounds the variable size of areas to be seeded and time when testing is completed to allow seeding makes it more practical to do this work with our own equipment and available manpower.

The author is at the Caterpillar Tractor Company, Peoria, IL 61602.

2. Contract seeding is done using the USDA guide specifications with only slight modifications. We are seeding at the rate of 40 PLS/sq ft with 2 of the PLS being forb seeds from the list of recommended forbs Dr. Schramm gave at the first Prairie Conference in Galesburg, Illinois in 1968. Straw mulch is applied within 24 hours after seeding is completed over all the areas seeded.

A side interest has developed in the use of mulching materials storage. Storage and availability of straw, plus need for additional equipment and manpower suggested the use of wood cellulose mulch as the more expedient method of mulching for our situation. Contractors are required to use straw-asphalt emulsion mulch. With the new EPA rules on burning trees cleared from construction areas we are now finding shredded wood or chips are equal or superior to straw.

One concern is the lack of good certification and germination testing for prairie seed. It costs just as much to seed with poor seed as good seed unless you have a failure and then it costs double. The little cost difference for good seed is cheap insurance for a successful stand. We think as others begin to recognize the potential for prairie seeding the need for uniform certification and testing will increase significantly, and this is something we all should be actively supporting now.

Each of us has our own personal objectives for attending this conference. Mine is design, but as part of a team effort to encourage and promote additional efforts for prairie restoration, I need the knowledge of both the technicians in this group and practitioners to be able to accomplish my design objectives.

We are here to learn from each other and anything that will help us understand what and why we do what we are doing will help us better to promote the team objective of broader prairies in our home states.

ABSTRACT

Caterpillar Tractor Company, in its quest for economical erosion control and landscaping materials with minimum maintenance at its Midwest proving grounds, has discovered the value of native prairie grasses. These are now being used to establish ground covers on spoil areas devoid of topsoil, with minimum fertilization and using existing seeding equipment. Studies of individual grasses are providing new landscape tools for both esthetics and erosion control at low costs with reduced maintenance.

RANGELAND – A PROPER PRAIRIE USE

C. M. Schumacher

Prairie is land on which the climax (natural potential) plant community is dominated by grasses. When land such as this is used for grazing by livestock and big game animals, the land use is designated as rangeland. Rangeland is a historical and proper land use of true and mixed prairies. These are lands on which grasses, grass-like plants, forbs, and shrubs evolved – while being used by grazing animals – to dominate the climax plant cover. In South Dakota 9 million hectares of private land are used as rangeland, in North Dakota, 4.5 million hectares. Nebraska, with its vast sandhills prairie, has nearly 10 million hectares. In the eastern prairie states, the total area of rangeland is much less: Minnesota has 28 thousand hectares, and Iowa only 11 thousand hectares.

Principles and techniques for the improvement or maintenance of this kind of land make up the science of range management. Range management is a young science that grew up with another young science called ecology. Ecological principles are an integral part of sound rangeland management.

The interest of the Soil Conservation Service (SCS) in rangeland management traces back to the origin of the Service. In 1935 Public Law No. 46 directed the establishment of SCS as an agency to carry out Congress' declared policy to provide permanently for the control and prevention of soil erosion and thereby to preserve natural resources. This law applies to rangeland as well as to other kinds of private land.

Generally, on rangeland, the greater the departure of the vegetative cover from climax the greater the exposure of the site itself to destruction by the elements. Therefore, climax has a meaning to the resource manager whose goal is the prevention of soil erosion.

In the late 1930's and early 1940's, plant scientists with SCS began to use condition classes as a measure of the health of rangeland. Gradually a range-site-and-condition concept was developed and put into general use when making inventories of the rangeland resource.

By definition, a range site is a distinctive kind of rangeland that differs from other kinds of rangeland in its ability to produce a characteristic natural plant community.

The range site is a product of all the environmental factors responsible for its development. In the absence of abnormal disturbance and significant physical deterioration, the site can be identified by the natural plant community growing on it. Where excessive livestock grazing or other disturbance has altered the plant community, the range site can be identified by such environmental factors as soil, climate, and topography. The assumption that similar soils having the same topography and the same climate have the same potential for climax vegetation is well established. Range site is used as a basic segment of the rangeland inventory. It is very useful for making essential interpretations for uses and benefits of rangeland other than livestock production.

By definition, range condition is the present state of the vegetation of a range site in relation to the climax plant community for that site.

Range condition is based on a comparison of existing plant communities with the presumed climax plant community for a specific range site regardless of the value of individual plants or of the plant community for specific uses. Departure from climax is measured in increments of 25 percent and range condition is then classified as being excellent, good, fair, or poor.

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One of the methods used to determine the climax plant community of a range site is the evaluation of relict vegetation and associated soils on areas that have been subjected to minimal abnormal disturbance. This poses a problem, as reliable relicts of prairie in eastern South Dakota are scarce and in some areas their existence is threatened.

When used as rangeland the usual goal of management is to restore or to maintain the climax plant community, or a plant community somewhat altered but still providing adequate resource conservation. When properly planned and carried out, such use preserves the potential of the site itself, and the site does not contribute appreciably to the pollution of adjacent lands or lands downstream.

On rangeland, the proper degree of use each year, including well-planned deferments, is the most effective and least expensive conservation practice. Such use permits secondary plant succession where needed.

As population increases, the pressure for more intensive land use increases. This pressure is evident in higher cost of land and higher prices paid for crops. Much land in South Dakota, an estimated 117 thousand hectares, went from grassland use to cropland use in the fall of 1973 and the spring of 1974. Some lands that do not have the capability for this more intensive land use have been broken out of grass. The 1967 Conservation Needs Inventory, made by SCS, indicates that South Dakota has 214 thousand hectares of cropland that should be converted to rangeland by reseeding. North Dakota has 299 thousand hectares and Nebraska over 400 thousand hectares of cropland that should be converted to rangeland.

When warranted, SCS encourages or may be asked to assist in the conversion of cropland to grass. Based on the capability of the land and the needs and desires of the landowner, SCS may recommend range seeding or pasture planting. Some lands have a capability for either of these uses. Production from well-managed pasture is greater on suitable lands, but this fact must be weighed against the greater inputs demanded and the season of the year when additional grazing is needed. Nearly all grasses used for tame pasture in this area are cool-season species that are most productive early in the season and less productive in July and August.

When establishing grass on lands not suitable for tame pasture, or where rangeland is the preferred land use, range seeding is the practice used. This practice aims at returning the site to a high range condition, generally as near climax as is practical. This necessitates the use of different species mixtures on different range sites.

Successful range seeding has been a relatively recent accomplishment. As recently as 1931 the renowned agrostologists A. S. Hitchcock and Agnes Chase wrote the following about the cultivation of native grasses:

> Only one of the fifty species (grasses) cultivated in the United States is a native of this country. This is slender wheatgrass (*Agropyron tenerum*), which is cultivated for hay to a very limited extent in the Northwestern States. Our prairies, plains, and upland meadows support numerous native species that are palatable and nutritious, but none of them has been found adapted to cultivation. This is due principally to the high cost of their seed. The grasses which best withstand grazing are sod formers. Perennials as a whole produce fewer and less viable seed than do annuals, and sod-forming grasses particularly, spreading vegetatively, do not produce large seed crops.

Only a few years after the above was written, the drouth of the 1930's emphasized the need for seed of grasses adapted to the Midwest and West. In response to this need, during the mid 1930's, some of the first plant science specialists employed by SCS began scouring the Great Plains for promising plant materials. A start was made in selecting and evaluating some

native species at SCS plant materials centers, but the production of adapted seed in quantity was still years in the future. Plant scientists called upon for plant materials to stabilize badly eroded areas in the Great Plains faced an enormous problem.

During this pioneer period, the inherent characteristics within native grass seed as well as its physical structure presented problems not fully understood. The truth that seed from a single native species could contain such divergent ecotypes was difficult to comprehend. Trial and error by some and research by others proved that for range seeding it was best not to move ecotypes of warm season native grasses more than 400 to 480 km (250 to 300 miles) north or 240 to 320 km (150 to 200 miles) south of their point of origin; also, that ecotypes should not be moved from one range site to another site having major soil or climatic differences. For prairie restoration, it would be better to further restrict distances of movement and differences in site.

Many native grasses have seeds that when threshed are fluffy or chaffy or contain much inert matter. For example, only a few years ago a seed dealer in South Dakota reported that seed of little bluestem (*Andropogon scoparius*) was returned. The reason given: "because it's hay, not seed." Special drills were developed; some built with a picker wheel like that in a cotton planter, that would evenly meter out nearly any of the native grass seeds.

Limitations caused by the small size of these seeds had to be considered. Farmers knew how to plant wheat (*Triticum* spp.). The seed kernel of wheat weighs 40 mg and can push a green shoot up through a considerable covering of soil. Seeding equipment used to plant wheat buried the seed of grasses such as western wheatgrass (*Agropyron smithii*) that weighs 4.26 mg, big bluestem (*Andropogon gerardi*) that weighs 2.98 mg, little bluestem that weighs 1.79 mg, or sideoats grama (*Bouteloua curtipendula*) that weighs 0.62 mg. Drills with depth bands were developed that were capable of placing these small seeds at a depth from which the new shoot could emerge.

It was true, as pointed out by Hitchcock and Chase, that the native grasses, especially the rhizomatous species, did not produce much seed. At least this was true of these plants when they grew in the wild. Seed producers learned that when properly spaced by planting in rows, given adequate water and fertilizer, and protected from competitive weeds, these grasses produce seed in economic quantities. Also, the removal of these competitive factors does much to improve the size of the caryopsis and thus the vigor of the seedling.

It has been found that seed of many prairie grasses collected in the wild can be increased under optimum conditions. The increase, after careful evaluation, can then go to seed producers who make it available commercially. This seed still contains the inherent characteristics of the native grass, and it has an increased food supply that enhances the chance of seedling emergence and survival when used in range seeding.

Range seeding does not restore prairie as it was in its pristine condition. When properly carried out, it does assure a plant cover of dominant prairie species that can be maintained by proper grazing management. This plant cover, with proper use, will protect and improve the soil resource so that associated plants native to the site can come back through secondary plant succession.

The vast prairie region of North America evolved under grazing use and occasional burning. In the early 1950's, I had the privilege of accompanying the ecologist, Dr. David Costello, of the U.S. Forest Service, when he was selecting a section of the Nebraska National Forest to be protected as a "natural area." This was in the heart of the Nebraska sandhills prairie and the site, still protected, is known as "Signal Hill Natural Area." I recall Dr. Costello's observation that protecting this section was a good thing to do but that it was improperly named. He said that when man kept grazing animals and fire out of a grassland ecosystem it should be called an "unnatural area."

It is my contention that proper grazing use and range seeding are compatible with the need expressed for the preservation of the genetic heritage contained within the prairie ecosystem. It is also my belief that the preservation of relict areas of climax vegetation is a great asset to the person managing the rangeland resource.

ABSTRACT

Prairie is land on which plants suitable for grazing evolved, with grazing use, to dominate the climax plant cover. Such land when used for grazing, by livestock or big game animals, is designated as rangeland. Management of rangeland is based upon sound ecological principles.

The Soil Conservation Service (SCS) provides the landowner with range site and condition information which is useful for making essential interpretations for the varied uses and benefits of rangeland. The usual goal of range management is to restore or to maintain the climax, or near climax, plant community.

Rangeland on which little or none of the climax vegetation remains can be partially restored by range seeding. Range seeding, when properly carried out, assures a plant cover of dominant prairie species that can be maintained by proper grazing management. This plant cover, with proper use, protects and improves the soil resource so that associated plants native to the site will be able to come back through secondary plant succession.

Proper grazing use and range seeding are conservation practices compatible with the need expressed for the preservation of the genetic heritage contained in the prairie ecosystem.

KEY WORDS

Prairie, climax, rangeland, range site, range condition, range seeding, proper grazing use.

LITERATURE CITED

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WHY LITTLE BLUESTEM IS A KEY PLANT IN THE COMPOSITION OF NEBRASKA'S RANGELANDS

Walter Fick

It can be said the grasslands of Nebraska are worth many times more than gold mines. For here grows a wide variety of grasses, mixed with native legumes, forbs and various other plants. Along with a favorable climate and sufficient rainfall, here has been created one of the greatest grass producing areas to be found anywhere. Nebraska's grasslands are as valuable as gold mines for her grasses are a renewable resource, and can be harvested again and again. They are truly green gold.

But we know the key to maintaining the highest production, and preserving this resource is through wise management. So it becomes necessary that every practicing rancher learns to recognize the different species of grass and plants that inhabit his range. He must know their value, which ones are palatable and nutritious and which are low in such values. For when he can recognize the different plants and knows their value, he can manage his grazing in a way that will help to increase the desirable plants, and to eliminate the low value invading species. Thus, he can increase his grass production to its highest potential.

Actually every ranch is a grass factory. Livestock are but the means to harvest it and convert it into a marketable product. It is not necessarily the number of livestock that he can run, but the pounds of beef he can produce that is important.

This is what I have tried to do on our small family size ranch in Holt County, Nebraska. I would like to share with you why I believe "Little Bluestem is a Key Plant in the Composition of Nebraska's Rangelands," my experiences and the observations I have made with the species little bluestem (*Andropogon scoparius*). I want to tell you why I believe little bluestem is the key plant in the composition of our range grasses and the one species that any rancher can use as a barometer to gauge the condition and productivity of his entire range, thus enabling him to achieve his rangelands' highest production.

Little bluestem, or commonly known as bunch grass, is a plant that I feel has been unjustly condemned by so many people, as having no value, and one that livestock will not eat. I feel it is merely a case of misunderstanding. For it is the key plant I have used in increasing the production and measuring the improvement I have made on my own ranch.

Observe this plant for a minute. It is as its name applies, a bunch grass: a thick, dense clump of grass. We find the little bluestem plant is capable of producing an enormous amount of forage. But like all living things it too exists under the laws of nature, where the strongest motivation of all life is self preservation, the urge and struggle to reach maturity, and then to reproduce itself and, thus, to fulfill its destiny as nature intended.

But in order to achieve this end, nature has given to all living things a means of defense. If too much of its growth is left ungrazed it becomes coarse and unpalatable and livestock will shy away if other more palatable forage is available. It is for this reason, I believe, it is condemned as of no value. But in reality it is the plant's first line of defense. For little bluestem cannot spread by an underground root system but must be allowed to reach maturity and produce its seed in order to survive and propagate itself.

If you would observe the area surrounding a mature parent plant, you will discover many young plants becoming established and replenishing the range with its own kind. As these young plants furnish nutritious forage they usually are closely grazed and the unobserving eye fails to see them.

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But again, my purpose is to show you that little bluestem can be used as a measuring stick, that by its presence, its absence, or the amount of grazing pressure it is receiving, as an indication of the total range condition.

On a site that is in good range condition you may find many little bluestem but animals do eat little bluestem for our rangeland is like a cafeteria, offering a wide selection of plants. The cattle graze along making a selection here and there. The next time they pass they do the same. As long as there are other species available, they take only the choicest parts of each. If the range is overstocked, or grazing pressure increased...each time around there is less choice until even the parent little bluestem plants are grubbed to the ground. Their root systems become weakened and eventually they die and disappear from the range. When you have no little bluestem left in the composition, all the desirable grasses will have been overgrazed too. You will have reached the point in time where you are beginning to harvest your factory. Little bluestem is the key plant and can be used to gauge the condition and productivity of your entire range. Here and there you may find a plant hardly grazed, but for every plant you see ungrazed, you will find six or a dozen grazed to varying degrees. Always remember to notice the condition and degree of use on the rest of the range as the grazing pressure increases on the little bluestem plants. Soon you will learn to recognize when you have achieved full use and yet maintain the highest total production.

We had an interesting experience in a pasture we purchased some years ago. The range condition was certainly down. Little bluestem plants were practically all gone. The predominant plant was green sagewort. Only here and there you would see a little bluestem plant, and it would be hiding beneath the protective surface of a prickly pear cactus. But on closer observation we found many dead clumps of little bluestem that had been grazed as close to the ground as possible. The leaf surface of these plants had been removed too long. No longer able to breathe or absorb the sun's energy, they became exhausted and had died. This was real evidence of continued overgrazing. Again, the absence of healthy little bluestem plants told us the low condition of the rest of the grasses in the composition.

We kept this pasture under light use and it was eight years later before we felt that little bluestem was becoming reestablished. By then too, we noticed that the green sagewort was thinning out as the other desirable grasses were returning and gaining in vigor.

We had a similar experience in another pasture that was in low to fair condition. Only here we started on a complete deferred program. It was left idle for eight complete growing seasons, and then was used only lightly in the fall for the last of the four years. What a transformation took place here. It had become a sea of grass. But the noticeable thing was as the pasture returned to full production so did little bluestem.

We then managed with what we thought was proper use, using little bluestem as the key plant to tell us when the range condition was going up or down, so we could now maintain full production.

A view across any adjoining fence line gave one quite a lesson too. As far as you could see across, there were no little bluestem plants and all other desirable plants were practically gone. Something had happened here and it all started when the operators failed to notice that little bluestem was beginning to disappear from the composition. Ten years prior, the condition in these two pastures was exactly reversed.

Working with nature teaches us that we live in a world of cause and effect relationships. Things do not just happen, but are made to happen. Every rancher is the absolute monarch in his grass land dynasty. He opens–and shuts the gates. He rules–and must assume responsibility. For when man abuses his range, nature quickly replaces it with undesirable plants in order to discourage further destruction by grazing animals. Every plant in nature's realm serves some useful purpose. Even yucca and cactus assume a protective role and assist desirable grasses in their struggle for survival. All grassland is a complex society of living plants: each struggling for

survival and domination. Every hillside is a written page and one every rancher can learn to read. The condition of your range today is the result of the management it has received in the past. The condition of your range in the future will depend on the kind of management you are giving it today.

We have seen that little bluestem is a desirable grass. That livestock do eat it—and can destroy it. That by its absence or presence you can measure the total condition of the range. But little bluestem offers other advantages as well, for its very presence in the composition denotes that you have a strong vigorous grass factory. When this condition exists all the grasses start earlier in the spring. A good grass cover affords protection from wind erosion. It helps to absorb the rain, thus helping recharge the ground water supply. It holds the winter snow to blanket the hills. Little bluestem is also recognized as one of our most important grasses in our native hay meadows, adding greatly to our winter feed supply. If all of these then are true..... why can we not accept little bluestem on its merits in our summer range?

ABSTRACT

Little bluestem is a desirable grass. Little bluestem is the key plant in the composition and can be used as a barometer to help you achieve the highest production possible. From practically nothing but your willingness to permit a few parent plants of little bluestem to go to seed each year, you too can eventually possess a virtual sea of grass. When you do, you will find that little bluestem has been with you all the way helping you to achieve that goal. Your grassland then will be like a gold mine and can be harvested again and again as long as you continue to manage it wisely.

MIDWEST LIVESTOCK PRODUCERS REDISCOVER THE PRAIRIE GRASSES

John K. Maddy

In the beginning, grass, trees, and shrubs covered the arable land of the vast midwest areas of the United States. These plants grew and died in natural succession, leaving their residue to the land. This helped develop deep and productive soils -- some of the most productive soils of our Nation. The grasses were also used by wild animals for both forage and cover. Wild buffalo, antelope, and the lowly prairie dog made their homes in this habitat.

This natural community of plants and animals was radically disturbed when immigrants from Europe came to our American shores. They brought with them a new life style and procedures for managing plants and animals. The immigrants soon discovered that the land on which these wild plants had grown could also grow more economical crops. The crops could be used by the grower, sold for money, or bartered for other needed products.

Native plants, both grass and trees, were plowed or removed to raise wheat and, later, corn and tobacco. Native grasses used for forage or pastures were not managed properly so they lost vigor. They were rapidly invaded by plants that were less desirable for grazing. To make these hay and pasture fields more productive and economical, new grasses were introduced to American agriculture. These introduced plants were plants that the early pioneers were familiar with in their home country. They knew how to plant, manage, and use them for forage production. They introduced timothy, orchardgrass, bromegrass, clovers, alfalfa, and many other species from their native lands. Unfortunately, some undesirable plants called weeds hitchhiked with the imported seeds.

These introduced plants spread rapidly across the United States as the prairie grasses were plowed or were grazed out with incorrect grazing systems. The introduced plants were those that made most of their growth in the early growing season and again in the fall months when the weather was cool and moisture was favorable. This was in contrast to most of the prairie grasses that made their most productive growth during the warm summer months.

Over time, the eastern livestock farmer learned more about how to seed, fertilize, and graze these cool-season species. Research was also helpful for farmers who raised row crops and small grain and used legume-grass mixtures for both hay and pasture. At the same time, the western rangeman was learning to manage the drier grassland of the plains. Some of these men learned how to manage communities of grasses and associated forbs for the production of livestock. Some learned that to maintain economical forage production, he must not be too greedy in his grazing program. And they learned to graze only half the production of his grass plants, leaving the other half to maintain stands of vigorous growing grass.

On the surface, all seemed to be going well as far as using plants and animals for producing beef and milk products was concerned. It soon became evident that there were flaws in grazing calendars that gave stocking rates for livestock on pastures. Although cool-season species produced well in spring and early fall months, production was inadequate during the hot and often dry summer grazing period. Likewise, rangemen in some areas of the West were having the same problem finding adequate forage in the early spring and fall grazing periods.

In the Midwest and particularly in Iowa, most cool-season pastures produce an overabundance of forage in June and often a sparse growth in August. In contrast, warm-season species like switchgrass, big bluestem, and indiangrass make their greatest production during the warm weather months of July and August.

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During the late 1960's, B. H. Rountree, plant materials specialist for the Soil Conservation Service, suggested that both the warm-season and cool-season grasses be grown on the same farm. They would be grown in separate pastures and grazed in such a manner that fresh, succulent forage would be available during the entire grazing period.

New selections of some of the warm-season species had been tested at the SCS plant materials center located at Elsberry, Missouri. These new accessions were available to midwestern farmers to compare with standard varieties on the commercial market.

Starting in 1970, a small number of Iowa livestock farmers were encouraged to use both warm- and cool-season grasses for full-season pastures. Warm-season pastures were established in *pure stands* in order to reduce the complication of growing mixed stands of grasses with different growth patterns, maturity and response to management techniques. Pure stands of switchgrass, big bluestem, or indiangrass were most commonly seeded in a separate pasture or grazing unit. Other pastures were seeded to pure stands of bromegrass, orchardgrass, tall fescue, or other suitable cool-season species.

The grazing schedule varied from farm to farm, but in general the livestock were turned into a cool-season pasture about May 1. The cattle were usually rotated from one cool-season pasture to another, depending on the growth of plants, size of fields, and numbers of livestock. Cool-season plants start to produce seedheads in late May and usually produce up to two-thirds of the season's production before July 1. Cool-season pastures deteriorate very rapidly after this date. They produce forage again when cool weather returns in late August or early September.

Warm-season species start to "green up" in late May. Depending on the species seeded, they are ready to graze in late June or early July. The midwestern livestock man learned that warm-season grasses respond favorably to commercial fertilizer. Fertilizer can double forage production on warm-season as well as on cool-season pastures. Again, livestock can be moved from one warm-season pasture to another in keeping with good grazing management. Like their cool-season cousins, warm-season plants decrease their forage production very rapidly after seedheads form. To maintain beef production, it is necessary to move to other pastures. The logical choice is back to the cool-season grasses, as their growth and production starts again in September.

Does this cool-season, warm-season combination pay off? A new system must not only prove as good, but must be better if livestock men are going to use it. Some research on this combination showed up well in Nebraska. For example, yearling steers grazed all season long (189 days) on cool-season grass, and produced 193 pounds of beef per acre. When grazed for the same number of days on both cool- and warm-season grass, the total gain was 267 pounds of beef per acre. This was an increase of 74 pounds for the season and did not require additional pasture acres.

Iowa livestock men are finding the same increase in production when integrating both plant species. Iowa does not yet have large acreages of native grass pastures, but the practice is increasing and interest is gaining each year.

In addition to the use of warm-season grasses for pasture, there are some other benefits that wildlife biologists are testing and becoming quite enthusiastic about. The ringneck pheasant has been finding less and less nesting cover, especially during the early spring months of the nesting season. Other wildlife species also need better habitat. Grazing cool-season grasses closely in the spring results in poor nesting cover, but the native grasses are not grazed until July and so maintain suitable cover into August. This gives the birds a chance to "bring off" a brood that otherwise would not have been possible. Also, since native grasses cannot be grazed closely and still maintain their usefulness, their ungrazed stubble remains as winter protection for many wild birds and animals.

Native grasses are also grown on many sites in Iowa for erosion control cover. They are grown in both pure stands and in mixtures. These grasses often prove a better choice on sites where low fertility and drought prevent the establishment or maintenance of long-time stands of cool-season plants.

Many schools, churches, youth camps, industries, and individuals are establishing native grasses on private lands. They call it "restoring the native prairie." These fields are providing good sites for outdoor classrooms.

Native grasses are returning to Iowa and the Midwest with a variety of uses. Thanks to recent grazing experiences in the use of warm-season, cool-season grass combinations for beef or milk production, they can be economical to landowners as well as providing protective cover for the land.

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