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Third Midwest Prairie Conference Proceedings

Kansas State University, Manhattan

September 22 — 23, 1972

Lloyd C. Hulbert, editor

Division of Biology, Kansas State University

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PREFACE

The location of this third midwest prairie conference resulted from being informed that a host for another conference was needed at about the time of our recent acquisition of Konza Prairie Research Natural Area, 916 acres of bluestem prairie which we are happy to show to those interested.

The response to the announcement was a surprise, so much so that we had to reschedule to larger rooms than originally planned. About 200 enthusiastic people participated in the two day sessions. The blend of papers from various disciplines and from both practitioners and researchers, rather than being dull as in some conferences, seemed stimulating and enriching, probably because of the common interest in the prairie.

The first prairie conference was held at Knox College, Galesburg, Illinois, in September, 1968, ably organized by Peter Schramm. Two years later a second highly successful conference at the University of Wisconsin was coordinated by James H. Zimmerman. A fourth conference is already being planned for North Dakota in 1974. Anyone interested that is not already on the mailing list should write to Mohan K. Wali, Department of Biology, University of North Dakota, Grand Forks, N. D. 58201 and ask to be put on the mailing list.

It is logical that those who are interested enough to attend a prairie conference would be interested in seeing that samples of prairie are preserved for the future. Thus an unplanned expression of support for a prairie national park appeared at the sessions, resulting in appointment of a committee to draft the following resolution which was adopted by the conference and sent to the news media and government officials.

The Third Midwest Prairie Conference with over 200 scientists from all over the Midwest, assembled at Manhattan, Kansas, September 22, 1972, is strongly aware of the rapid disappearance of one of our irreplaceable national resources, the prairies of North America.

These are very diverse types of habitats of our native plants and animals and extend over a vast area from Canada to Texas. Representative areas of these prairie ecosystems need to be incorporated into a National Park system. As an initial step in this direction the Prairie Conference endorses strongly the incorporation into the National Park system of the proposed Tallgrass Prairie National Park in Kansas (House Bill H. R. 9621 and Senate Bill H. S. 2149). It further suggests that other portions of the prairies be sought in other states as necessary parts of a North American Prairie National Park system.

Not represented in these proceedings is the display "The Spirit of the Savanna - the Invisible Landscape from Alberta to Texas" which Dr. Robert W. Dyas and students of the Landscape Architecture Department, Iowa State University, Ames, brought and set up at the conference, much to our edification and enjoyment.

Many at the conference attended the field trips to Konza Prairie Research Natural Area and the Soil Conservation Service Plant Materials Center where a large number of native prairie plants are being raised.

The participants made the conference possible, their enthusiasm made it a pleasure, and the cooperation of the authors facilitated publication of these proceedings. To all go a sincere thanks.

Lloyd C. Hulbert, coordinator
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Manhattan, Kansas 66506

SESSION CHAIRMEN:

T. M. Barkley, Associate Director, Division of Biology, K.S.U.
G. W. Tomanek, Vice-President, Fort Hays Kansas State College, Hays
Peter Schramm, Director, Knox College Biological Field Station, Galesburg, Illinois
Roger Q. Landers, Department of Botany and Plant Pathology, Iowa State University, Ames.

Management of Prairies and Prairie Species

BURNING TRUE PRAIRIE¹

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Abstract. True prairie grasslands evolved under conditions which included fire. Fire's use as a management tool has been investigated at Kansas State University since 1923. Time of range burning has a profound influence on its effect. Generally the closer time of burning is to time of spring growth the more favorable the responses for domestic livestock production. Higher forage yields, higher range condition, lower soil moisture losses are associated with late spring burning (May 1) when compared to earlier burning dates. Many weedy grass, tree, and shrub species can be controlled by use of fire. Soil temperatures are higher throughout the growing season following a spring burn. Soil chemical properties are altered little in grasslands following long-term annual burning.

True Prairie is a fire-derived and fire-maintained grassland. Adaptations of grasses such as apical meristem placement, intercalary meristem, and rhizomatous habit likely have occurred in response to fire and grazing pressures. True Prairie, dominated largely by warm-season perennial grasses, is invaded rather quickly by cool-season grasses, shrubs, and trees in the absence of fire. Grazing impedes but does not eliminate invasion of some woody species (Blan 1970).

Bluestem range has been burned as a management practice since presettlement days. Lewis and Clark (Coues 1893) reported widespread use of fire by indigenous tribes of the central United States. Their use of fire to attract large herbivores, primarily bison, led to use of fire as a tool for domestic livestock operations that developed in the Midwest in the late 19th century. Cattlemen trailing herds from the southwest to fatten in the bluestem regions observed increased livestock gains on burned areas as opposed to unburned areas. Later leasing agreements stipulated burned grassland and fairly liberal acre allotments for each animal to insure high gains. The combination of fire and liberal acreage maintained the True Prairie in excellent condition.

More intensive use of the prairie with cattle confined by barbed-wire fences made overgrazing a serious problem. Overgrazing and improper timing of range burning lowered livestocks gains and countered the benefits of burning.

TIMING RANGE BURNING

In the early 1900's prairie usually was burned in late fall to late winter; very little was burned as late as March or April.

Herbage yield.

Research begun at Kansas State University in 1923 by A. E. Aldous led him to consider effects of time of burning on

Grasses and Prairie Species

Owensby

City, Manhattan 66506

bluestem range productivity (Aldous 1934). His ungrazed plots have been burned annually since then except from 1945 through 1952. Aldous (1934) and McMurphy and Anderson (1963) have reported herbage yield data from those plots (Table 1). As time of burning neared when warm-season dominants started growth, forage yield was reduced less.

Table 1. Grass and weed yields (lb per acre, air-dry) from plots burned at indicated times on Aldous plots.

Time of burning	Grass	Weeds
Aldous (1927-1933)		
December 1	1519	95
March 20	1643	115
April 10	1888	76
May 5	2017	34
Unburned	2926	113
McMurphy and Anderson (1929-44, 1953-60)		
December 1	1975	
March 20	1979	
April 10	2090	
May 1	2280	
Unburned	2550	

Studies on grazed pastures were initiated in 1950 on the Donaldson Pastures (Range Research Unit) 5 miles northwest of Manhattan to determine effects of burning date on livestock performance, botanical composition, and herbage yields. Early-spring (March 20), mid-spring (April 10), and late-spring (May

¹Contribution No. 1325, Department of Agronomy, No. 449, Department of Animal Science and Industry, Kansas Agricultural Experiment Station, KSU.

1) burned, and unburned pastures were studied. As with the ungrazed plots, forage yield was reduced less with later burning. However, forage yields on grazed, late-spring-burned pastures did not differ from those on grazed, unburned pastures (Owensby and Anderson 1967). Weed yields were less on mid- and late-spring burned pastures than on unburned pastures.

Soil moisture.

Exposure of the soil surface to raindrop action reduces soil's infiltration capacity by reducing noncapillary porosity. The longer the soil remains barren, the greater is the risk of puddling and reduced soil moisture for plant growth. Burning removes not only the standing dead material, but also most of the mulch. Mulch provides the cushioning necessary to maintain good granular structure for high infiltration.

Anderson (1965) reported on how burning dates affected total soil moisture in the ungrazed Aldous plots, as measured by a neutron moisture gauge. Soil moisture generally increased in burned plots as burning date approached start of spring growth, and unburned plots had the highest soil moisture (Fig. 1).

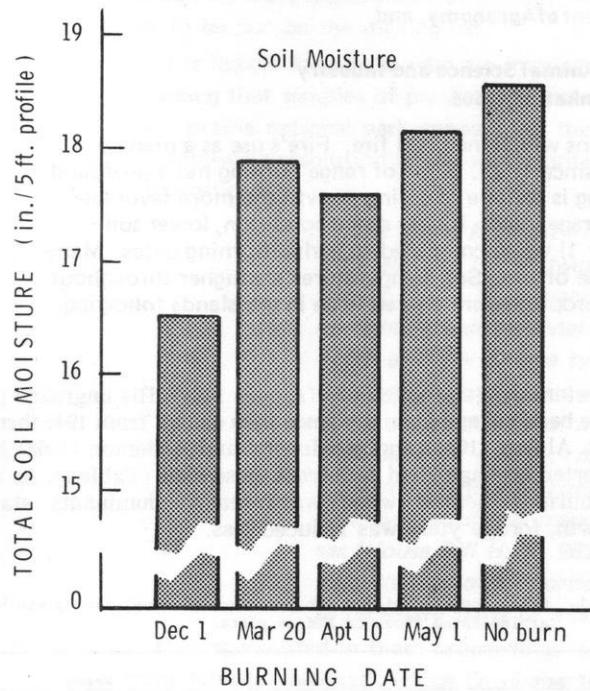


Figure 1

On grazed units soil moisture was highest on the late spring burned pasture and lowest on the unburned area; early- and mid-spring burned pastures were intermediate (Anderson et al. 1970). Apparently greater growth by forbs and woody species increased moisture use on the unburned area.

Botanical census

Species responses to burning date under grazing were reported by Anderson et al. (1970) as follows.

Decreasers. Major warm-season dominants tend to decrease under excessive grazing and are used as primary indicators of bluestem range conditions.

Higher percentages of decreaser species [big bluestem (*Andropogon gerardii* Vitman), little bluestem (*A. scoparius* Michx.), switchgrass (*Panicum virgatum* L.) and indiangrass (*Sorghastrum nutans* (L.) Nash)] were found on grazed mid- and late-spring burned pastures than on unburned or early-spring burned ones (Fig. 2). More big bluestem and indiangrass accounted for the differences in decreaser amounts. Little bluestem percentages were essentially the same in all study pastures. As little bluestem is a bunchgrass with dead material in the center, fire burns into the crown and kills some plants.

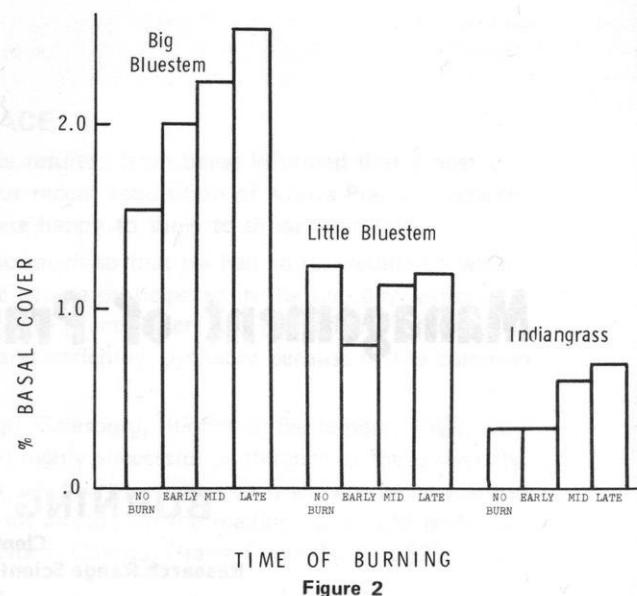


Figure 2

Increases. Secondary species in the stand that tend to increase with heavy grazing are termed increases. Sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], blue grama [*B. gracilis* (H.B.K.) Lag ex Steud.], and Kentucky bluegrass (*Poa pratensis* L.) are the primary increaser species in western True Prairie. Sideoats grama increased in the early-spring burned, grazed pastures, probably in response to a reduced herbage yield and subsequent overgrazing. Herbel and Anderson (1959) indicated that sideoats grama increased under heavy grazing pressure. Spring burning essentially eliminated Kentucky bluegrass because it was actively growing and susceptible to fire injury (Fig. 3).

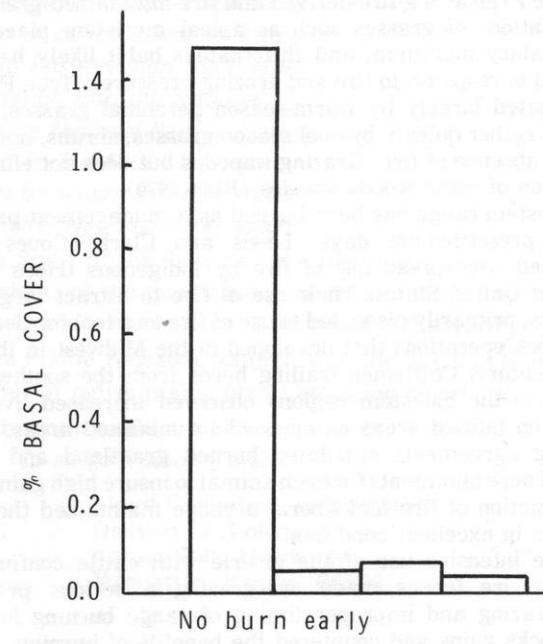


Figure 3

Sedges and Rushes. Mid- and late-spring burning reduced sedge and rush amounts more than early-spring burning or not burning. Growing season of the dominant genus, *Carex*, begins in late March, making it susceptible to fire injury by mid- and late-spring burning.

Annual Grasses. Spring burning on grazed pastures drastically reduced basal cover of annual grasses [sixweeks

fescue (*Festuca octoflora* Walt.), annual brome (*Bromus* sp.), and little barley (*Hordeum pusillum* Nutt.)] (fig. 4). As most annuals in True Prairie are cool-season, fire injury is severer in spring.

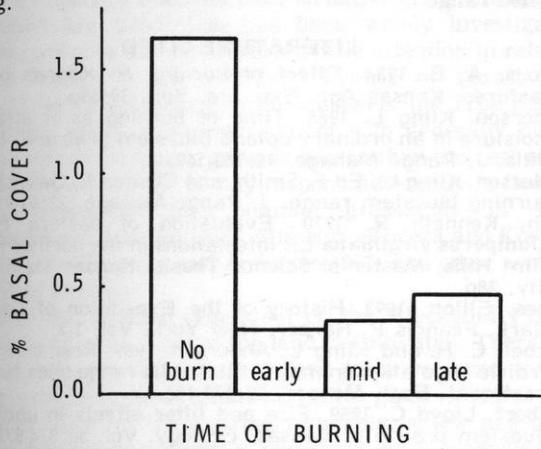


Figure 4

Perennial Forbs. Mid- and late-spring burned pastures had lower perennial forb basal cover than unburned or early-spring burned pastures. Many prairie forbs complete their life cycle before competition by major warm-season, perennial grass dominants is intense, so forbs are susceptible to fire injury by spring burning.

Shrubs. Smooth sumac (*Rhus glabra* L.) and leadplant (*Amorpha canescens* Pursh) increased but buckbrush (*Symporicarpos orbiculatus* Moench) declined in the burned pastures more than in the unburned pasture. Aldous (1934) reported on burning to control smooth sumac and buckbrush (Figs. 5 and 6). Smooth sumac reserve carbohydrates (CHO) are depleted and stored at essentially the same time as those of warm-season perennial grass dominants, so burning to favor warm-season perennial grasses also favors smooth sumac. Buckbrush phenology is such that CHO reserves are depleted four to six weeks earlier than in warm-season perennial grasses, so buckbrush is susceptible to injury from late-spring burning.

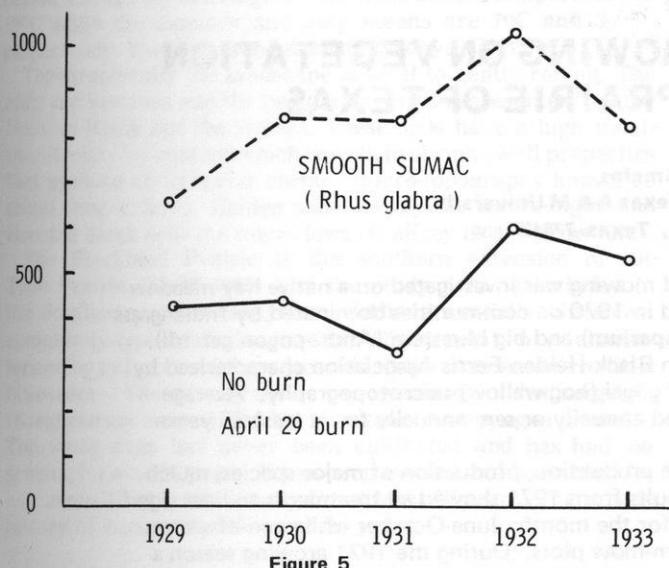


Figure 5

Eastern Redcedar. Eastern redcedar (*Juniperus virginiana* L.) commonly invades unburned True Prairie. Because it does not resprout from roots following death of tops, fire can essentially eliminate it from bluestem grassland. Blan (1970) reported that all redcedar-free pastures he studied had burning or mechanical removal in their management histories.

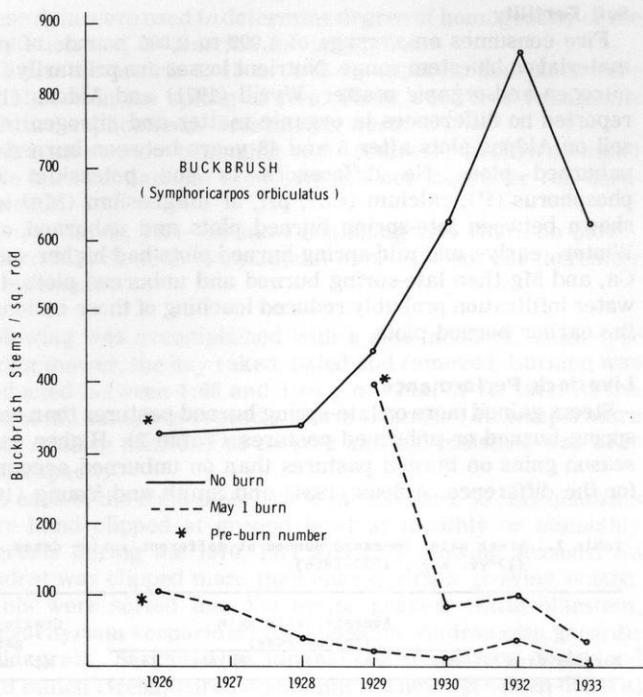


Figure 6

Soil Temperature

Removing the insulating mulch and darkening the soil surface increases soil temperatures. Aldous (1934) reported higher soil temperatures at 1, 3, and 7 inches deep from early spring to mid-summer on areas burned in early spring than on unburned areas (Fig. 7). Hulbert (1969) reported similar trends with a later spring burn. Soil temperature affects microorganism activity, evaporation, and plant growth and development and probably is basic to many of the differences from range burning.

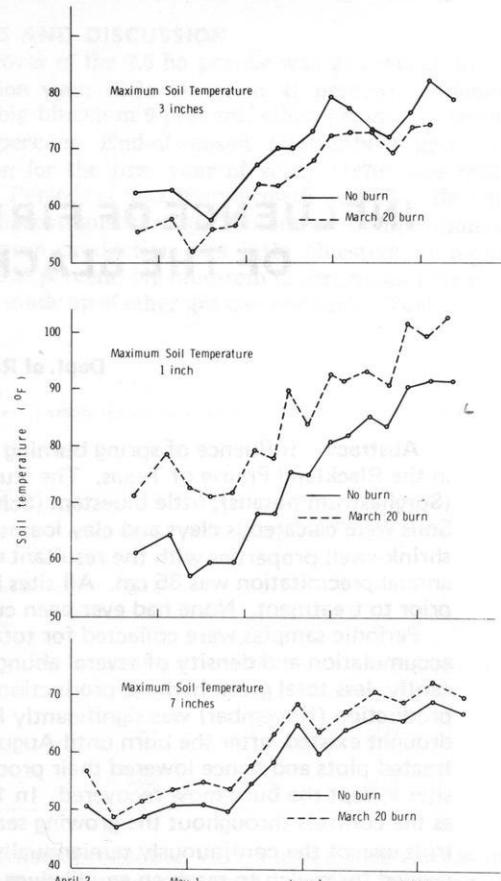


Figure 7

Soil Fertility

Fire consumes an average of 1,000 to 2,000 pounds of plant material on bluestem range. Nutrient losses are primarily from nitrogen and organic matter. Wyrill (1971) and Aldous (1934) reported no differences in organic matter and nitrogen in the soil on Aldous plots after 5 and 48 years between burned and unburned plots. No differences in soil potassium (K), phosphorus (P), calcium (Ca), pH, or magnesium (Mg) were shown between late-spring burned plots and unburned ones. Winter-, early-, and mid-spring burned plots had higher soil K, Ca, and Mg than late-spring burned and unburned plots. Less water infiltration probably reduced leaching of those cations on the earlier burned plots.

Livestock Performance

Steers gained more on late-spring burned pastures than early-spring burned or unburned pastures (Table 2). Higher early-season gains on burned pastures than on unburned accounted for the difference. Aldous (1934) and Smith and Young (1959)

Table 2. Steer gains on range burned at different spring dates (17 yr. avg., 1950-1966).

Burning date	Average daily gain (lb/head/day)					Grazing season gain (lb/head)
	May	June	July	August	Sept.	
Unburned	1.83	1.74	1.58	1.24	1.44	233
March 20	2.42	1.90	1.56	1.13	1.12	238
April 10	2.50	2.01	1.64	1.28	1.19	253
May 1	2.36	2.06	1.75	1.28	1.28	259

found that burning increased protein and ash content of bluestem forage. Smith et al. (1960) found bluestem dry matter and crude fiber digestibility to be higher on burned than unburned range.

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INFLUENCE OF FIRE AND MOWING ON VEGETATION OF THE BLACKLAND PRAIRIE OF TEXAS

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Abstract. Influence of spring burning and semiannual mowing was investigated on a native hay meadow in the Blackland Prairie of Texas. The study was initiated in 1970 on communities dominated by Indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*) and big bluestem (*Andropogon gerardii*). Soils were calcareous clays and clay loams of the Houston Black-Heiden-Ferris Association characterized by shrink-swell properties with the resultant development of gilgai (hog-wallow) microtopography. Average annual precipitation was 85 cm. All sites had been mowed annually or semiannually for at least 30 years prior to treatment. None had ever been cultivated.

Periodic samples were collected for total green herbage production, production of major species, mulch accumulation and density of several abundant forbs. Results from 1971 showed all treatments to have significantly less total green herbage production than controls for the months June-October while end-of-season production (November) was significantly less only on burn-mow plots. During the 1971 growing season a drought existed after the burn until August. This may have caused a severe micro-environment on exposed, treated plots and hence lowered their production. When above normal fall precipitation occurred nearly all sites except the burn-mow recovered. In 1972 total production on all treated sites was essentially the same as the controls throughout the growing season. By 1972 all sites had the same amount of mulch as the controls except the continuously semiannually mowed sites. It appears that approximately three years are needed for mulch to reach an equilibrium. A noticeable reaction to burning and release from mowing was a decrease in density of certain abundant forbs. Semiannual mowing enhanced forb numbers.

INTRODUCTION

The influence of fire (Daubenmire 1968) and mowing (Merrill and Young 1959, Jameson and Huss 1959, Ehrenreich and Aikman 1963, Vogel and Bjugstad 1968) on native grassland species composition and production has been widely investigated. However, one area that has received little attention in relation to these factors is the Blackland Prairie of Texas. This grassland, which is the southern extension of the True Prairie (Dodd 1968), exists in an environment with generally higher temperatures and a longer growing season than the rest of the True Prairie. As a result, it may respond differently to fire and mowing treatments than similar grasslands in Iowa (Ehrenreich and Aikman 1963), Missouri (Kucera and Koelling 1964), Kansas (Owensby and Anderson 1967) and other portions of the True Prairie.

Little of the original vegetation of the Blackland Prairie remains today since most of the land is cultivated. There is a tendency, however, for some cropland to be returned to permanent grass and in some situations native grass mixtures may be utilized. Also, of the existing remnants, a few are being considered as nature preserves and some have already been purchased by the Nature Conservancy. Many of the remnants are being destroyed and it seems desirable to document their vegetational characteristics and their responses to the influence of fire, mowing and total protection while sufficient examples remain.

A description of the remnants of the Blackland Prairie is provided elsewhere (Collins 1972). The purpose of this report is to evaluate the response of spring burning and semiannual mowing (July and October) on the species composition, production and mulch structure of native Blackland Prairie. The results will hopefully provide implications for management of native preserves and for re-established native grass pastures. The results are to be considered preliminary.

STUDY AREA

The study area is a 2.5 hectare (ha) native grassland located near the center of the Blackland Prairie Resource Area of Texas (Godfrey, Carter and McKee 1970). It is on the USDA, Blackland Conservation Research Center at Riesel, Texas.

Mean annual precipitation is 85 cm with two peaks in May (10.7 cm) and September (7.1 cm) and generally a hot, dry period during July and August. The mean annual temperature is 19°C while the January and July means are 7°C and 30°C, respectively. The frost-free season is 250 days (Carr 1967).

Topographically the landscape is level to gently rolling. The soils are Vertisols and the two major series represented are the Houston Black and the Heiden. These soils have a high montmorillonite clay content which results in shrink-swell properties that produce an irregular surface micro-topography known as gilgai (hog-wallow). Heiden soils occupy the micro-highs and Houston Black soils the micro-lows (Godfrey 1964, Collins 1972).

The Blackland Prairie is the southern extension of the True Prairie (Dodd 1968) and the study area is included in the *Sorghastrum-Schizachyrium* (Indiangrass-little bluestem) community-type of Collins (1972). The vegetation is characterized by tall, perennial grasses and major dominants are little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*) and big bluestem (*Andropogon gerardii*). The study area has never been cultivated and has had no grazing for over 30 years. It has been mowed and harvested for hay annually or semiannually for at least 30 years. There is no history of burning for the past 30 years.

METHODS

The 2.5 hectare prairie was sampled in June, 1972 for basal cover with 2000 single, vertically placed point quadrats and for frequency with 120, 25 cm x 50 cm quadrats. A stratified random sampling procedure was used. Samples were randomly placed along several parallel compass lines sighted across the area.

These data were used to determine degree of homogeneity of the vegetation and to describe the vegetation.

Within the prairie 8, 15 m x 15 m experimental plots were established in the spring of 1970. There were four treatments with two replications. Treatments were:

1. No burn-no mow beginning 1970 (control) (no burn-no mow)
2. No burn-semiannual mow 1970 but not thereafter (no burn-mow)
3. Burn March, 1971—no mow beginning 1970 (burn-no mow)
4. Burn March, 1971—semiannual mow 1970 but not thereafter (burn-mow)

Mowing was accomplished with a side-mounted, sickle-type tractor mower, the hay raked, baled and removed. Burning was conducted between 1:00 and 3:00 p.m., March 15, 1971. At the time of the burn, wind speed was 8 to 13 km/hr, air temperature 21°C, relative humidity 60 percent and soil moisture was near field capacity.

In each of the eight plots five 1/8 m² (25 cm x 50 cm) quadrats were hand clipped at ground level at monthly or bimonthly intervals during the 1970, 1971 and 1972 growing seasons. No quadrat was clipped more than once during a growing season. Plants were sorted into the major grasses (little bluestem, *Schizachyrium scoparium*; big bluestem, *Andropogon gerardii*; Indiangrass, *Sorghastrum nutans*), other grasses, forbs and total mulch (fresh, cured and humic). They were oven-dried at 27°C for 48 hr and the results reported in kg/ha.

During August, 1972 stem counts were made in all plots of some of the more numerous forbs. Ten 25 cm x 50 cm quadrats were counted in each plot. In addition, 20 quadrats were taken in adjacent plots with a continuous history of semiannual mowing.

Precipitation records were obtained from the Blackland Conservation Research Center which is located within 2 km of the study site. Soil moisture was determined gravimetrically (NAS-NRC 1962) in all plots on May 15 and July 15, 1971.

Taxonomic nomenclature follows Gould (1969).

RESULTS AND DISCUSSION

Basal cover of the 2.5 ha prairie was 23 percent and percent composition was: little bluestem 41 percent, Indiangrass 32 percent, big bluestem 9 percent, other grasses 11 percent and forbs 7 percent. End-of-season (November) green herbage production for the first year of study (1970) was 6682 kg/ha (Table 1). Periods of maximum growth were May through early June and late August through September. Composition based on end-of-season production was little bluestem 61 percent, Indiangrass 20 percent, big bluestem 12 percent and the remaining 7 percent made up of other grasses and forbs (Table 1).

TABLE 1

Seasonal green herbage production (kg/ha) during 1970 for a Blackland Prairie in Texas.

Species	June	August	October	November
Little bluestem	1618	2240	3330	4046
Big bluestem	222	320	697	800
Indiangrass	293	660	1175	1310
Misc. grass	202	106	181	444
Forbs	666	142	200	82
Total	3006	3468	5583	6682

End-of-season production values agree with studies of other central bluestem prairies with similar composition and precipitation. Values range from 4000 to 8000 kg/ha for sites in

North Dakota (Hadley 1970), Minnesota (Smeins and Olsen 1970), Iowa (Ehrenreich and Aikman 1963), Missouri (Kucera and Ehrenreich 1962) and Kansas (Owensby and Anderson 1967). Generally production of the present study is somewhat greater compared to other reports.

Control plots (no burn-no mow) has significantly greater production than other treatments for all dates except April and November during 1971 (Table 2). By November all treatments were the same except burn-mow plots which were 2590 kg/ha or 37 percent lower in production than controls. It appeared that either mowing or burning had a depressant influence on production while a combination of the two yielded the most pronounced reductions (Table 2).

TABLE 2

Total seasonal green herbage production (kg/ha) for the year of the burn (March 15, 1971). All plots were mowed semiannually for 30 years prior to 1970. Mow plots were mowed semiannually through the 1970 growing season while mowing ceased in no mow plots the fall of 1969.

Date	Treatment				Cumulative Precipitation (cm)	
	No Burn No Mow	Burn No Mow	No Burn Mow	Burn Mow	35 Year Average	1971
April	276a*	119a	504b	192a	29	14
June	2348a	1850b	1568b	1389b	48	22
August	4165a	2613b	3150c	2435b	57	57
October	5678a	4028b	4015b	3545b	71	74
November	6750a	6374a	6535a	4160b	78	86
Total Annual Precipitation				85	103	

* Values within each date followed by the same letter are not significantly different at the 0.05 level.

Cause of reduced production, particularly on the burn-mow plots is difficult to ascertain. Seasonal precipitation, soil moisture and time of burn may be involved. Seasonal precipitation for 1971 deviated considerably from the 35 year averages (Table 2). Longterm cumulative precipitation for June is 48 cm while in 1971 it was 22 cm or less than half of normal. By the end of August, 1971 precipitation equalled the 35 year average and by the end of the year it exceeded the average by 18 cm.

Limited precipitation early in the growing season may have produced a severe environment that retarded plant development particularly where the mulch had been removed by mowing and burning. Plant development on treated plots was from 1 to 2 weeks behind controls the first 6 weeks of the growing season. This is contrary to the results of Ehrenreich and Aikman (1963), Hadley and Kieckhefer (1963) and others who have shown burn plots to start growth earlier and develop faster. In the present study, however, timing of the burn just prior to an unseasonal drought may have produced opposite results. As indicated by Aldous (1934) and Owensby and Anderson (1967) as time between burning and beginning of spring growth lengthens, forage yield diminishes. Although time of burn in this investigation coincided with growth initiation, limited precipitation reduced growth rates for nearly 3 months.

Why all treatments except the burn-mow eventually caught up with the controls after favorable precipitation occurred in August is not apparent. Perhaps the double treatment so impaired growth that the plants were unable to respond. The data show, however, that all treatments were essentially the same until October and thereafter the burn-mow plots failed to keep

pace with the others. An obvious difference observed in the field was reduction in number of flowering culms of the major grasses on the burn-mow plots. It was estimated that reduction was at least 50 percent of other treatments. This reduction of course, lowered production but again it is difficult to propose a reason for the limited flowering behavior of plants in these plots.

Surface soil moisture (0-15 cm) showed no significant differences between treatments during May and July of 1971. All plots were at or near the permanent wilting point (15 bars) during both of these months but growth continued. This suggests that most of the species are able to remove moisture from the soil at tensions much greater than the standard 15 bar value. Soil moisture does not explain the production differences between plots for 1971.

Many studies have shown fire to increase production (Ehrenreich and Aikman 1963, Hadley and Kieckhefer 1963, Kucera and Koelling 1964) while others (Aldous 1934, Owensby and Anderson 1967) indicate that burning, particularly at the wrong time, may reduce production. The results of this study agree with the latter.

During the 1972 growing season all treatments produced the same amount of green herbage for all sample dates. Thus, one year after the treatments were applied all plots had returned to the same level of production. Yields for November, 1972 samples varied from 6300 to 7100 kg/ha with no significant differences between treatments.

Total mulch present on plots is presented in Table 3. The no burn-no mow plots had 2935 kg/ha of mulch in June of 1970. This was primarily the litter left after the last mowing in November, 1969 as well as some late fall growth that was added to the standing dead material. In 1971, the year of the burn, burn plots had significantly less mulch than other treatments. The no burn-mow treatment had 1612 kg/ha while the no burn-no mow, in its second year with no mulch removal, had 3720 kg/ha. By 1972 the no burn-no mow, in its third year with no harvest, had reached 6484 kg/ha by June. The other treatments had also reached similar values. By comparison, adjacent plots that had continued under a semiannual mow regime had only 2683 kg/ha or 41 percent of the no burn-no mow. The burn-mow was still lagging behind other treatments with only 5871 kg/ha.

TABLE 3

Total mulch (fresh, cured and humic) weight (kg/ha).

Date	Treatment				
	No Burn No Mow	Burn No Mow	No Burn Mow	Burn Mow	Semiannually
1970 June	2935	---	---	---	---
1971 June	3720a*	487b	1612c	431b	---
1972 June	6484a	6715a	7170a	5871b	2683c
August	7652a	7667a	7039a	6255b	3440c

* Values within each date followed by the same letter are not significantly different at the 0.05 level.

Dyksterhuis and Schmutz (1947) found relict little bluestem communities of the Fort Worth Prairie of Texas to have approximately 8000 kg/ha total mulch. This would suggest that mulch accumulation on sites in this study might increase slightly with one more year of protection. Thus, 3 to 4 years appear to be necessary for mulch to reach an equilibrium in this grassland. Ehrenreich and Aikman (1963) indicate that 4 to 6 years are necessary to reach this state in Iowa prairies.

Results of this investigation are preliminary and as additional data are collected answers to some of the questions may become apparent. Because of the preliminary nature of the study, little

can be surmised about composition shifts but some obvious changes have occurred (Table 4). A comparison of all treated plots with adjacent plots that continued to be mowed semiannually showed a significant reduction in densities of some of the more conspicuous forbs. It appears that *Centaurea americana* (American basketflower) is greatly enhanced by semiannual mowing. This is a somewhat weedy annual that seems to prefer well-lighted sites where little mulch accumulates. *Gaillardia pulchella* (Indian blanket) had a similar, though a not so obvious, trend. On treated plots that were burned or where some accumulation of mulch occurred these species were greatly reduced in density. *Shrankia uncinata* (catclaw sensitivebriar) was little influenced by any treatment. Little bluestem was unaffected by treatments except the no burn-no mow which had the lowest density of flowering culms which is attributed to greater accumulation of mulch on these plots.

TABLE 4

Density (stems/m²) of selected species during August, 1972. Each value represents the average for twenty quadrats.

Species	Treatment				
	No Burn No Mow	Burn No Mow	No Burn Mow	Burn Mow	Mow Semianually
<i>Centaurea americana</i>	3	3	3	0	26
<i>Gaillardia pulchella</i>	0	0	2	4	5
<i>Shrankia uncinata</i>	2	3	2	2	3
<i>Schizachyrium scoparium</i> (flowering culms)	15	37	26	21	25

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PROGRESS REPORT ON THE EFFECTS OF MOWING ON WILD FLOWERS¹

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Sweet Rocket (*Hesperis matronalis*, Linn.), butterfly milkweed (*Asclepias tuberosa*, Linn.), and Gray goldenrod (*Solidago nemoralis*, Ait.), were subjected to 13 mowing treatments spaced at two week intervals throughout the 1972 growing season. These treatments consisted of one control and 12 mowing dates and a clipping height of four inches was used for each mowing date. The 12 mowing dates employed are listed

as follows:

1. May 1	5. June 26	9. August 21
2. May 15	6. July 10	10. September 4
3. May 29	7. July 24	11. September 18
4. June 12	8. August 7	12. October 2

Data were collected by measuring the parameters listed as follows: (1), survival, (2), height and number of lateral shoots forced, (3), date and duration of bloom, and (4), general rating of the esthetic values of plants in each treatment.

SURVIVAL

During the 1972 growing season, no detrimental effect was noted among the three species of wild flowers as a result of mowing. A survival of 100 percent in each species was noted

¹Conducted for the Nebraska Department of Roads by the Department of Horticulture and Forestry, University of Nebraska, in cooperation with the U.S. Department of Transportation, Bureau of Public Roads. The opinions, findings, and conclusions expressed in this report are those of the authors and not necessarily those of the Nebraska Department of Roads and Bureau of Public Roads.

among the plants that were mowed and unmowed.

HEIGHT OF LATERAL SHOOTS

Without exception, mowing significantly reduced the height of the lateral shoots that were forced in all species. The reduction in height was more pronounced in sweet rocket and Gray goldenrod plants. Butterfly milkweed plants showed a reduction but it was not as pronounced as in the case of the other two species. The results also showed that the later the mowing treatment was employed the shorter the height of the lateral shoots that were forced.

NUMBER OF LATERAL BUDS FORCED

Lateral buds were forced in all three species when the apical dominance was broken by the mowing treatments. Analysis of the difference between the different mowing dates reveal that there was a significant increase in number of lateral buds forced in some of the mowing treatments.

DATE AND DURATION OF BLOOMING

Delayed and extended blooming was noted in all three species as a result of mowing. Blooming was extended one and one-half months for butterfly milkweed and Gray goldenrod and one month for sweet rocket.

NUMBER OF FLOWERS

Generally, a reduction in the number of flowers produced per plant was noted in sweet rocket and Gray goldenrod. In the case of butterfly milkweed, however, there was no correlation between the mowing dates and the number of flowers produced per plant.

ESTHETIC VALUE

Certain mowing dates improved the esthetic value of mowed over the unmowed plants. Appropriate mowing dates improved the esthetic values because plants had more compact growth and were not susceptible to lodging.

WILD FLOWERS FOR NEBRASKA ROADSIDES

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Abstract. The wild flower research project in Nebraska covers many phases of research activities. Criteria for selection of species, procedures employed in collecting plant propagules, results of germination studies, and results of investigations regarding roadside establishment were discussed. Studies which will be conducted in the future also were discussed.

LANDSCAPING WITH NATIVES

D. E. Hutchinson

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George D. Aiken, now a U.S. Senator from Vermont, began the propagating and culture of wildflowers in the early 1920's. He says "I did this partly because of an innate love for all things of the wild and partly to accept the challenge of those who said it couldn't be done." He published the first edition of "Pioneering with Wildflowers" in 1933, in order to provide information on the culture and use of wildflowers.

"Wild Flowers for your Garden" by Helen S. Hull is a book on using wildflowers in landscaping.

One of the outstanding architects in the use of native plants is Neil Porterfield of the firm Hellmuth, Obata, and Kassabaum, Inc., architects of St. Louis, Missouri. Associated with Porterfield in this work was C. Robert Belden.

Robert J. Dodson, landscape architect, Parks and Recreation Department, Kansas City, Missouri, has a real interest in the use of native grasses and wildflowers in the city parks.

Dr. Sotero Salac and James F. Hesse, University of Nebraska, Department of Horticulture and Forestry, are doing much needed research work with wildflowers.

There is a real opportunity to use drouth tolerant, disease resistant native grasses in landscaping. Native grasses such as: The bluestems (*Andropogon*)

Grazes (*Bouteloua*)

Switchgrass (*Panicum*)

Indiangrass (*Sorghastrum nutans*) and others.

Little bluestem (*Andropogon scoparius*) is found in 45 states. Many of the other native grasses are found in most of the states.

Little bluestem, a warm season bunch grass with varying shades of blue and green, has much potential for use in landscaping. The height will usually vary from 12-30 inches depending upon the site and precipitation. It will take the heat of south and west exposures. In the fall the white colored seed heads and red foliage are beautiful. The plants remain upright all winter. The red color of the foliage and stems stays all winter until it needs to be clipped back when the new growth starts. The red color makes a striking contrast against the snow.

Most landscaping lacks winter color other than green. Little bluestem can help add this winter color. The variety of bluestem named "Blaze" was developed by Dr. L. C. Newell. It has a significant name in that it has exceptional red foliage in the fall and winter. In landscaping it has been used in groupings of single clones and in banks of plants. It will do well on all exposures, being able to survive on hot south and west exposures. Little bluestem is the state native grass of Nebraska.

Sideoats grama (*Bouteloua curtipendula*), the state native grass of Texas, can be used in about the same situations outlined for little bluestem. The maximum height is about 24 inches. Sideoats grama may also be used as a turf.

Blue grama (*Bouteloua gracilis*) a short warm season native grass will stand much heat and drouth. The flag-like purplish

white heads on each stem are attractive in summer, fall and winter. The heads will stand upright during the winter. It makes a good foundation plant in dry hot sites. It is used in turf seedings in combination with buffalograss (*Buchloe dactyloides*). It is also used in recreation areas and highway medians.

The tall warm season grasses—big bluestem (*Andropogon gerardii*), sand bluestem (*Andropogon hallii*), switchgrass (*Panicum virgatum*), indiangrass (*Sorghastrum nutans*) all have a place in background situations, for accent and for beautification and for fall and winter color.

These native grasses for landscaping are easy to propagate from seed or clones. One Nebraska nursery puts single clones of little bluestem in gallon cans for sale in the Omaha, Nebraska area. There is a place and a need for nurseries to establish banks of native grasses for landscaping and availability.

There is a need for more emphasis on the use of native grasses in landscaping.

In every town and county we find garden clubs with members interested in and using native grasses along with other native plants. There is much interest, too, in the use of native plants and grasses in floral arrangements.

There are many wildflowers which can be used in landscaping. Bloodroot (*Sanguinaria canadensis*) and Jack-in-the-pulpit (*Arisaema triphyllum*) have been rated high by some groups. They have a place, but in the middle USA we have butterfly milkweed (*Asclepias tuberosa*). I would rate this the most beautiful flower of all. It fits in with most types of flowers in landscaping.

We have several species of *Liatris* which add much summer and fall color and receive ready acceptance. The coneflowers (*Rudbeckia*), sage (*Salvia pitcherii*) and other prairie wild-

flowers may be used in landscaping and native plant gardens.

The Plant Introduction Center at Ames, Iowa is increasing Jerseytea (*Ceanothus americanus*) for a potential release. This is a low growing forb with white flowers and semi-glossy leaves. It is drought tolerant.

Leadplant (*Amorpha canescens*) with gray leaves and purple flowers adds distinctive color when landscaping.

Roundhead lespedeza (*Lespedeza capitata*) with gray foliage and round brown seed heads provides winter contrast as well as summer color. The stiff stems with the brown heads stand upright all winter. They are especially nice when viewed against the snow.

Buffaloberry (*Shepherdia argentea*)—a native shrub with gray leaves similar to Russian olive and has red fruit. It could be used as a medium height shrub.

The Fragrant sumac (*Rhus aromatica*) and skunkbush sumac (*Rhus trilobata*) are very hardy and have attractive foliage and fruit and will survive where many other shrubs fail.

Eastern wahoo (*Euonymus atropurpureus*) a medium tall native has done well in my landscaping for over 30 years.

We need to take a better look at the native shrubs available for landscaping.

The Dutch elm disease and the many costly problems associated with Siberian elm should prove to homeowners, parks departments, cities and towns the fallacy of using single species and especially the use of Siberian elm. Many states are putting on campaigns to use primarily native trees in landscaping.

In all our landscaping we should become acquainted with the natural vegetation and then use it as it fits the site and climatic conditions.

THE ROLE OF THE SOIL CONSERVATION SERVICE'S WORK WITH PLANT MATERIALS

by

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Abstract. The Soil Conservation Service operates 20 plant materials centers in the U.S. to assemble, evaluate, select, and provide for the increase of native and introduced plants needed for wind and water erosion control and sediment reduction. Selected plants are used for range seedings, pasture improvement, grassed waterways, gully stabilization, roadside development, urban land stabilization and beautification, streambank protection, strip mined land improvement, disposal and use of agricultural solid and liquid wastes, dune and shoreline stabilization, wildlife food and cover, and noise abatement. Over 100 improved varieties, 47 of native plants, have been selected and released during 35 years of such work.

In discussing the role of the Soil Conservation Service's work with plant materials, consider the concept of "diversity." According to some ecologists, diversity is the key to protecting the environment—diversity in soils, plants, animals, water, air, climate, and man's uses of these resources. Plants—their development; their interrelationships with other plants, soils, humans, and animals; their establishment and their uses; and their tie-in with other technical, economic, and social phases are all part and parcel of insuring diversity in the environment.

The benefits of plants are generally recognized, but the challenge to plant scientists is to maintain a balanced

ecosystem by preventing or controlling soil erosion, reducing or stopping other forms of agricultural pollution, keeping the landscape green, and so improving the quality of the environment in general.

We know that soil erosion caused by water runoff from cropland and grassland is responsible for sediment—the major pollutant of surface waters.

Wind erosion also contributes a significant share of agricultural pollution. It is estimated that of the total sediment produced in this country each year, wind erosion contributes about 15 percent.

Plants—grasses, legumes, trees and shrubs—used as natural engineering materials, offer one of the most practical methods of controlling sedimentation.

The Soil Conservation Service's **National Handbook of Conservation Practices** lists 121 treatment measures. These measures are designed to control erosion by wind and water and to make the best use of crops, grass, timber, and other organic cover. Forty-eight of these treatment measures are vegetative or cultural; and an additional 34 use vegetation as a supplementary practice. This means that vegetation is involved in 82 of the 121 treatment measures with which we work.

To help meet the many and diverse needs for plant materials in conservation work, the Soil Conservation Service operates 20 plant materials centers. These centers assemble, evaluate, select, and provide for the increase of grasses, legumes, shrubs, and trees needed for erosion control, good land use, wildlife food and cover, and beautification; that is, for improving our environment.

PROCEDURES

All work done at plant materials centers is consistent with specific, high priority, plant material needs for the conservation, development, and productive use of soil, water and related resources of the area served. Needs and priorities are established for each state by committees, with interdisciplinary representation, consistent with the mission of the Soil Conservation Service's Framework Plan. . . for quality in the resource base, the environment, and the standard of living.

Several steps make up the system used at the centers.

The first step in carrying out a project at the center is to gather and compare plant materials that may have value for meeting the conservation objective. These materials are obtained from foreign plant introductions, from collections of promising ecotypes from native vegetation, from naturalized aliens of unknown origin that have survived in out-of-the-way places, and from improved strains produced by plant breeders. A single plant materials center may have assembled and comparatively screened as many as 20,000 different samples.

The second step is to place the few plants selected from the comparative screening into initial seed increase in order to make more precise comparisons or to study cultural methods. This is known as secondary testing. This can be done either at the center or in outlying areas called "land resource areas" (LRAs) when the soil and climate are different from those represented at the center. This step is also comparative in that the newly selected materials are compared with a standard plant presently in use. Usually yield information, botanical composition, etc., are determined by this secondary testing.

The third step is to compare selected plant materials under actual use conditions on farms and ranches of soil conservation district cooperators. Here again, the plants are compared with a standard, and the adaptation and performance correlated with soils, climate, and use.

The fourth and final step is to cooperatively release the adequately proven material and to distribute foundation seed or stock to soil and water conservation districts. This in turn encourages commercial growers to increase the materials.

All these steps are taken whenever possible in cooperation with state experiment stations, the Agricultural Research Service, and private research agencies, which helps assure that the highest standards are maintained.

During the 35 years that the plant materials centers have been operated, more than 100 improved plants have been selected and introduced into the soil and water conservation program. Many of the selected grass and legume varieties have been registered with the Crop Science Society of America and are produced under certification programs. More than 50 million pounds of seed of these plants are on the market. In addition, millions of seedlings of SCS-selected woody plants are produced annually by state and private nurseries.

Of the 100-plus improved plants introduced into conservation

use by the plant materials centers, 47 have been selected from native plant materials. In addition, SCS through earlier production and field plantings has created a demand, resulting in the commercial production of 23 other native trees and shrubs. SCS plant materials centers also have selected over 200 other promising accessions of native plants for further evaluation, and several of these will be named, released, and used in resource conservation and development in the future.

A few examples of new plant materials selected, with special emphasis on native plants, will help illustrate the contributions of the plant materials program to resource conservation and environmental improvement during the past 35 years.

EROSION CONTROL AND RANGE SEEDINGS

The emphasis of plant materials work in the earlier years was on suitable plants for protecting agricultural land from damage. While wind erosion was devastating large areas of land in the Great Plains states, huge quantities of seed of adapted grasses were needed for proper land use and erosion control. Here native plants proved superior to introduced species for converting cropland to grass. Seed was harvested from native stands by soil conservation districts, individuals, and commercial companies. Personnel of the plant materials centers located areas with good seed and helped develop special machinery to do the job.

It was soon learned that plants native to certain regions performed poorly or often failed when moved too far from the point of origin. To meet the needs in the Great Plains, many improved varieties of native warm-season grasses were developed through the cooperative work of the Agricultural Experiment Stations, Agricultural Research Service, and/or Soil Conservation Service. Such varieties as 'Pathfinder' and 'Blackwell' switchgrass, *Panicum virgatum*; 'Pawnee' and 'Kaw' big bluestem, *Andropogon gerardii*; and 'Aldous' and 'Blaze' little bluestem, *Andropogon scoparius*, for example, have become well known and are extensively used in range reseeding. Three to four million pounds of seed of improved native grasses is harvested each year now in the Great Plains.

Varieties developed from introduced plant materials are probably best known in the West. Examples of widely known and extensively used varieties include 'Greenar' intermediate wheatgrass, *Agropyron intermedium*, from the Northwest; 'Luna' pubescent wheatgrass, *Agropyron trichophorum*, from the Southwest; and 'Blando' brome, *Bromus mollis*, and 'Lana' vetch, *Vicia dasycarpa*, from California. While perhaps less well known, improved varieties from native plants, such as 'Whitmar' beardless wheatgrass, *Agropyron inerme*, and 'Sherman' big bluegrass, *Poa ampla*, have contributed to range revegetation in the West.

PASTURE

The greatest contribution by plant materials centers to improvement of pastures has been the selection of superior varieties from introduced plant materials. A few examples will illustrate the scope of this contribution.

'Manchar' smooth brome, *Bromus inermis*, and 'Latar' orchardgrass, *Dactylis glomerata*, were selected by the plant materials centers and released with the state experiment stations of the Northwest, specifically to meet the conservation needs of that region. Their use has extended throughout the northern tier of states. For example in 1970, 1,600 acres of 'Latar' orchardgrass seed was produced in Oregon alone. This volume of seed was enough to seed approximately 100,000 acres to this improved variety.

'Pensacola' bahiagrass, *Paspalum notatum*, was extensively tested by the plant materials centers in the South and jointly released with the Florida and Georgia Experiment Stations in 1944. Today its use has mushroomed to more than 10 million acres in the Southeast.

The plant materials center serving New York played a major role in the rapid increase of birdsfoot trefoil, *Lotus corniculatus*,

starting in 1936 with seed collected from an old pasture. The first field planting was made in 1937. Today the total area planted to birdsfoot trefoil is about 2 million acres.

Interest in the use of native warm-season grasses for summer pasture is rapidly expanding in the southern Corn Belt. Studies at the Elsberry Plant Materials Center in Missouri have shown that 75 percent of the forage production of such warm-season grasses as big bluestem, indiangrass, *Sorghastrum nutans*, and switchgrass is after July 1. This is the period when the commonly used cool-season pasture grasses, such as tall fescue and smooth brome are practically dormant. Expanding interest in warm-season grasses has resulted in the cooperative selection and recent release of 'Cave-In-Rock' switchgrass by the Soil Conservation Service and the Missouri State Agricultural Experiment Station.

GRASSED WATERWAYS

Good grassed waterways are essential in many cropland areas not only to provide a safe watercourse for disposal of runoff water, but also to filter out much of the sediment being carried in the water. Conservationists in the Corn Belt are experiencing a relatively new problem in maintaining adequate vegetative cover in waterways due to the susceptibility of the commonly used cool-season grasses to currently-used herbicides. Work conducted at SCS plant centers, however, has shown that the native warm-season grasses are more tolerant of herbicides. Consequently these grasses are now being included in mixtures for grassed waterways.

Other plant materials center contributions in the development of improved grasses for waterways include 'Sodar' streambank wheatgrass, *Agropyron riparium*, 'Tegmar' intermediate wheatgrass; 'Kent's dwarf' reed canarygrass, *Phalaris arundinacea*; and 'Garrison' creeping foxtail, *Alopecurus arundinaceus*.

WIND EROSION AND CONTROL

Wind erosion is still a problem. There are still 55 million acres with serious wind erosion problems, and approximately 5 million acres are damaged annually. In addition to being responsible for considerable sediment in our surface waters, dust storms pollute the air to the extent of 300 to 1500 tons of soil particles per cubic mile. Although complete ground cover with grasses is the ultimate defense against any kind of soil erosion, suitable plant materials are used in other ways to control wind erosion. Windbreaks, for example, help control soil blowing, reduce the drying effects of wind on soil and plants, and help prevent the abrasive action of rapidly moving soil particles on young tender seedlings. In addition to such widely used foreign introductions as Russian olive and Siberian elm, field plantings by the Soil Conservation Service have resulted in the commercial production and extensive use of such native trees and shrubs as green ash, *Fraxinus pensylvanica*; hackberry, *Celtis occidentalis*; American elm, *Ulmus americana*; Amur honeysuckle, *Lonicera maackii podocarpa*; American plum, *Prunus americana*; silky dogwood, *Cornus amomum*; and ponderosa pine, *Pinus ponderosa*, in windbreaks and shelterbelts. The use of herbaceous plants in one or several-row windstrips or barriers is gaining in popularity. Such barriers effectively reduce wind velocities for a distance of 8 to 12 times their height. Tall-growing, stiff-strawed native grasses such as switchgrass and indiangrass, and introduced grasses such as tall wheatgrass, *Agropyron elongatum*, have real potential for use as wind barriers. In the northern Plains states these wind barriers can serve double duty by trapping snow for much needed soil moisture and effecting a more even spread across a field.

COVER CROPS

Cover crops are needed on highly erosive soils for adequate protection, especially in orchards. Uncontrolled runoff water has resulted in soil losses exceeding 200 tons per acre per year in

young citrus orchards in California. The California Plant Materials Center helped solve one such problem with the selection of a native, self-reseeding, annual brome grass, *Bromus carinatus*, released as 'Cucamonga', which is being used in strips to control erosion between the tree rows. Volunteer weed growth within the tree row is controlled by selective chemicals.

GULLIES

Gullies are sources of continuing erosion and sediment. Often they have been neglected to the point where mechanical reshaping is very difficult and costly. Fortunately, plant materials and techniques are available for stabilizing such heavy silt-producing areas. Such native plants as black locust, *Robinia pseudoacacia*, and Virginia pine, *Pinus virginiana*, have proven valuable for planting on such critical areas.

SEDIMENT

Today there is a growing awareness of the off-site or downstream impacts of sediment, the result of soil erosion. Many people once believed that farms and ranches were responsible for all of the discharge of sediment into our surface water. They do account for at least 50 percent of the more than 4 billion tons of sediment produced each year. Therefore, improved plant materials for such practices as grassed waterways, field windbreaks, conversion of marginal agricultural land to pasture or range, cover crops, and critical area stabilization will continue to receive emphasis.

There are, however, other very serious sediment sources. Plant centers have broadened their programs to search for suitable materials for other uses including roadside development, mine spoil revegetation, streambank stabilization, and waste disposal areas. Emphasis is also given to the selection of improved plants for wildlife habitat improvement, and environmental and beautification plantings.

HIGHWAYS

Highways and airports outside of urban areas are taking an estimated 160,000 acres of new land each year. While the primary 4-lane highways are being effectively stabilized, much greater attention must be given to the vegetation of state highways and particularly of secondary paved roads. A road erosion study in one state showed that soil losses from secondary roads were 121 tons per mile and that 33,000 of the 45,000 miles of road in the state were secondary roads.

Plant centers are searching for suitable plant materials for erosion control on road cuts and fills. In several states the respective state highway agency and the Soil Conservation Service have developed cooperative agreements relating to testing and selecting improved plants for roadside development.

Several improved SCS developed plant materials from introduced plant materials are now extensively used in the vegetative stabilization of roadsides. These include 'Emerald' crownvetch, *Coronilla varia*; 'Lana' vetch; and 'Durar' hard fescue, *Festuca ovina duriuscula*. Again, SCS-selected native plants are making a real contribution. 'Sodar' streambank wheatgrass, *Agropyron riparium*, and 'Critana' thickspike wheatgrass, *Agropyron dasystachyum*, are extensively used in the Northwest. In the Central Plains States improved native grasses are being used more and more extensively because, once established, they require very little maintenance and they offer a real contrast of textures and colors, adding substantially to roadside aesthetics.

In Nebraska alone, the use of low-maintenance grasses combined with a limited mowing program has resulted in an annual savings of \$500,000 and returned over 50,000 acres to wildlife habitat.

Interest is also increasing in the use of native wildflowers in roadside development, critical area stabilization, and natural area restoration. The plant materials center at Manhattan, Kansas, is currently evaluating over 180 collections of selected

wildflowers in cooperation with the University of Nebraska and the Nebraska and Kansas State Road Departments. This Center and others, including Knox City, Texas are determining the techniques for mechanically harvesting seed of promising native forbs to accomplish the commercial production necessary for their widespread conservation use.

URBANIZATION

Erosion losses from housing and industrial and institutional developments are often more serious than from roads. The process of reshaping land for urban uses is taking an estimated 2,000 acres of farm and open land each day. Steep slopes and complete removal of vegetation on large areas result in sediment yields from 10 to 40,000 times as much as those of adjacent farm or ranch land. Vegetation—both temporary and permanent—with engineering practices is definitely needed. Here again, we are experiencing an increasing interest in the use of low-maintenance plant materials. Several natives, such as buffalograss, *Buchloe dactyloides*; blue grama, *Bouteloua gracilis*; sideoats grama, *Bouteloua curtipendula*; and western wheatgrass, *Agropyron smithii*, are being used.

STREAMBANKS

Of the 7 million miles of streambanks in this country, approximately one-half million miles are undergoing serious erosion problems. These unprotected channel banks are unsightly, in addition to being serious sediment-producing areas. Fortunately, through field trials and research, technical knowledge, equipment, and materials are available for solving many of these erosion problems. Adapted plant materials play an important role in supplementing proper design and, where needed, mechanical protection. Although many introduced species of grasses and legumes such as bermudagrass, *Cynodon dactylon*; tall fescue, *Festuca arundinacea*; and crownvetch are used for stream and channel bank stabilization, a number of native plants also make a contribution. Reed canarygrass has been extensively used for bank stabilization when taller growth has not been objectionable. Plant centers are currently attempting to find low-growing or dwarf forms that produce adequate viable seed. "Maidencane" a native panicgrass, *Panicum hemitomon*, selected by the Coffeeville, Mississippi, Plant Materials Center, offers possibilities for streambank stabilization in the South, and switchgrass is used for stabilization in the northeast, southeast and southern Plains.

STRIPMINING

The National Mine Law Study recently concluded showed that 2 million acres would benefit from conservation treatment, mostly in the form of vegetation, to restore the disturbed areas to stabilized and attractive conditions. In addition to such well-adapted introduced grasses as weeping lovegrass, *Eragrostis curvula*, and tall fescue, native plants such as switchgrass play an important role in mine spoil restoration. Two native plants, recently selected by the Big Flats, New York, Plant Materials Center, appear very promising for mine soil revegetation. These are 'Arnot' bristly locust, *Robinia fertilis*, and a native panicgrass, *Panicum clandestinum*, known as deertongue.

These same introduced and native plants can be used in reclaiming sanitary landfills and developing these areas for agricultural and/or recreational areas.

AGRICULTURAL SOLID AND LIQUID WASTE

Most authorities on the subject agree that disposal of agricultural solid and liquid waste will ultimately be on the land. One method that has been used to a limited extent for many years, but is now spreading more rapidly, is the use of "living filter systems" or "irrigation land disposal systems." There are about 500 canneries in the United States that are using living filter systems for effluent disposal from their products. These systems are very effective with grasses. In one installation a native grass, reed canarygrass, yielded between 6 to 8 tons of hay per acre per year and in 7 years removed 2,733 pounds of nitrogen. Plant centers are beginning to search for plants tolerant of various types of waste.

DUNES AND SHORELINES

Grasses and woody plants, usually supplemented with engineering measures, are used for dune and shoreline stabilization. Beachgrass and dune grasses have been most successful in providing initial control by stilling the sand. These plantings are followed by the growth of woody plants, either through manmade plantings or natural successions. 'Cape' American beachgrass, *Ammophila breviligulata*, and 'Clatsop' red fescue, *Festuca rubra*, are examples of SCS-selected native plants for converting shifting sands to stabilized areas capable of supporting wildlife and recreation.

WILDLIFE

All properly managed plant materials are beneficial to wildlife. Some such as 'Cardinal' autumnolive, *Eleagnus umbellata*, have been planted by the millions for wildlife food and cover. A single autumnolive shrub can produce up to 80 pounds of fruit which is used by 15 species of birds. Indiana alone now plants over 300,000 autumnolive each year and to date, after 10 years of planting has not had a single complaint against this shrub. 'Rem Red' Amur honeysuckle is a newly released addition to this group of wildlife food plants and is particularly valuable since uneaten "raisined" fruit persists on the plant throughout much of the winter. Whereas these two examples have both been selections from introduced materials, plant centers are working with many promising natives including elderberry, *Sambucus* spp.; sumac, *Rhus* spp.; American plum; chokecherry, *Prunus virginiana*; silky dogwood; Florida chinquapin, *Castanea alnifolia* var.-*floridana*; and runner oak, *Quercus pumila*.

ENVIRONMENTAL PLANTINGS

SCS is also experiencing a much greater interest in the use of improved plant materials for environmental or multiple-use plantings. Interrelated objectives include soil stabilization, living screens, noise abatement, songbird habitat enhancement, and beautification. Here SCS-improved herbaceous and woody plants are being used to provide more attractive, convenient, and satisfying places to live, work, and play. For example, plants absorb polluted air and emit air that not only is richer in oxygen but also somewhat freer of pollutants. Plants help too by screening out and/or collecting some particulates.

Plants also produce a native sound barrier because they dilute sound energy or loudness. With proper design, tree and shrub screens can reduce noise levels by as much as 50 percent.

These have been only a few examples of how the Soil Conservation Service's plant materials centers are contributing to the quality of the resource base, the quality of the environment and the quality of the standards of living for a better America.

INTRODUCTION TO NATIONAL GRASSLANDS ADMINISTERED BY THE CUSTER NATIONAL FOREST RELATIONSHIPS OF GRASSLANDS TO AVAILABLE BENCHMARKS

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Abstract. This slide presentation covered the location and characteristics of the four National Grasslands on Custer National Forest; how they were established, how they are administered, uses and demands being made of the land, the relationships that appear to exist between "benchmark" areas and the present mid-grass prairie. The complexities of present day management on lands of mixed ownership and the need for land use planning based on land capability and public inputs were touched on in this presentation.

The location of these public lands within North and South Dakota is shown on the accompanying map. The four National Grasslands of the Custer National Forest total 2,333,944 acres of which 1,258,390 acres are Federal public land, and 1,075,554 acres are land of other ownerships intermingled in a complex irregular pattern. These National Grasslands are divided into three Forest Service Ranger Districts. The McKenzie District with headquarters at Watford City, North Dakota, and the Medora District headquartered in Dickinson, North Dakota, are collectively called the Little Missouri National Grasslands. The Cedar River National Grasslands in South Dakota are administered out of Lemmon, South Dakota. The Sheyenne National Grasslands are administered from nearby Lisbon, North Dakota. The Sheyenne Grasslands are within the tall-grass prairie, while the other Grasslands exhibit mid-grass prairie vegetation. Grand River and Cedar River typify the rolling midgrass prairie. The larger Little Missouri National Grasslands are more diverse with the majority of the area in badlands of intricate, erosional pattern surrounded by a band of plateau prairie.

The benchmark mesas, protected by the steep badlands clay escarpments surrounding them, are well described in "Relicts of Climax Vegetation on Two Mesas in Western North Dakota" by Clayton L. Quinnild and Hugh E. Cosby in "Ecology" Vol. 39 No. 1, Jan. 1958. These are classified as managed natural areas in the Soil Conservation Society of America publication of February 1972, page 4, and have been submitted for Research Natural Area designation.

The impression that a layman gets when viewing these areas for the first time is that here in undisturbed condition the climax vegetation is not spectacular, although quite diverse. Here this midgrass prairie is not "stirrup deep to a tall horse" and, surprisingly, it does contain some of the species common in overgrazed ranges. Fringed-sage and cactus are present in the stand that is predominantly western wheatgrass and blue gramma. The litter and humic mulch is amazing in quantity, and the production is great, as quantified in the "Ecology" article, though the area does not appear to be much more productive than are many areas open to grazing. The contrast to sites adjacent to stockwater that are subject to annual growing season use is acute, however.

Historically, the grasslands have felt the pressure of man's demands in three times: first came the days of overgrazing by the Texas trailherds; second, the overplowing of the homestead era, and third, the increase of diverse demands in recent years for the energy reserves of lignite coal and oil, as well as recreational, grazing and other agricultural values.

The land ownership status of the National Grasslands is extremely complex. Ownership by the Federal Government was obtained by outright purchase, condemnation, exchange, and transfer by Executive Order from the public domain. Most of the acreage, consisting of submarginal farming land,

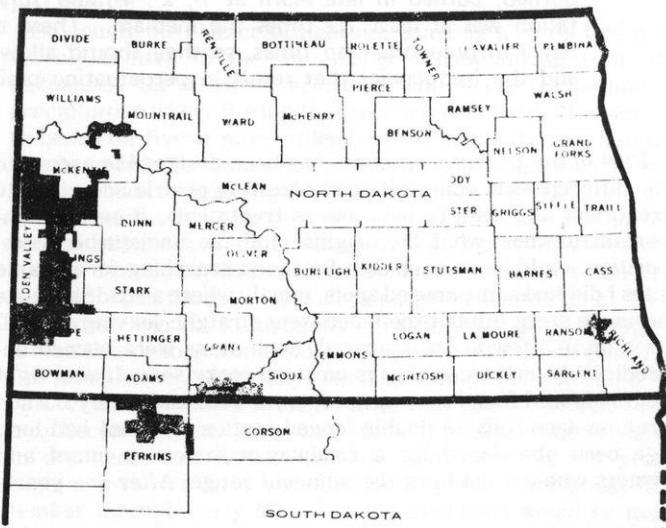
grasslands, and badlands, was obtained in 1938 and 1939 under Title III of the Bankhead-Jones Farm Tenant Act. Administration of Title III lands remained with the Soil Conservation Service until transferred to the Forest Service in 1954. Much of the depleted farmland was reseeded, pasture fences built, stockwater was developed and the forage was made available to grazing associations for administration of grazing use.

The basic mission has been to hasten the recovery of the soil and vegetative cover of these lands and to develop a healthy rural economy.

The blowing plowed land soil of the 1930's has been largely controlled by reestablished vegetation and the stability of the ranch economy now exceeds that of other occupations here; though total population is declining in this area.

The total Federal acreage is now under at least one formal permitted use. Thus, there are no "non-committed" areas. The area which has remained unplowed constitutes one of the largest areas of prairie in the country. Vegetative composition here has been altered by grazing, but because of variations in intensity and time of use, the pattern of change is also varied. Management of grazing can assure continued diversity of prairie species, and could influence change toward desired combinations.

The perpetuation of a natural prairie environment here is an idea that meets with much competition from other demands. For example, today there are 138 active oil wells, 240 miles of pipeline, and 1,200 miles of oil service roads. Exploratory interest continues at a high level as about half of the 1,100,000



GRASSLANDS OF THE CUSTER NATIONAL FOREST

acres are underlain with coal which is a major power reserve. There are major proposals to transport water from Lake Sakakawea to potential minemouth generator sites and to irrigate land. The Little Missouri River has been proposed as a candidate for formal classification as a Scenic River. Organizations have requested that wilderness or open space values be classified. There are accelerating interests in tourism and historical sites. Archeologists have made significant discoveries here. Snowmobile use has tripled in two years, as well as increasing use by motorcycles, horseback riders and hunters. Furthermore, the existence and needs of the livestock industry cannot be forgotten in the press to deal somehow with these other values and demands. More than 610 rancher-permittees now graze 77,000 cattle on the National Grasslands of North Dakota. They have had a long-term share in the battle to reclaim and manage these lands properly.

Many of these uses can be quite compatible or complimentary if they are properly planned and integrated. With the endorsement of the Governor, North Dakota State University has obtained funds for, and is underway on, Phase I of a three-phase study of the nine southwestern counties of the State, which in-

clude the Little Missouri National Grasslands. Phase I is tentatively scheduled for completion in about 16 months. Another significant part of the planning effort related to the National Grasslands is the Multiple Use Plan being prepared by the Forest Service. Part I, covering the whole area, is being revised to incorporate public comments to the draft copy. Part II will be specific plans for high priority parts of the area.

The Environmental Protection Act requires Federal administrators to evaluate proposed activities on Federal lands for major impacts to the quality of the environment. This sets the stage for either modification, approval, or disapproval of any proposals of a controversial nature.

With a staff basically designed and financed for a grazing economy, and with the speeding confluence of demands apparent, the Forest Service should not commit the land to any further major encumbrances or new impacts now. The study and response from the people will indicate needs and areas of relative suitability or nonsuitability for various types of development. Public comment is invited as an essential part of this effort.

MANAGEMENT OF KONZA PRAIRIE TO APPROXIMATE PRE-WHITE-MAN FIRE INFLUENCES*

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Abstract. Konza Prairie Research Natural Area, 916 acres (370.9 hectares) of unplowed native bluestem prairie, 10 miles south of Manhattan, Kansas, was purchased in 1971 by The Nature Conservancy and given to the Kansas State University Endowment Association for ecological research. The objective of management is to approximate the pre-white-man prairie ecosystem. Fires in that system were caused by lightning and Indians. Although lightning occurs primarily during the growing season, lightning storms have been recorded every month of the year. Spring has a slightly higher incidence of lightning than autumn.

A burning plan has been developed for Konza Prairie with four replications of six treatments: unburned, burned in late April at 1-, 2-, 4-, and 10-year intervals, and burned after years when precipitation was at least 1.2 times the median. These treatments include the possible range of fire occurrence in pre-white-man times, so they should allow us to assess both the ways that fire affects prairie and the frequencies that result in perpetuating prairie in good condition.

Part of my previous research has been designed to ascertain the differences in composition of bluestem prairie according to treatment and soil. To help assess treatments, it seemed important to know what the original and the undisturbed composition would be on each soil. By much searching for suitable sites I did find some unused spots, mostly where a road had gone around a steep hill but the fence went straight, leaving a small area up to a few acres ungrazed. Such areas were burned unpredictably, and were always on steep rocky soils. It was eight years before I found an ungrazed, unmowed, and rarely burned area on deep soils—a double fenced section line that had long ago been abandoned for a roadway with fences intact and owners who did not burn the adjacent range. After one year's

study, I found that a herd of cattle had been trailed down it in the spring when the soil was unusually soft and wet.

Clearly we needed a natural area for ecological research on the bluestem prairie. Efforts to secure one began about 1957, when a group from several departments of Arts and Sciences and Agriculture drew up a report citing the need and asking the administration for help. The effort intensified about 10 years later, and a thorough inventory of possible sites in an area within 30 to 50 miles of Manhattan was made. The criteria desired in an area were:

1. Biota as natural as possible. Available areas never plowed and moderately stocked were examined to see how well they met the other criteria.
2. Soils of agricultural quality in addition to steep, rocky soils.
3. Large enough to support small animals in natural conditions.
4. Close enough to KSU to facilitate research.

*Contribution No. 1187, Division of Biology and
Kansas Agricultural Experiment Station.

The second criterion gave the most difficulty. Large unplowed acreages existed in the Flint Hills because they were too steep or rocky to plow, but generally any area that was plowable had been plowed. We finally found a few rare areas that had some patches of unplowed agricultural soils, then checked ownership and negotiated for acquisition. For a long period it seemed hopeless.

Finally through the efforts of many people in the KSU administration and in The Nature Conservancy, we secured a 915-acre (370.9-hectare) tract that met these criteria rather well. The Nature Conservancy purchased the area in December, 1971, using funds generously donated by Miss Katharine Ordway, whereby the area became another unit in the Ordway Prairie Preserve System. The Nature Conservancy immediately transferred title to the KSU Endowment Association for use in ecological research.

Because the donor asked that we use an Indian name, we chose to name the area after the tribe that inhabited the area well before it was disturbed by white men. This also is the tribe from which the state of Kansas derived its name. Using "Kansas Prairie" would have implied a state-owned prairie, rather than an Indian name, so we chose Konza (short o), one of the 50 variants of the spelling of the tribe.

KONZA PRAIRIE RESEARCH NATURAL AREA

One of the differences between Konza Prairie and most natural areas is that it was selected to be representative of the widely occurring bluestem prairie, whereas many natural areas are (properly) selected and preserved because they are unique or unusual. We need the characteristic as well as the unusual areas for scientific study.

Konza Prairie Research Natural Area, 10 miles south of KSU, can be reached in 20 minutes from the campus (Fig. 1). It is about 3 miles long by one-half mile wide (0.8 by 4.8 km) in the north edge of Geary County, Kansas. Management is designed to reestablish as closely as possible the pre-white-man bluestem prairie ecosystem, because that will give us a chance to evaluate the changes man has induced by his manipulations, and because study of the natural, self-sustaining ecosystem can help us learn principles concerning the functioning of the many parts of a stable system. The climate, topography, soils, and most of the native biota are there, and nothing need be done concerning them to reestablish the original prairie. However, leaving the area alone will not satisfactorily reestablish the original prairie because the large herbivores, bison, elk, and antelope formerly present are absent, and because fire would rarely occur naturally.

Reintroduction of large native herbivores was rejected because the area is too small for such animals to move around in even a semblance of their natural state. It was deemed better to exclude all large herbivores and to make comparisons with the experimental cattle-grazed ranges owned by KSU to evaluate grazing influences.

FIRE IN PRESETTLEMENT PRAIRIES

That fire was a part of the original prairie is attested by records of early naturalists and explorers, and by studies on the vegetation of prairie areas unburned for long periods. Bragg (1971) documented forest invasion of prairie in Geary County, Kansas, by using U.S. Land Office Survey records made in 1856 and 1857 and U.S. Department of Agriculture aerial photographs made from 1937 to 1969. The surveyors in 1856 and 1857 recorded when they entered and left timber on section and township lines, and they used trees as witnesses for survey markers. Using those sources of information Bragg found no detectable difference in the amount of area in forest today and in 1857 on bluestem ranges regularly burned, but he found marked increases (up to nearly continuous forest) on some soils that had not been burned for many years.

Clearly then we need to burn Konza Prairie to approximate the original conditions. We know that the American Indian and

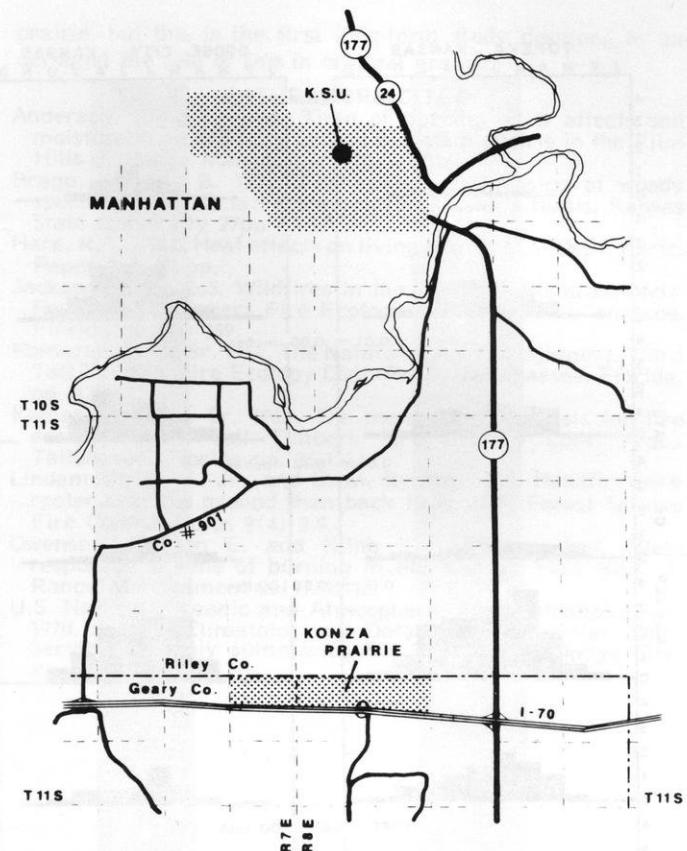


Fig. 1. Konza Prairie, 916 acres of unplowed bluestem prairie, ten miles south of Kansas State University.

lightning (Komarek 1964, 1966, Jackson 1965) started fires in the prairie, but we do not know how often, at what season, or how erratically fires occurred. No records have been kept in the grassland of the occurrence of lightning-caused fires, as the U.S. Forest Service has done in forests. To get some indication of the likelihood of lightning-caused fires, records of thunder were compiled from daily weather records of first-order weather stations where the occurrence of thunder as well as the amount of precipitation was recorded. (Visible lightning was also recorded for a number of years, but since lightning can be seen for long distances, those records were not used) (U.S. NOAA 1951-1970).

Obviously the chance of lightning starting a grass fire is inversely related to the amount of accompanying rain. Unfortunately the weather records do not record the amount of precipitation where the lightning occurred, because thunder can be heard for five or more miles from the place the precipitation was recorded. The data can be used only as a rough indication of the likelihood of lightning-caused grass fires, but the number of thunderstorms with no rain, a trace, or less than 0.05 inch of precipitation makes it reasonable to expect that thunderstorms occurred each year with so little rain that a grass fire could have resulted when the grass was dry enough to burn (Fig. 2). Most years prairie grasses start active growth about the end of April. If standing-dead grass is small compared with green growth, a fire is unlikely by early May: but if standing dead is great, a fire can occur for at least a month after new growth starts. Grass may become dry enough to burn as early as sometime in August in dry years and as late as late September in wet years. Lightning-caused fires could occur anytime from about September through early May, but the likelihood would be much higher in autumn and spring, with spring appearing to have a higher probability than autumn because of the more frequent thunderstorms.

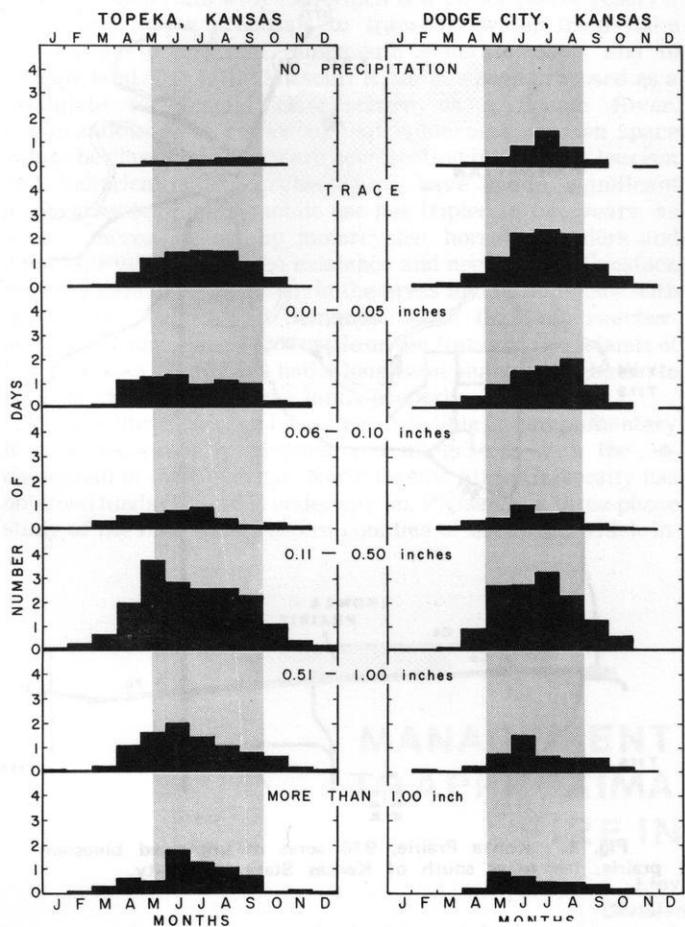


Fig. 2. Seasonal occurrence of thunderstorms associated with various amounts of precipitation at Topeka and Dodge City, Kansas, from 1951 through 1970.

With evidence that April would be as likely or more likely than other times for lightning-caused fires, and with the evidence that late-spring burning results in higher grass yields than earlier burning does (Anderson 1965, Owensby and Anderson 1967), we decided that the main time for burning should be spring, preferably late April.

BURNING PLAN

The burning plan developed for Konza Prairie encompasses the range of burning frequencies possible in pre-white-man times, from unburned to burned every year (Fig. 3). Unburned areas are expected to become forested; and in those areas we will study the rate of invasion by each species. We are interested to learn if 4- and 10-year intervals between fires will keep out woody plants, as well as learning effects of those intervals on herbaceous species. Burning after years when precipitation was at least 1.2 times the median probably will be more like the original than burning at uniform intervals. Precipitation records at Manhattan for the last 100 years indicate that precipitation is at least 1.2 times normal about one year in four. The interval between such years varied from 1 to 18.

This plan will allow us to ascertain which burning treatments allow the prairie to persist and which ones do not, thereby helping us to understand the likely fire frequency before European man settled the area. Also, by comparing various treatments, we will gain considerable information on the way that fire affects grassland. A deficiency of the plan is lack of burning at other times in the year, so we expect to add some small plots burned in autumn and early spring. We also intend to add some small plots burned with the wind and others burned against the wind, because the effects differ (Lindemuth and Byram 1948, Hare 1961).

For this plan to succeed we must successfully control our prescribed burns and prevent wild fire from occurring, at least on most of the area. Fire fighting equipment is being procured, and efforts are underway to obtain funds to build a headquarters part of which will include quarters for a caretaker, one of whose duties will be fire detection and control. We plan to mow a wide strip, perhaps 25 meters wide, in late July around the periphery of the area, and to mow some strips through the area. In the strips fires can be more readily stopped than where unmowed. If experience indicates the need, we will burn a narrow band perhaps 2 meters wide, within the mowed strips each autumn making an effective fire barrier. In addition to being an aid in fire control, mowing in late July is a desired treatment, as it results in favorable conditions for many prairie species. We will use a sickle bar mower on the nonrocky soil, but something like a flail mower on the rocky sites. Where a sickle-bar is used, we plan to remove the cut grass for hay on half the area and leave it on the other half. After a number of years, we may be able to assess the change in fertility due to removal of nutrients in the hay.

Results of fire studies on Konza Prairie will have many applications. For example, the results will be useful in managing a



Fig. 3. Konza Prairie burning plan. The four replications of six treatments occupy small watersheds as much as possible, so that nutrient and soil losses in runoff may be measured.

prairie national park. Opponents of a prairie national park have used the threat of fire to park visitors and to adjacent property as reasons for not having such a park. Results on Konza Prairie should help evaluate those objections. It appears that use of procedures outlined for Konza Prairie will be applicable in a park also. For example, mowing a wide strip around the periphery should make the threat to adjacent property no greater than at present, and it would be possible to burn a narrow strip each autumn within the mowed area to further reduce the threat of fire to adjacent property to less than under present grazing management. Along roads, visitor centers, and campsites, mowing annually would effectively remove fire as a serious threat to people in those locations. A prairie national park should have large native herbivores like bison, so the grassland would be grazed appreciably, although probably less intensely than ranches grazed by domestic livestock. Deciding how often a prairie national park should be burned will be greatly helped by the results on Konza Prairie. If a part of the park is burned each year, herbivores will graze mostly on the burned area, resulting in rotation of the area grazed. If the stocking rate is reasonable that might be good management.

We hope Konza Prairie can be a stimulus for long-range plans for other areas. Certainly the value of the area will increase proportionately to the length of the time the treatments are continued. Other studies of fire have been made in bluestem

prairie, but this is the first long-term study designed to understand the role of fire in original prairie.

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APPROXIMATING PRE-WHITE-MAN ANIMAL INFLUENCES AND RELATIONSHIPS IN PRAIRIE NATURAL AREAS¹

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Shelford (1963:329) depicts a "common morning scene" on the prairie before the coming of the white man as "a herd of bison or pronghorns in the distance, jack rabbits returning to their forms, a wolf or coyote trotting to its den, several small birds flying overhead and singing, and locally a prairie dog or a ground squirrel sitting upright at its burrow."

Today, when one looks out over the prairie lands of this country, he sees a different scene. We have traveled well over a century through time since the temperate grasslands of North America carried vast herds of bison and pronghorn. The burrowing animals such as the prairie dog have been effectively removed. Predators such as the wolf and primitive man are gone, and the black-footed ferret is on the endangered list. The coyote has remained and thrived despite man's efforts to eliminate him. The prairie chicken remains only in remnant populations.

The creation of a national or state area designed to approximate native prairie conditions brings up some interesting management problems. We cannot just select an appropriate

vegetative area and then leave it alone. At least certain animal species that we know once roamed the pristine grasslands must be reintroduced. Since a selected area has some size limitation, it must be enclosed with a fence or have some natural barrier to prevent depredation on nearby private ranges by large herbivores. This simple act of fencing off an area makes a sound management plan necessary.

In this paper, we will comment on large herbivores and predators as they relate to native prairies. Much of the information presented here is based on our bison-behavior research at Wind Cave National Park in South Dakota. We shall also attempt to point out some of the management problems that might be anticipated and suggest some possible solutions.

THE HERBIVORES

There can be little doubt that the two major prairie dominants among large herbivores was the bison and the pronghorn. Estimates vary, but at least 60 million bison once roamed over North America, with at least 45 million occurring in all parts of the grasslands except California (Shelford 1963). Pronghorn populations have been estimated at between 20 and 100 million (Seton 1929). Although some authors indicate that pronghorns tended to occupy drier portions of the grasslands than did the bison, these two species shared much of the same range.

Bison feed primarily on grass. In terms of animal units, they are considered nearly equal to domestic cattle. That is, stocking

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and the mountain lion, preyed on the bison occasionally, they were not significant in the way that the wolf was. Coyotes can not be considered seriously as bison predators, although they have been demonstrated to affect pronghorn populations under certain conditions (Einarsen 1948).

If we wish to closely approximate pre-white-man conditions on a national or state prairie park area, we must carefully weigh any thought of reintroducing these predators that played a vital role in the original grassland ecosystems. We must recognize that such an area will probably be an island surrounded by private land. Therefore, we must consider the sentiment and ultimate problems of the neighboring landowners.

Most of us are aware of the present status of predator management. It is an issue of emotion as well as of logic and fact. It seems almost certain that reintroduction of large mammalian predators into a region where livestock is a major enterprise will meet firm and vociferous opposition. And, in all honesty, the landowner cannot be blamed for being apprehensive because it is not possible to guarantee that there will be no depredations by these predators. If the system could be physically closed, thereby preventing egress of these predators onto private land, a reintroduction could be justified. Or, as with the coyote, if the predators are already present in the system without having to bring them in, there would be fewer problems. The question is one of values. It is not one of magnitude. If one wolf should take one calf, the fat would be in the fire and possibly rightfully so.

In view of the situation, we can draw a few conclusions. Certainly the reintroduction of mammalian predators would more closely approximate the pristine condition. Unless there is no danger of depredation or if there is a general willingness on the part of the public, including involved landowners, to accept possible depredations, however, perhaps the best solution would be to settle for something less. After all, it is virtually impossible to reintroduce at least one of the major predatory species. The American Indian as he was before the white man cannot be returned to the scene although his absence means a lesser approximation of the original condition. For these reasons, we do not recommend reintroduction of the wolf, bear, or cougar into a prairie park surrounded by private livestock ranges.

POPULATION CONTROL

In view of the facts that the limiting effect of predators is doubtful and that our prairie approximation is finite within the boundaries of a fence or other barrier, the problem of disposing of surplus herbivores to hold populations within the carrying capacity becomes a real one.

One possibility is trapping animals and removing them from the area. This technique is frequently proposed by those concerned about humane treatment for animals or interested in obtaining live animals themselves. It has serious drawbacks. A few are mentioned below.

First, and perhaps most important, trapping and transporting live animals is not as humane as some people believe. There is a great deal of stress on the animals involved in a trapping operation, and the risk of serious injury or mortality is high. In working with bison and elk roundups at Wind Cave, it is evident that, no matter how careful handlers attempt to be, the handling experience is a difficult one for wild animals.

Second, trapping and removal may result in distorted sex and age ratios if all animals trapped are removed. For instance, in a corral and wing-fence operation, cow-calf bison groups are much easier to capture than lone bulls or bull groups. At Wind Cave, this was due to the habitat preference of these groups and their gregariousness during the trapping season. The groups could not be gathered during the breeding season when the bulls were courting without greatly increasing opportunities for injury. This same problem occurred with elk trappings. Also, when animals are trapped periodically and then released, they will become harder to trap if the same facilities are used time

after time. Some people call this being "trap wise." The Indian probably did not face this problem when he trapped animals or drove them over cliffs because there were few, if any, survivors to be conditioned to continued trapping attempts. Today, it can be a real problem.

Finally, trapping is expensive in time and equipment. Even if surplus animals were sold, it would be difficult to justify the expenses of such an operation on an annual basis.

The alternative to this is a direct-cull, with animals shot on the range. This technique has the advantage of being more humane in the treatment of the animals. Also, it allows a careful selection of the animals to be removed and thereby avoids the problem of distorted sex and age ratios. Disposal of the carcasses presents a problem that must be worked out in accordance with local conditions. At Wind Cave, the surplus bison are given to the Bureau of Indian Affairs and thus go to the Sioux Indians of South Dakota.

We would suggest that such population control on an area designated as "natural" be carried out by qualified personnel employed by the administrating agency. This will insure a more accurate harvest with a minimum of disturbance on the area. Provisions for such a population-control system should be carefully spelled out in agreements between state authorities and the federal administrative agencies.

SUMMARY

Any attempts to approximate pristine prairie conditions would be incomplete without including herbivores and, possibly, predators that are known to have existed on early grasslands. The inclusions of these species, however, necessitates sound management plans.

The food habits and consumption rates of the species introduced must be considered in adjusting population ratios to the forage supply. Supplemental feeding is not a sound practice for native conditions. Adequate water and salt may be used as tools for population dispersal. Data on behavior of the species involved provide information on range-use patterns that influence the choice management practices. This is true for both inter- and intra-specific behavior. Mammalian predators, such as the wolf, grizzly bear, and mountain lion, should not be introduced on an area surrounded by private lands unless all depredations can be prevented or private landowners are willing to suffer these depredations. Management plans for population control of large herbivores should be spelled out in prior agreements between state authorities and federal agencies.

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Prairie Preservation and Restoration

THE SANDHILLS OF NEBRASKA AS A LOCATION FOR A NATIONAL PARK

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photographs by the author

The only major biome types in the United States not represented by any national park include what are generally termed prairielands. Among these are recognized three basic types: one is tallgrass prairie, another is shortgrass prairie, and the third—intermediate between the other two—is usually known as midgrass prairie. Ecologists advocate that sizeable remnants of each basic type be preserved within a system of national parks. So far, though, the only effort in this direction has been toward possible establishment of a Tallgrass Prairie National Park in the Flint Hills region of Kansas.

This report is not intended to promote an alternative for the Kansas proposal, but instead to publicize an additional prospect for a national park within another prairie biome, one farther to the west and north.

To many people the Sandhills region of Nebraska brings to mind visions of barren, unstable sand dunes; yet nothing could be more misleading. Much of the Sandhills region is dune-like in topography, but all of it is well carpeted with native grasses and well endowed with hundreds of lakes and a varied wildlife resource.



A typical scene in the Sandhills where overgrazing is not evident; the grass in the foreground is sand reedgrass (*Calamovilfa longifolia*).

More than 10,000,000 acres in size, the Sandhills region extends across nearly 200 miles of westcentral Nebraska and roughly 100 miles north and south between the Niobrara and Platte rivers. The topography consists largely of postglacial dunes that have since become stabilized with grass; these are interspersed with constructional alluvial plains which contain numerous lakes. The sandy soil, averaging 60 to 200 feet in depth, is underlaid with thick beds of porous sandstone which are excellent aquifers. Most of the annual precipitation, averaging 22 inches along the east and 17 inches along the western edge, infiltrates directly into the sandy soil. Large areas of the region have no surface drainage and what streams do occur have a remarkably constant flow. Thus the entire region is endowed with a high water table and most Sandhills lakes are, in fact, natural surface extensions of that water table. On the grass-covered dunes—locally known as “choppies”—moist sand can be found within one foot of the surface even during the drier periods of summer.

Due primarily to favorable water conditions, dominant plants of the Sandhills are the tallgrass species, except where overgrazing has occurred. On the dune areas they include sand bluestem (*Andropogon hallii*), little bluestem (*Andropogon scoparius*), sand lovegrass (*Eragrostis trichodes*) and—most widespread and abundant of all—sand reedgrass (*Calamovilfa longifolia*). On the alluvial plains the dominants include big bluestem (*Andropogon gerardi*), switchgrass (*Panicum virgatum*), western wheatgrass (*Agropyron smithii*), prairie cordgrass (*Spartina pectinata*) and indiangrass (*Sorghastrum nutans*). The two common shortgrass species, blue grama (*Bouteloua gracilis*) and buffalograss (*Buchloe dactyloides*) appear commonly as increasers on those dunes areas which have been overgrazed.

There are many species of forbs native to the Sandhills; some are indicators of overgrazing on certain sites, others thrive best among tall grasses protected from overgrazing, while still others are pioneer plants on wind-eroded blowouts. A sampling of unique species includes: sand begonia (*Rumex venenosus*), butte primrose (*Oenothera caespitosa*), bush morning-glory (*Ipomoea leptophylla*) and sandhills sunflower (*Helianthus petiolaris*).

The entire Sandhills region is excellent wildlife habitat. Big game mammals include both mule and whitetail deer and, in

localized populations, the pronghorn. Coyotes are everywhere abundant and the smaller mammals include such unlikely prairie species as raccoon, skunk, beaver and—where sizeable groves of trees have been planted—even the porcupine. The prairie dog, however, is not native to the Sandhills; apparently it is unable to dig suitable tunnels in the loose, sandy soils of the region.



The Sandhills region supports the largest nesting population of long-billed curlews remaining in North America.

An outstanding attraction of the Sandhills is the varied abundance of bird life. Game species include an abundance of sharp-tailed grouse, local populations of prairie chickens and ring-necked pheasants, many nesting species of ducks, and several established flocks of Canada geese. Nesters also include the following shorebirds: avocet, upland plover, Wilson's phalarope, killdeer, and the largest of all American shorebirds, the handsome long-billed curlew. The latter is of special significance because the epicenter of its entire breeding range lies within the western half of the Sandhills.

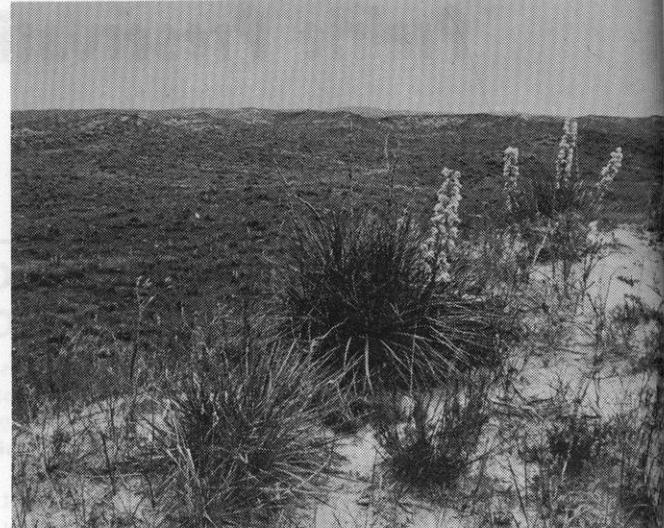
Economy of the Sandhills region is based almost entirely upon the grazing and breeding of beef cattle; the only other source of income, a minor one, occurs through leasing of privileges for hunting and fishing.

Abundant water and native grasses, plus certain topographic features, combine to make the region one of the finest cattle grazing areas and alluvial meadows which usually surround one or more shallow lakes. Cattle are usually confined to summer pasturing in dunes areas while the flat meadows are allowed to produce a wild hay crop for mowing in July; the hay is then stacked in the meadows and provides feed for cattle which are returned there for winter pasturing.

Sandhills ranchers all recognize the threat of wind erosion and thus are careful to guard against sand blowouts; however, many of them do allow their ranges to deteriorate from various degrees of overgrazing. Another and recent ecological threat to the region, especially along its eastern edge, is the increasing use of pivot irrigation to supplement hay production or to try converting meadows to cornfields. This trend may prove to be self-defeating, though, for Sandhills soils are not inherently rich and do require artificial fertilizing for high-yield cropping. Such fertilizer, when applied with irrigation water, tends to leach out

too fast for efficient plant use and has even caused nitrate pollution in wells supplying the drinking water for ranches and small towns.

Although none of the Sandhills can be regarded free from man's influences, sandy soils have precluded almost all use of the plow. Thus the region can boast the largest area of unbroken prairie remaining in North America. Furthermore, it is a type of prairie which can maintain itself without fire which is so necessary to prevent encroachment of woody vegetation in the true tallgrass prairies farther to the east.



The drier, western portion of the Sandhills exhibits quite a bit of yucca especially as an indicator of moderate overgrazing.



The Sandhills region is endowed with a high, dome-shaped water table and numerous shallow lakes.

With the above facts in mind, it is now possible to conclude that a prairie national park in the Sandhills of Nebraska may be practical for the following reasons:

(1) The region is extensive enough to encompass an unbroken unit of unplowed prairie of at least 200,000 acres. Such an area would likely permit native flora and fauna—including bison to be introduced—to attain their own levels of dynamic, natural balance with a minimum of human interference; it would nevertheless, occupy no more than two percent of the region's total acreage.

(2) Due to a high water table, many lakes and a varied topography, a Sandhills National Park would preserve and exhibit major associations of tall, mixed, and shortgrass prairie; it would also preserve a diverse and abundant fauna of both terrestrial and aquatic animal life.

(3) The region already encompasses two sizeable areas in federal ownership—Valentine National Wildlife Refuge of 71,000 acres, and Crescent Lake National Wildlife Refuge of 46,000 acres—and either one could become the nucleus for a national park of considerably greater acreage. This would preclude having to depend entirely on private land for acquiring the necessary acreage for a national park.

(4) The sandhills region is unsuitable economically for anything but cattle grazing, contains no known mineral deposits, and is not immediately threatened by any cities, power plants, dams or other encroachments of modern technology; these facts would assure a protective buffer to any national park established well within the region's periphery.

TALLGRASS PRAIRIE NATIONAL PARK

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Abstract. Prospects for establishing the Tallgrass Prairie National Park in the near future are improved by the introduction of bills in Congress in 1971 by Senator James B. Pearson (S.2149, on June 24) and Congressman Larry Winn, Jr. (H.R.9621, on July 7) calling for the establishment of such a park in Eastern Kansas.

Hearings have not yet been scheduled on these two bills. Support for them is broadly based. The U. S. Dept. of Interior, its National Park Service, and conservation organizations, almost without exception, favor the establishment of the Park in order to preserve a sample of both the plant and animal components of the Tallgrass Prairie, about as it was at the time European man first came on the scene.

ECOSYSTEM RESTORATION

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Abstract. The Nature Conservancy has acquired more than 800 areas in the last 20 years in its effort to preserve all of the U. S. ecosystem types as reservoirs of biological species and genetic diversity and as benchmarks of naturalness against which we can measure the effects of our pervasive experiments in environmental alteration. Undisturbed samples are not always available, and so it has become increasingly evident that some efforts at manipulation and restoration of disturbed areas is necessary. The reasons for, the difficulties in, and the methods of such restoration are discussed and exemplified by the experimental studies of the Center for Applied Research in Environmental Sciences (now reorganized as Environmental Concern, Inc.) in restoration of salt marshes along the Atlantic Coast.

The Nature Conservancy has an active program of preservation of natural areas throughout the United States. Over the last 20 years, over 800 preserves have been established through gifts of land, purchases made with money raised from private sources, or preacquisitions with later transfer to a government agency. The total saved now approaches 400,000 acres of ecologically significant landscape. As a matter of relevance to the subject of this conference, we now own and manage more prairie areas and types than anyone outside the federal government.

The rationale for this land saving effort has varied among the different participants and from project to project, from aesthetic and open space considerations to a concern for scientific research and education. The fundamental goal has been to preserve examples of all of the ecosystem types represented in the United States as reservoirs of biological species and genetic diversity and as benchmarks of naturalness against which we can measure the effects of our pervasive experiments in environmental alteration.

Initially, our theory of action was that the Conservancy would

save undisturbed tracts such as virgin forests and protect these in perpetuity. This concept has evolved as fewer and fewer undisturbed areas were to be found. Today we are also land banking areas which have been disturbed, which are in various stages of ecological succession, and in some cases areas which have been substantially altered. In many areas of the country, this is about all that is left. What then do you do when pristine habitats are no longer available and the job of saving representative ecosystems is far from completed? The answer, I think, is that you work on improvement and restoration of disturbed areas to assist in the recreation of disappearing and vanished habitat types.

The approach being discussed, it should be noted, is not widely appreciated or practiced at this time. In spite of considerable agitation and activity in the environmental quality field, the giant federal agencies, other governmental bodies, university departments, and other institutions show relatively little concern with environmental naturalness. Efforts at soil conservation, reforestation, reclamation, air and water quality improvement are, for the most part, simply efforts to improve

and extend manipulative controls and in many cases cause additional artificialization of the environments they treat. There is much talk of the integrity of ecosystems and of the functional continuity of all organic existence, but much of what passes for environmentalism today continues to ignore such considerations, focusing instead on processes of simplification, substitution, and homogenization tied to the unabated exploitation of resources. In contradistinction to the above, the restoration effort with which we are involved is a part of the larger preservation effort attempting to maintain the diversity of our biological capital as a long-term contribution to ecological stability and function. When the deficiencies of artificial systems catch up with them, this biological capital is all that we will have to fall back on.

WHY RESTORE ECOSYSTEMS?

We have in mind serving three principal purposes by restoring ecosystems. The first involves providing habitat for the preservation of species and ecological phenomena. In the Conservancy we have been attempting this by establishing preserves, but we know that many of these have deficiencies which diminish their utility for that purpose. Some can be improved through enlargement and restoration of degraded adjacent lands. Some can be improved through certain management manipulations on existing lands. Some kinds of ecosystems may not even be preserved in damaged form, and we would like to attempt the recreation of such communities through the reassembly of their scattered components. Who knows what the functional natural ecosystem should be on Iowa cornlands, for example, since all of the high potential sites have long been subjugated to the plow. The same fate has overtaken many eastern forest types so that what remains hardly measures up to the descriptions of the early explorers. We only have to look around to see what happened to the tall grass prairies everywhere. We may need these lost and vanishing ecosystems one of these days and whatever we can do to save or restore them will be appreciated by future generations.

The second reason we are so interested in restoration is the process itself. We would like to find techniques for restoring sound ecological function to badly damaged landscapes. We are aware of the dysfunctions in our contrived systems and we have reason to be fearful of their deterioration and collapse. Lacking complete knowledge, failsafe considerations must be important components of any system of management and to utilize such strategies demands not only that we bank our ecological capital, but that we find out how it may be employed when the need arises. We need to apply our own theoretical knowledge to the reconstruction of natural systems before we are compelled to do our experimentation under a state of emergency. Of course it may be that such human systems as intensive agriculture will prove themselves to be interminably viable and we may then never face a life and death need for our reconstitution efforts. Nevertheless, prudence dictates that we learn what we can in anticipation of such a need.

The third goal of restoration should be the reestablishment of diversity for diversity's sake in the environments in which most people must spend their time. Brushing aside the question of long term stability of our contrived systems, it is an observable fact that most of them are unnecessarily ugly and depressing. Organic diversity and landscape variation have often been thoughtlessly eliminated simply as the path of least resistance and then we are all left to live with the results. Highway rights-of-way, for example, needn't be monocultured, if only we would take the time and effort to explore alternatives. It would be enriching, to say the least, to reintroduce ecosystem diversity into managed systems. One way of accomplishing this is to find applied uses for natural diversity within such managed systems. Such applications could help to overcome the economic cost-benefit deterrents to maintenance of diversity. The ideal situation would be to find ways to couple ecosystem restoration with economic motivation—to make restoration pay. We may

find that we have often been economically unwise in crushing nature out of the picture. With a better knowledge of alternative uses of diversity, as in pest control, modulation of microclimates, or effects of environmental amenities on property value, we could make restoration attractive to the motive of self interest. Then we would really see some action.

HOW TO RESTORE ECOSYSTEMS

An immediate caveat is appropriate at this point. I don't know how to restore ecosystems nor does anyone else. Part of the reason for restoring them is our knowledge that we don't understand them and that we need to keep them around so that we can study them and become wiser. Therefore, we can not be arrogant in our approach to restoration. For the most part ecosystems must restore themselves and our role should be to subsidize more than to guide. There may be a number of obvious barriers to natural ecological recovery and by removing them we may essentially hasten natural succession processes.

1) The first step in the restoration of an ecosystem is to remove the disturbance or source of disturbance which caused the original alteration. This could be as simple as halting logging or farming operations and allowing secondary succession to begin the revegetation of the site. In some cases, it might be considerably more complex. Structures may have to be removed, pavement may need to be broken, the original hydrology may need to be restored. Hydrological restoration for example, may involve blocking of drainage ditches, increasing the size of culverts, perforating levees, destroying dams, or adding contour to a modified water course.

In some instances, there may be runaway processes of destabilization at work which require considerably greater exertion to eliminate. Crude processes of reclamation may be required to negate such malign influences as gully erosion or continuing pollution. Such insidious problems as acid mine drainage may be simply insurmountable given the economic resources available for the project. For the most part, the feasibility or infeasibility of a restoration project will be determined at this point in the process.

2) After eliminating sources of disturbance, the next problem might be to correct the damage that the disturbance effected in the physical environment. In some cases, this will take care of itself. Drained swamps, for example, should fill up again once the drainage structures are destroyed. In some cases, however an additional subsidy may be required. A stream may have to be redirected into its old channel after the mill race is destroyed. Potholes and ponds may need to be redug. Frequently fertility and natural qualities of the soil may require some careful attention. Salinized areas might need to be flushed. Hard pan may require mechanical maceration. The nutrient balance may need to be reapproximated. We know, for example, that even grazing or mowing will seriously deplete certain nutrients in a prairie soil, though this may not be evident from inspection of the vegetation. Since the rate of nutrient migration into many areas is extremely slow, resupply of certain key nutrient concentrations could be important for the purpose of foreshortening the time span required for ecological recovery.

3) The next and most central element in ecosystem restoration involves the biological components. Disturbed sites will almost always show marked changes in the species composition and/or population distribution of the plant and animal inhabitants of the site. Usually many native species will have been eliminated and some exotics introduced. Some native species will reinvade the area from nearby refugia as soon as the sources of disturbance are removed. Other ordinary components of the system may no longer exist near at hand. Their nearest population may be so far away that it exceeds the dispersal capacity of the species to cover the distance in any reasonable time span. Therefore, one of the most important subsidies supplied in a restoration program will involve the reassembly of the biological components from the scattered locations where they still exist (if they still exist).

Though all of our efforts at restoration are unrefined, this may

be the area where the greatest expertise is required. Careful studies should be made to try to determine which species were formerly known or reasonably expected to exist on the site. There should be advantages to reintroducing locally adapted stock insofar as possible by obtaining propagules from the nearest remaining populations or those from the most similar ecological surroundings. Some remarkable community reassembly jobs have been done, particularly with prairies, and in the genetic reservoir sense, some of the restored prairies in the mid-west may be among the best that now exist.

The other side of the biological coin is represented by the exotic species which may have invaded the site during the time of disturbance and elimination of exotics may be a simple or difficult task. Some may be self-eliminating, being dependent upon their adaptations to the former disturbance and being unable to compete against native species once that disturbance is removed. Others will be tougher and may themselves constitute an effective barrier to the reintroduction of certain of the native species. My personal belief is that in most instances ecosystems have considerable "niche space" available for additional species, though niches may overlap with natives and the continued presence of exotics may result in a very different spacial and numerical distribution among species present. On small isolated sites, as on islands, where the scope of interspecies dynamics is considerably restricted, the effect of exotic species may be considerably more serious.

One problem with reestablishing a natural biological composition is the abundance of species. A species-by-species approach is likely to be insufficient for the restoration of the total ecosystem. For instance, it would rarely be possible even to reconstruct a catalog of the preexisting invertebrates, and it is even more unlikely that they could all be found and deliberately reintroduced with available resources. There are other species, such as soil fungi, of which we may not even know, but which have important functions within the ecosystem. Even pathogens and parasites may play a role and the ecosystem will not truly be restored until they are once more among its viable components. A partial solution to this problem might be the mass introduction of undifferentiated materials from natural ecosystem refugia. A few bales of raw sod, fresh cut hay, leaf litter, or what have you transported into the site of restoration might succeed where the most precise sorting and targeting of materials never could. It is unlikely that we will ever be able to perfectly recreate the species composition which previously existed and we will probably have to reconcile ourselves to compromising on a decent approximation.

4) The last readily apparent aspect of the restoration process involves the possible necessity of continuous intervention. In addition to malign influences which may have to be removed, there are other influences which might have to be restored for normal ecosystem function. Many systems are adapted to certain forms of periodic redisturbance, as in the case of tall grass prairies and fires, and an unnatural degree of protection from such influences may be a barrier to the achievement of the desired restorative results. It may even be necessary on small and fragmentary sites to set up an artificial regime of periodic burning, flooding, or whatever it is that is necessary to promote the proper circumstances for the adapted communities.

5) One of the important questions which must be asked is how do we know when we are done? This question can not be answered with any certainty. After all, the concept of a "natural" ecosystem is itself an obvious abstraction and can be variously defined, depending on the frame of reference. Since our reference is diversity, stability, and function, I would say that the ecosystem is restored to the extent that human intervention can assist such restoration when these qualities have been restored. When the full array of biological species appropriate to the site again exists in viable populations and when the biogeochemical cycles are again adequately functioning, I would say that the task of restoration is over and the job of maintenance begins. This is not to imply that no further

biological effects are expected, since natural ecosystems are quite dynamic. Population numbers may fluctuate and the physiognomy of the association may itself be changing with age in a continuous or irregular manner. Some species may even pass out of existence on the site, being unable to maintain themselves through time. This might justify second attempts or investigations into the reasons for such a development. However, I would say that in no case should an attempt be made to fine-tune the ecosystem or any of its processes. Our knowledge of systems is gross and we should not deceive ourselves with illusory precision. These are not gardens we are seeking to recreate but living communities of species, continuously interacting with their environments.

6) There are obvious limits to our capacity for restoration. Some of these limits vary with the ecosystem type. For example, it seems likely that prairies can be more quickly restored than forests, simply because of the comparatively short generation time of most prairie species. Where species are extinct, the ecosystem in question will never be recreated to its former condition and this is one of the limits which we will simply have to put up with. Individual sites may show their own limitations relating to size, variability, and the size and diversity of populations which they could be expected to maintain. It would seem most reasonable to judge the site's potential and the success of the restoration program by the status of those species which can most suitably act as indicators. These would be the rarest species in the community or the most fragile or intolerant. In many instances these characteristics will coincide, as in the case of top predatory animals, which characteristically are very infrequent and are the end-point accumulators of whatever malign influences are imposed on the system.

WHAT WE ARE DOING

In a general sense, the Conservancy, like most other such groups, has more need than it has capabilities. We own hundreds of natural areas of many sorts. Even those preserves representing the best remaining remnants are often degraded, simplified, and devoid of many of their expected biological components. Where possible, we have taken (or will take) steps to rectify these circumstances. We have acquired additional buffer lands and done at least the preliminary tasks necessary to promote their recovery. We have reintroduced species and attempted to eradicate others. We make our lands available for use by other groups, and various institutions, private groups, or individuals are conducting efforts at restoration on our lands. We have adopted a variety of restorative management practices, such as fire management of some prairies and pine lands, with marked effects on the reconstitution of natural ecosystem types.

We have also initiated an intensive new program in this field under the auspices of our Science Department. The Center for Applied Research in Environmental Sciences (CARES) of The Nature Conservancy was established in October, 1971, under the direction of Dr. Edgar Garisch. The Center is not presently restoring prairies, as would be most appropriate to this conference, but is working on grasslands of a sort—salt marshes in the Chesapeake Bay. It is intended that in the future the project will be expanded to other kinds of ecosystems, including prairies, forests, and inland aquatic sites. CARES is still a small organization, but it has a professional staff of six, ample facilities, and a tremendous opportunity for rapid growth in its project activity. So far as I know, it is the only such center wholly devoted to ecosystem restoration in existence anywhere, though hopefully it will not be the last.

Salt marshes were chosen as the first subject for restoration investigations for a variety of reasons. A little work has been done at other institutions on restoration of the type and a considerable amount of ecosystem analysis has been conducted. Floristically, salt marshes represent very undiverse communities which considerably simplifies our task. Some salt

marshes are almost a monoculture and even the most diverse along the eastern seaboard rarely contain more than a half a dozen species below mean high tide. The faunistic part of the community, due to its water-borne mobility, can be expected with considerable confidence to recolonize restored marshes with little or no outside assistance.

Another reason for working on salt marshes is because they have been one of the most underappreciated, abused and yet important ecosystems in the country. Great portions of the Atlantic coast salt marshes, as much as 50 percent of the original in some states, have been destroyed, primarily in the last couple decades by dredging, filling, and other destructive practices. Yet they are tremendously important to the ecosystems of the entire Atlantic, since they are a productive nutrient sink between land and ocean, utilized by a great number of species as breeding or nursery grounds and by some as permanent habitats.

Not the least of the attractions of salt marsh for the restoration program is the fact that it offers tremendous opportunities for the kinds of applications mentioned earlier in the paper. In addition to its productivity and importance to the ecology of land and sea, it has an outstanding potential for the kinds of coupling to economic motivators that could promote effective use of the techniques being developed. For example, one of the pervasive problems in the human occupancy of the coasts is the natural shoreline erosion that occurs in many areas. Once the unwise decision is made to construct expensive improvements on the shoreline, there is often an attendant necessity for continued and strenuous efforts to keep the water from undermining the investment. Mostly, erosion is resisted with expensive engineering structures, such as bulkheads, groins, and sea walls, which are themselves additionally destructive to the ecology of the area. Salt marshes offer a likely biological alternative which, in many instances, could more cheaply abate shoreline erosion by reducing wave energies. There are additional applications for salt marshes in water quality, wildlife management, mariculture, etc.

Because of this, a great many people may elect the strategy of creating marshlands along their shores rather than building bulkheads or employing engineering practices. Though this decision may be made mostly on economic grounds, they can be enhancing environmental quality in spite of themselves. All of this is not to suggest that restoration or creation of salt marshes could not itself become environmentally abusive if carried to excess, but there is hardly any expectation that this will occur. It is far more likely that we will continue to do less than we should in the way of creating or maintaining this type of ecosystem.

The experimental marsh so far constructed should serve as an example of a typical restoration effort. The site chosen, on an island presently owned by The Nature Conservancy, is one where the rate of erosion is extreme and has been much aggravated by boat traffic, mismanagement, and possibly by deliberate efforts to eliminate the island as an obstruction to water traffic. Before the project began there were remnants of *Juncus roemerianus* high marsh on the island's perimeter, but whether or not low salt marsh on a graded flat ever existed on the island is unclear. Nevertheless, the site was suitable for marsh establishment but this was hindered by water dynamics and bottom contours.

The first form of subsidization involved the transport of substrate from other areas onto the site where the marsh was to be built. This substrate was then gradually graded from above mean high tide to below mean low tide. The next step was to assemble the biological materials, and seeds of some eleven plant species were collected from various sources (*Spartina alterniflora*, *S. patens*, *S. cynosuroides*, *Distichlis spicata*, *Juncus roemerianus*, *Phragmites communis*, *Typha latifolia*, *Typha angustifolia*, *Panicum virgatum*, *Scirpus robustus*, and *Ammophila breviligulata*—all found in lower salinity marshes of the Chesapeake or on dunes above it.). Finding it infeasible

for the most part to plant seeds directly on the flat, the seeds were germinated in growth chambers and grown in greenhouses until they reached a certain size. They were then transplanted in peat pots to the graded tidal flat. A variety of variables were manipulated during this process, searching for the best ways to gather, store, and germinate seeds, and other propagules; proper methods of green house cultivation and planting techniques, etc. Some planting of rhizomes and plants taken whole from natural marshes was also tried. On the flat the distribution of plant species was arranged in an experimental mosaic so that future marshes can be created with a better understanding of which plants should be placed where. One additional form of subsidization provided for the marsh was in the form of protection against destabilizing wave action. Portable breakwaters of unique design have been placed strategically to protect the flat until vegetative cover is complete. These will be removed when vegetative spread has sufficiently stabilized the flat to provide its own internal cohesion (Figures 1-6).



Figure 1. Building graded tidal flat by barging in new substrate.



Figure 2. Collecting seeds of marsh plants for use in restoration.



Figure 3. Plant Propagation in the greenhouse.



Figure 4. Grasses being transplanted to graded tidal flat.

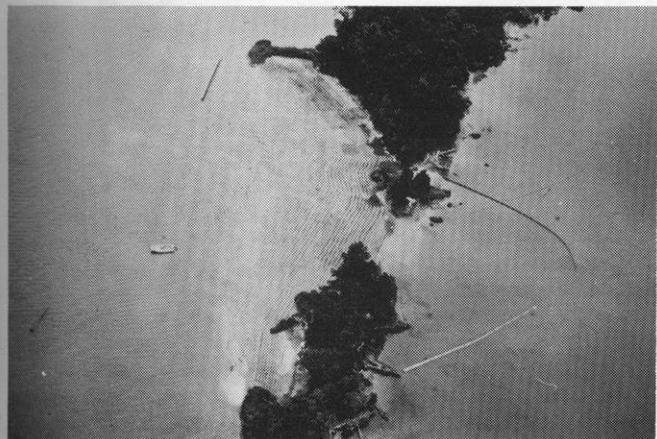


Figure 5. Transplanting of 100,000+ seedlings of nine species completed. Aerial view of flat, portable breakwaters on right.

FUTURE OPPORTUNITIES

The Nature Conservancy intends to expand the scope of its restoration efforts. Indeed, as the opportunity to acquire pristine natural areas continues to diminish, it is apparent that we must, particularly in regard to improving the viability and quality of our existing preserves. We would welcome the assistance and participation of anyone or any group with parallel interests. There is a pressing need for restoration of ecosystem types for which few or no natural representative sites exist and in which whole assemblies of species or locally adapted populations are endangered. These types are specialized regarding particular species and environmental



Figure 6. Flat about two months after planting, showing growth and spread of vegetation.

phenomena. There are particular sites which merit restoration attention because of their utility in research on ecosystem function or management.

It is encouraging to note a continuing and growing interest of certain universities and other institutions in ecosystem restoration, particularly of the much diminished prairie types in the middle of the continent. We would be exceptionally pleased to help these groups in whatever way we could by offering them the use of existing preserves for utilization in their programs or by the acquisition of new sites in which they may have already identified an interest. It is hoped that close ties of cooperation and communication will develop between the Center for Applied Research and some of these existing interested groups. There are a few steps which can be taken in the field of environmental improvement with such long term potential as the development and implementation of successful strategies in restoration of this kind.

Note: Since this paper was first given, the CARES program has elicited such a large and varied amount of public interest that it was felt that a separate organization could best promote the rapid spread of the concept of ecosystem restoration. Therefore, the Center for Applied Research in Environmental Sciences has been separated from The Nature Conservancy and will be established as a separate non-profit organization called Environmental Concern, Inc. The project continues under the direction of Dr. Garbisch and is currently expanding to include new restoration efforts. Insofar as Conservancy preserves might be benefited by restoration activity in the coastal zone or elsewhere, continued cooperation with Environmental Concern is expected.

THE BEAUTY OF PRAIRIE

Photographs by Patricia Caulfield
New York City

Patricia Caulfield developed a love of prairies as she grew up in Iowa. Her abilities to express her feelings and capture the beauty of prairies with a camera are evident in the accompanying photographs, which are a sample of those shown at the banquet of the conference. She is spending much time and energy trying to show others the value of prairie and why

samples, including a prairie national park, should be preserved. Those of us who study grasslands know the variety in appearance and composition, but most of us are less effective than Patricia Caulfield at helping others to see the differences and the beauty. (Editor)

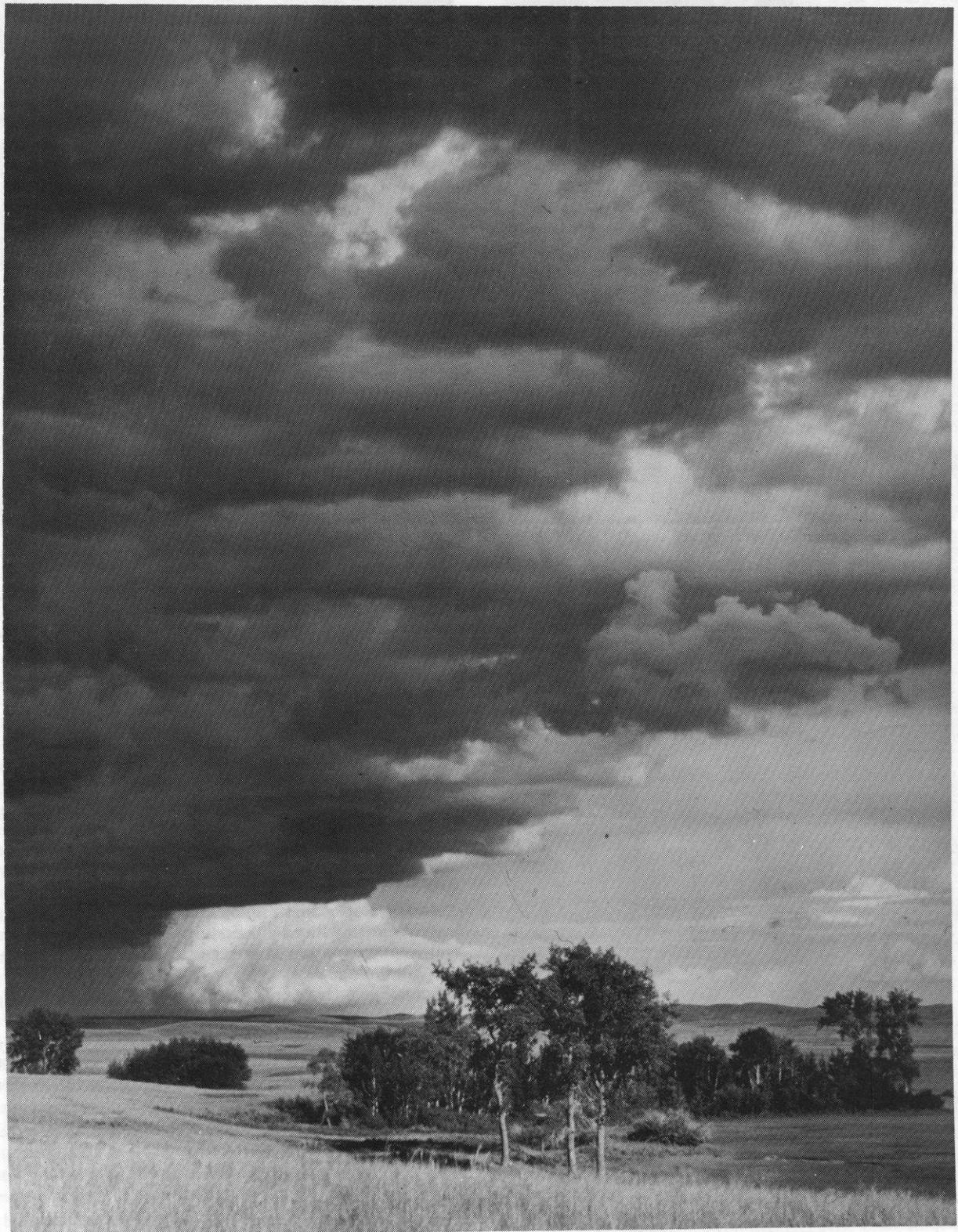


Figure 1. Storm, midsummer night, North Dakota, 1971. Copyright 1973 Patricia Caulfield.



Figure 2. Canada wild rye, South Dakota, 1971. Copyright 1973 Patricia Caulfield.

THE BEAUTY OF PRAIRIE



Figure 3. Sunflowers, dawn, Kansas, 1971. Copyright 1973 Patricia Caulfield.



Figure 4. Switchgrass, sunset, Missouri, 1971. Copyright 1973 Patricia Caulfield.



Figure 5. Prairie smoke, Iowa, 1971. Copyright 1973 Patricia Caulfield.



Figure 6. Big bluestem, sandhills, Nebraska, 1971. Copyright 1973 Patricia Caulfield.

Kansas State University, Manhattan, September 22-23, 1972

thirty-three



Figure 7. Canada geese, Missouri, 1971. Copyright 1973 Patricia Caulfield.



Figure 8. Fallow field, fall, Missouri, 1971. Copyright 1973 Patricia Caulfield.

Kansas State University, Manhattan, September 22-23, 1972

thirty-five

TO HEAL THE EARTH

Lorrie Otto
Milwaukee, Wisconsin

Since childhood we've been taught that one form of life depends upon another. In adulthood we in turn preach it to the young. Yet in the areas where we could put our learning and teaching into practice—school yards, churches, hospitals, roadsides, and most obvious of all, our own yards—we neaten and bleach, consistently and relentlessly destroying habitat for almost all life. If man pauses to think better, he is intimidated by neighbors or officials who feel threatened by change, or are unaware of the problem, or lack the talent to remedy it.

Some of us have joined Nature Conservancy and have ferociously fought to preserve unspoiled islands of land. But these acquisitions alone will not be sufficient to support the life systems of the earth. Like an enormous amoeba, a mass of unthinking or unknowing humanity oozes over the country, scraping off the hills, filling the valleys and then covering the flatness with concrete and mowed grass. This process wouldn't be so devastating if we had ribbons of restored acreage supporting and buffering the Nature Conservancy sanctuaries. If houses in suburbia were nestled in forests or prairies, water tables would be preserved, pollution of the environment would be dramatically curtailed, and in time we would have an educated and delighted citizenry better equipped to make environmental decisions. Suburbia could become the only quiet refuge left for man, where power equipment would be banned and the need for vacation homes would be obviated (removing another heinous disturbance to the wildlings).

The Nature Conservancy preserves, the midwest prairie conferences and our nature centers give us almost all of the ideas and tools we need to revitalize a great portion of our earth. Environmental concern since the first Earth Day in 1970 has brought many people to the threshold of action. Quite obviously these conditions and opportunities now need catalysts and translators.

At the Riveredge Nature Center in Newburg near Milwaukee, Wisc. we offer a course for suburban homemakers. The slide presentation includes some of the following:

1. Artists' yards tousled with prairie flowers
 - a—Encourages students to see plants through the eyes of designers (not farmers, parents or neighbors).
2. Suburban houses swathed in woodland growth, and others

where owners have destroyed woods with lawns and saved only the trees.

3. Bayside Grade School where P.T.A. landscaped with tree shrubs and prairie flowers indigenous to Wisconsin. (Helps children recognize plants described in American history and literature).
 - a—Concluding slides reflect aesthetics of suburbia where janitor sprayed with herbicides and pruned in a manner which has almost destroyed the entire project.
4. Psychiatric hospital in Oconomowoc (Rogers Memorial) where acres of formal lawns are becoming woods, meadows and restored prairie. (Sods removed and areas 18" by 3' lined with flattened cans which hold back the grass roots while prairie seeds and seedlings establish themselves).

I have designed this course and I teach it. I could not have done this without the information which the prairie conference have accumulated and made available. I use the names of artists with pictures of their yards in bloom and in seed, hoping that this will act upon the public with the force of fashions that led millions of women into pointed-toed and stiletto-heeled shoes, and then changed them into square-toed, high, chunky boots.

I suggest that to heal the earth is such a natural role for woman. It is an extension of motherhood as we try to insure continuation of human life by taking better care of its supporting structure. We must have places where soil is made, and materials and organisms to make it. We must have creatures and their processes to freshen air and purify water. We must have scavengers. We must have predators. We should know that some prairie plants should have holes in their leaves from feasting larvae which become butterflies and that they then pollinate the flowers so that seeds can form from which we get more plants for us to eat or for animals that we in turn eat and on and on!

All of the classes are fun to teach because basic to each idea is aesthetic delight for the individual. However, on the prairie days, the pleasures are peaked when we visualize the replacement of lot line to lot line grass carpeting with a glorious extravaganza of prairie flowers throughout the suburban midwest. And what makes that vision really shimmer is that it is all so possible!

THE VALUES OF SMALL PRAIRIE GARDENS

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Only rare, small relict "unbroken" prairie areas remain in eastern South Dakota. Most of the state residents, including the rural group, are unaware of the magnificence of the early tall grass prairie and are not able typically to recognize or identify native prairie grass species. In the hope that this neglect and ignorance might be corrected gradually, small prairie grass gardens have been planted as educational tools. It is hoped that these will stimulate the planting of others.

Two small gardens have been planted and are growing well at Vermillion, South Dakota, one on The University of South Dakota campus and one near a tourist camp. The former is sponsored by the University and the latter is sponsored by the City of Vermillion. Two more are planned, one on the high school and another on the middle school grounds. These are to be planted and cared for by students as school science projects.

Species used thus far are planted in 8 ft. rows, in 4-row blocks

and include: *Andropogon scoparius* (little bluestem), *Sorghastrum nutans* (indiangrass), *Andropogon hallii* (sand bluestem), *Panicum virgatum* (switchgrass), *Stipa viridula* (greenneedle grass), *Andropogon gerardi* (big bluestem), *Agropyron smithii* (western wheatgrass), *Bouteloua curtipendula* (sideoats grama), and a clover *Petalostemon purpureum* (purple prairieclover), plus some native prairie forbs. Planting procedures recommended by Jim Wilson of Polk, Nebraska were followed. In the gardens each species is marked and explanations of the significance of native prairie plant

species are available to interested people.

A surprising number of students, local people and tourists have indicated a strong interest in the prairie grasses and considerable unsolicited publicity has developed. We feel the development of similar small prairie gardens throughout the plains states would be of great help in kindling an interest in increased planting of these magnificent prairie species. In addition, we believe these gardens will be valuable tools in the education of school children concerning the early American prairie.

WHAT ARE OUR RESPONSIBILITIES IN PRAIRIE RESTORATION?

by
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Abstract. The extent to which native integrity would be lost indirectly in ecosystems of reference natural areas has been presented as the basic criterion for judging the suitability of large-scale restoration approaches. Evaluating current prairie restoration seed source trends within this context by examining nine key ecosystem concepts, indicates not only that these trends may damage prairie remnants, but also that this matter is only one part of a little recognized, but potentially very serious environmental crisis. The conclusion is that this crisis of mounting degradation, due to poor control over the artificial spreading of organisms in general, is large enough to warrant a new regulatory agency.

This paper presents the view that our primary responsibility in sound land-use is to preserve the highest quality possible in the stands of a program of reference natural areas. Quality is taken to be proportional to what Leopold (1949) called "land health", or the degree to which native mechanisms operate. Sound land-use, especially as related to its dependence on reference natural areas, is regarded to need an ecosystem basis (Pruitt 1970). Since the ecosystem has been regarded as the most complex system, aside from human society, which science investigates (Macfayden 1957 in Kendeigh 1961), the need to integrate concepts as the following for the proper application of any one of them, should be apparent. They are some of the key concepts that underlie the specific concern over the eventual effects of the large-scale spreading of ecotypes in prairie restoration.

ECOSYSTEM CONCEPTS

1. **Ecosystem concept** (Oosting 1956).
2. **Recent, intermediate view of the ecosystem** (Daubenmire 1968, Kendeigh 1961, McIntosh 1970). Kendeigh (p 26), also gives succinct versions of the earlier views.
3. **Regional nature of the ecosystem.** Since many of the stands designated as natural areas in programs like Wisconsin's (Scientific Areas Preservation Council), are so small that their wide-ranging animal components depend on other areas, the idea that they are best located along environmental corridors, seems very sound. Such locating should also alleviate the other frequent concern in scientific circles, that of maintaining good gene flow between stands of the same ecosystem type.
4. **Micro-gap-phase succession** Curtis (1959, p. 292-3) describes the nature of the countless, inconspicuous spots having

temporarily-open niche space in even "climax" prairies.

5. **Parameters of colonization** (adapted from Curtis 1959, p. 50; Daubenmire 1968)

%RP—relative number of a species (or strain) propagules available in a given region as affected by agents of dispersal; the gap is considered the center of the region.
cc—coefficient of colonization is the probability of a species invading the gap, given an equal entry of propagules from all species; it is a composite function of growth rates, phenologic behavior, antibiosis, leaf width, etc.
d—probability of the average unit propagule reaching the gap as affected by local dispersal and micro-habitat barriers.

PC—probability of cap colonization.
$$= d \times (\%RP) \times cc$$

6. **Ecotype** (Cain 1944). Curtis (1959) defined it simply as "a strain or race of a species which is differently adapted to the environment than other populations of the same species." Cain (1944) said their "individuality is maintained only because of habitat isolation." Regarding ecologic studies, Curtis (1959) said "Recognition of this situation and the solution of the problems it raises are among the greatest questions faced by vegetation ecologists today." This view was undoubtedly tempered by the considerable evidence he also presented which indicates ecotypic differentiation is the rule in natural upland communities. Its truth has already been pointed out by Goff (1971) who indicated that the International Biological Program cannot extend certain species association relationships from region to region because of the genetic differences within species.
7. **Niche** (Anderson 1956, Wuenscher 1969). The key part of this concept is that niches in ecosystems are actually filled by

ecotypes. Its significance, when considered with the widely-recognized exclusional nature of the niche, has been stated by Dice (1952). He said "Two different ecotypes, theoretically, cannot long exist together in the same population. Competition between them will be expected quickly to eliminate one or the other."

A simplified model of a niche (adapted from Anderson 1959, Wuenscher 1969) in an hypothetical plane is presented in fig. 1. The distance from the center of the polygon to a given vertex is a balance between a population's genetic potential to compete for the trait involved and the average collective ability of all associated species to do like wise.

Because of co-adaptive, genetically-maintained niches, a crude analogy will be made to a puzzle only to help clarify somewhat how the entry of one of Rudd's (1964) "biological weeds" in degraded conditions, can affect additional and severe damage to the system. Fig. 2 (adapted from Anderson 1956) shows how all of the pieces (native populations) might fit together in an average configuration of shared niche space that would be demonstrated in the long-term stability of a native ecosystem. Land sickness in this context can be viewed as having more un-occupied space in some niche plane than would occur with the oscillations of only native dynamics.

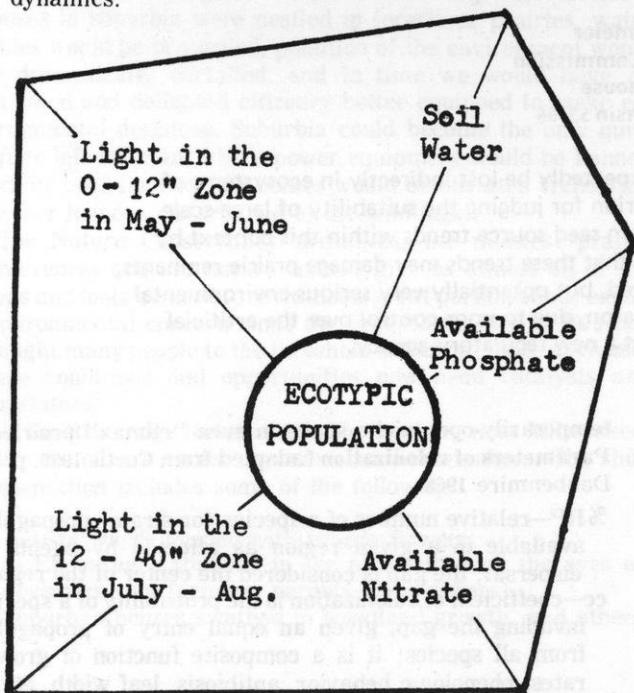


Figure 1. Schematic model of a species' niche in an ecosystem. This represents only one hypothetical plane of its total niche space in that ecosystem.

Alien invasion is not only much more likely in such a weakened ecosystem, but a slight edge in an alien's coefficient of colonization, may allow its niche to grow, like an infection, by constantly-increasing "%RP" values, until it crowds the space of many native niches in regional ecosystems. An example of such niche boundaries as they might be drawn for the Eurasian race of canary grass (*Phalaris arundinacea*) has also been shown in fig. 2. This is based on Fassett's (1951) observations in Wisconsin lowlands. Note that the degrees of niche encroachment include eliminations of some local native populations.

8. **Hybrid Swarms** (Anderson 1956, Stebbins 1966). This concept shows how man has created many of the weeds by mixing originally disjunct populations in conditions of land sickness. Anderson (1956) explains how the process of hybrid swarming in creating many new types of offspring greatly increases the chances that one particular type will be able to

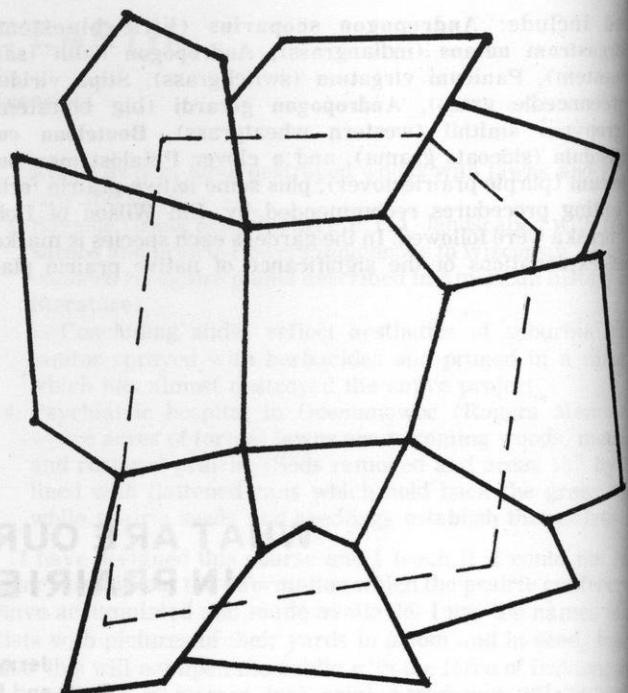


Figure 2. Schematic model of shared niche space in an hypothetical plane for 10 co-adapted ecotypic populations of an ecosystem. The dashed-line polygon represents niche intrusion like that described for the Eurasian race of canary grass.

invade open niche space. Such swarming can occur between ecotypes too. Stebbins (1966) said that a number of hybrids between plant races have given vigorous, intermediate and highly variable offspring. It should be pointed out that the USDA (1948) has considered key restoration grasses as the following to be mostly cross-fertilized: *Andropogon gerardii*, *A. scoparius*, *Bouteloua curtipendula*, and *Panicum virgatum*.

9. **Recent successional-refuges.** This term has been adopted as a label for the often unrecognized thousands of retired strips and odd corners, where native prairie is actually expanding largely unaided. They are usually in old-field habitats near original prairies. Judging by the scores we have recently found with little effort in the 600 square mile Waukesha County, hundreds of those spots exist there alone. Thomson (1940) provides details on the successional processes involved. These spots are good local seed sources and many should have seed which is less inbred than that of isolated remnants.

DISCUSSION

Integrating the preceding concepts with my restoration research (Schwarzmeier 1972) and with my involvement with Wisconsin's Scientific Areas program, has produced considerable apprehension as regards the ultimate fate of the prairie-related reference stands if current seed spreading trends continue. The various concerns with minimal elaboration follow.

1. An imminent usurpation of many potential prairie sites in the prairie corridors due to large alien strain plantings nearby. This could occur even if only the relative propagule value of those strains were significantly raised.
2. Contamination of the ecotypic integrity of reference areas by cross-pollination.
3. Reference area contamination by alien strain seeds. Initially, this may be an effect of the early usurpation on the regional probabilities of remnant gap colonization, where a region consists of a portion of a prairie corridor and the

adjacent areas containing several alien strain plantings.

4. Development of hybrid forms within the dominant species may occur as a result of conditions 2 and 3. These may be more aggressive than the earlier-growing original alien strains.
5. As a result of conditions 2, 3 and 4, the micro-environment of the average gap may become so severe that little niche space would be left for many non-dominant species.

Since some basic original objectives of scientific area use, describing original native ecotypes and their roles, will already be lost by stages 2 and 3 (may be impossible to avoid if stage 1 is once reached), the final several stages of possible degradation will be omitted in this paper.

All of the preceding underlies a rather startling hypothesis which I now offer:

Using alien ecotypes for upland restorations in regions containing reference natural areas, may be more damaging than using strains of species like quack grass (*Agropyron repens*) or timothy (*Phleum pratense*) that are already established in the region.

The hypothesis mainly concerns regions having reference area communities of the same general type from which the alien ecotype originally came.

Recommended approach to prairie restoration

This involved topic is only touched on to indicate that safe methods do exist within our society's means to deal with the restorational needs of the prairie as related to its long-term preservation in regions like Wisconsin, where prairie national parks would be impossible. It really does not seem as crucial to sound prairie conservation right now. If the ecologically-minded prairie people were to concentrate on it to the exclusion of regulating the commercial trends, their efforts could all be in vain. These people must first make sure that the serious natural area impacts of those trends are identified and checked in time. Also the rate of deterioration in many of our semi-isolated remnants seems low enough to allow the time expectedly needed to rebuild a devasted complex system. It certainly takes much longer to rebuild a smashed clock than it did for someone to smash it in the first place. Finally, since community structure affects survival of non-dominants and itself is a function of the amount of time between seeding and arrival of late-successional stages (Schwarzmeier 1972), use of the more natural restoration approaches may have great practical value in even urban landscaping considerations.

Evaluating, typing and mapping all prairie-related remnants.

Ideally this would include collection and description of all common ecotypes in each stand and preservation of nearly all stands.

Environmental corridor considerations.

1. Give special recognition to remnants within environmental corridor zones.
2. Give high priority to management of degraded prairie stands located between good remnants in such zones.
3. Give high priority to burning-expansion of remnants on their edges.
4. Encourage seeded-restorations in old-field areas between widely-spaced good remnants using mostly seed from the two flanking remnants.

General restoration.

1. Old-field maintenance even without regard to identifying prairie species is one of the simplest and best things a lay land manager can do (Zimmerman 1971). It usually amounts to doing nothing more than periodic burning or mowing to prevent the brushy stages from becoming dominant. This management does the following:

- a. replaces in effect, the partial loss of ecosystem initiators of succession (wildfires, etc.).
- b. recognizes and respects the great significance of the early stages of natural successional processes.
- c. automatically increases the regional propagule values for many aggressive but early-successional native plants that often are prairie species or good for wildlife.
- d. encourages natural outbreeding processes for prairie plants.

For a good example of how this simple approach was applied on a large scale, in Nebraska, see Nelson (1972).

2. Seeded restoration suggestions.

- a. remember that the term "native seed" really should be reserved for the most local ecotypes remaining for a given type of site.
- b. with only a little professional guidance, lay enthusiasts can often do very well by collecting from local "recent successional-refuges" and remnants; in prairie dominated spots, they can usually collect all available seed with little regard to identification except for avoidance of weed seeds; collecting and spreading prairie hay is a quick and often suitable version of this method; this approach can be turned into a good hobby since many of the species that seemingly should be dominant in early stages (e.g., *Oenothera biennis*, *Rudbeckia hirta*, *Monarda fistulosa*, *Elymus canadensis* and *Aster laevis*) are very easy to propagate; use of a seeding mixture applying these natural principles of succession (Curtis 1959, p. 292-3), will encourage a long-term attachment to the project because the late-successional plants (as the bluestems and *Silphiums*) by having low initial seedling densities, will demonstrate an exciting, constant expansion and successional refinement as they progressively take over; this process can be as short as 10 years in suitable conditions; see Thomson (1940).
- c. the most important practical consideration in most cases is soil preparation; unless a completely-natural invasional product is desired, plowing and a whole year of fallowing, is one of the most important steps, at least in the Great Lakes region; for details see (Wilson 1970, Rock 1971, Schwarzmeier, 1972).

CONCLUSIONS

Although this brief paper can be criticized for incomplete scientific presentation of the concepts and concerns on which it is based, it should be pointed out that its main object is to call attention to what seems to be one of our most critical environmental crisis areas relative to its recognition. Indeed if many of our greatest ecologists of the last three decades were right in their agreement on the necessity of a system of natural ecosystem banks (Graham 1944, Leopold 1949, Curtis 1959, Pruitt 1970, Loucks 1971), then the least we can do is work for a thorough evaluation of the whole complex matter of organism introductions, by a group of professional experts in the various relevant disciplines.

The lack of publicly expressed concern seems to be a result of inadequate professional machinery to deal with the complexity and size of the problem. Bates (1956) presented a good explanation for the large differences between ecologists and evolutionists in their findings and opinions concerning the role of equilibria in ecosystem dynamics. From it, one can see that the needed integration of the many concepts, from both disciplines, is more than most specialists can approach on a part-time basis.

If the proper, integrated approach is applied to examination of many of our present organism introduction trends, a very alarming picture begins to form. One facet is recognizing our continuation of technologically-augmented dispersals as presented by Anderson (1956) and Bates (1956) for plants, vertebrates, insects and microorganisms into both terrestrial and aquatic environments (e.g., downy chess, carp, Colorado potato beetle and yellow fever).

Another facet is our accelerating trends of landscape simplification. Finally, integrating these trend considerations with

an understanding of the hybrid swarm process of weed creation, leads to the conclusion that lack of better regulation will eventually result in a landscape dominated at every level by irruptive, oscillatory, weedy organisms.

The proper solution then would actually appear to be creation of a strong national agency having charge over the transmission of all organisms, especially as regards restricting any new type as long as that type appears to be a potential degradational infector of land systems. This agency would be similar to the present U.S. Customs Bureau, but would also regulate strongly on an interstate basis and be very alert for potential contaminants of natural areas.

When matters of great environmental urgency are considered by diverse philosophies, some polemics are bound to occur. Since we are dealing with the fate of many irreplaceables, the natural inclination to neglect information that threatens our views, now more than ever must be considered very secondary to the objective application of the best current knowledge. This is not to chide those who appear to be blocking the recommended approach of minimal departure from natural processes, or even those promoting seemingly-damaging dissemination trends. It was through the early efforts of some in the latter category that we still have many of the native prairie mechanisms which we now seek to preserve in highly different land-use circumstances. Rather the intent is to underscore the need for all to approach these crucial questions as objectively as possible, so that each of us will be able to accept new information should our methods ever lose their relevance.

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THE PRAIRIE AS AN ESTHETIC EXPERIENCE AND A TOOL FOR PUBLIC ENLIGHTENMENT

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Have you ever asked yourself why people grow flowers around their houses? It seems rather remarkable, considering the chores of preparing the land, sowing and planting, weeding and watering and trimming, to say nothing about the cost. But people do it and even compete with one another for the most beautiful flower garden in town. The reason is, of course, that so many of us have a keen sense of esthetics. We enjoy beautiful things so much that we are willing to work and pay for them, and our reward is the pleasure of beholding lovely flowers.

The relation of these observations to the topic of our symposium on "Approximating the original prairie ecosystem" surely is obvious. There is hardly a place on earth where so many beautiful flowers grow throughout the growing season as on the prairie. That the prairie is beautiful was already observed by Clements and many pioneers before him. It is a genuine thrill to experience the esthetic delights of the flowering prairie from the earliest spring blossoms to the time when the bluestems turn so red that they might better be called redstems! The flowers come in all sorts and sizes, shapes and designs and

colors, a continuous procession of delight. And the beauty of the prairie is not limited to the forbs. Even many grasses have beautiful flowers for bouquets that will grace any living room. As long ago as the late 15th century, Albrecht Dürer, one of the greatest artists of the Renaissance period, painted a bouquet with *Poa pratensis*, thereby focusing the attention of the beholders of nearly five centuries on the beauty of our grasses. And still, it is ignored so often.

But times have changed. The prairie in all its glory is now threatened with extinction, and most of it is already gone. Only precious bits remain. Our symposium is therefore timely. We still find pieces of prairie of various size and quality, but even the best preserved ones may not be exactly what they were in their pristine state. In that state, the prairie was grazed by roaming, unfenced bison, antelopes and other herbivores which, in turn, were kept in check by cougars, wolves and other predators. Lightning fires occasionally swept across vast expanses with no one to put them out, and wet years alternated

with droughts. In such a setting the prairie evolved, perfectly adapted, and flexible in its herbaceous character to meet the constantly changing conditions. The wolves are gone, the cougars are hunted and destroyed as if they were Satan himself, and fences limit the circulation of grazing animals, frequently leading to serious overgrazing. And of course, most of the prairie has been consumed by a rapacious plough.

Approximating the original prairie ecosystem is a challenging task, and the chances for success vary according to the prevailing conditions. Some prairies are in relatively good condition, others are more or less badly overgrazed. Therefore, approximating the original prairie ecosystem means above all nursing the damaged prairies back into the closest approximation of pristine conditions. That this can be done has been demonstrated. But it is extremely difficult to establish a prairie with all its forbs on cultivated land, although even this seems possible with the right leadership and expertise, patience and support.

It does indeed require the support of the people, morally, financially and in every other way. Conservation is meaningless unless it serves the people, but it must be understood that serving the people does not always mean a net profit of so many dollars. The esthetic and spiritual qualities of the prairie must be appreciated as much as those of art museums, for in fact, our bits of prairie are now museum pieces, unique, priceless and to be cared for, so that they may justify their existence by serving their purpose. That purpose is to teach us about life on earth, about ecosystems and how to manage our resources. And in addition, that purpose is to give us those inestimable qualities of life, of joy and enjoyment, of knowledge and of beauty. Said Frank Egler (1972): "There has always been a tradition in ecological circles of the pursuit of knowledge for its own sake, of an esthetic enjoyment of the intellectual. I think we should be very proud of this tradition and seek to maintain it."

If the support of the people has become necessary, the time is also peculiarly auspicious. The disastrous decline in the quality of our environment has so aroused the people that they are much more willing to learn about our real needs and how to serve them. Terms like conservation, ecology, even ecosystems have become fashionable, and more and more people are trying to discover just what is involved. But if they are willing to learn, there must be those who teach them. Let us therefore find people with knowledge and experience, willing to help. Let them teach all who are willing to listen, teachers and students alike, members of clubs and societies concerned with gardens, flowers, nature, conservation, wilderness, etc. Teach them not just what ecology and conservation are all about; they can learn that from many sources. But demonstrate how the PRAIRIE can serve their needs, how the PRAIRIE must be preserved and admired and loved. Teach them to observe it in all seasons, and awaken joy and interest in it among all the people around us. On carefully planned field trips, point out all there is to see, place it in its proper setting in time and place, arouse enthusiasm and curiosity. Then people will support the effort to approximate the original prairie ecosystem because they learn to appreciate the return; a return more profitable than most forms of entertainment on which huge sums are spent, a return of much more lasting and satisfying quality. But the people must be taught to appreciate what they see, and what they now refer to as grass and weeds must turn into living, enjoyable and useful organisms by which they become fascinated.

No two pieces of prairie are exactly alike, and if we are to improve our damaged prairie remnants, we may as well focus on those features to which people respond most readily. This is undoubtedly the beauty of the forbs in bloom. But forbs can give a lot of trouble and many are not cooperative at all. Their seeds may not germinate readily and they resent being transplanted. Here I should like to appeal to my scientific colleagues to carry on much needed research on the life histories of forbs, their behavior and their needs.

We need to know more about the natural ecesis of forbs under

the impact of competition, about their longevity and the longevity of their seeds, about their resistance to drought in various ontogenetic phases and to transplanting. Such research projects should be carried out separately in the bluestem or tall grass prairie, the mixed prairie and the grama-buffalograss or short grass prairie.

On the basis of my experiments I can suggest mowing at the end of the growing season with a rotary mower that shreds everything, but nothing is removed. In theory, there is no need for mowing as there was none in the original prairie ecosystem. But as long as nothing is removed and the growing season is over, mowing does help to give the resting prairie a more attractive appearance and also to keep down woody invaders. There will, therefore, be no financial return but the esthetic reward is great. For example, on the various prairies in Douglas County, the spring flowering *Lithospermum* has one to eight flower stalks whereas on my prairie it has eight to fifteen!

We need to know more about the relation of forbs to grazing animals for Hetzer and McGregor (1951) have shown how grazing reduces first of all the number of forb species in the natural plant communities. They divided the prairie into five types according to the pressure of grazing animals, i.e. fenced cattle. They found that the first type approximates the natural prairie. If ungrazed for a year or more, it appears to be an undisturbed grassland. But already in the second type, they observed that the forbs which are so characteristic of the prairie, have nearly disappeared! Only a few relic forbs remain in the third type, and that is the end. There are practically no prairie forbs left in the fourth and fifth types. Systematic grazing by fenced animals therefore impoverishes the prairie where it hurts most.

Nowadays the application of herbicidal sprays is practiced by many farmers. The use of such sprays on the prairie is, of course, unacceptable because it kills the forbs first. Where brush invades the prairie, it can be suppressed by cutting the woody plants individually. They should be cut flush with the soil surface, and the stumps should be painted immediately with a brush killer. This is a very tedious task but it is effective without hurting the forbs.

Mulch helps to retain soil moisture and prevent excessively high summer soil temperatures. It also reduces soil erosion to a minimum and is sooner or later incorporated into the humus rich horizons of the prairie soils. Where prairie plants are allowed to grow unchecked, they will produce a considerable biomass. When this accumulates enough and more or less falls over during the winter, it will retard spring growth notably by densely shading the soil, keeping it cool, but also preventing damage by late frosts. The occasional prairie fires, however, reduced the amount of mulch at irregular intervals and thus helped to restore and maintain a healthy balance.

Prairie fires are therefore important and many experiments have been made to understand the effects of fire on the prairie (I need only recall the splendid work by Owensby). Large parts of the Flint Hills prairies are burned annually or nearly so but the fires of cattle ranchers are set for economic reasons and relate little to our considerations. Approximating the original prairie ecosystem includes fires but the story told by past experiments is not necessarily the one that interests us here.

It seems unlikely that fires occurred annually on the same piece of pristine prairie; intervals of five to ten years seem more probable. Furthermore, fires are usually set before the beginning of the growing season although natural prairie fires are unlikely at this time of year. Spring and early summer is the rainy season, and when the prairie with its mulch is soaked by the heavy downpours of thunderstorms, it does not burn well if at all. But later in the summer, when all is dry and when the so-called dry thunderstorms roll across the landscape, then the prairie can be ignited more readily. Fires at this time are fatal to woody invaders whereas the herbaceous vegetation remains relatively unharmed. This helps to maintain the extent of the prairie. Deliberate burning in late summer is unpopular

because it interferes with the economic use of the prairie. But economic use and approximating the original prairie ecosystem are not at all the same, neither in method nor in goal. This must be emphasized.

Where fire experiments are to be carried out in connection with approximating the original prairie ecosystem, I should like to suggest that fires are set only once in five years and others at even greater intervals. For the sake of gathering scientific information, it seems desirable that some fires are set in early spring and others during a late summer drought. I venture to guess that these latter fires will be the most telling ones.

The intervals of at least five years are necessary because it is important that the mulch be restored for the protection and enrichment of the soil. Fire stimulates erosion, and frequent burning, especially on hill sides, can only lead to undue sheet erosion which can remain inconspicuous until serious damage is done, and then it is too late. The years of rest from burning strengthen the grasses and forbs alike and permit them to sprout vigorously after the fires. Frequent burning weakens the plants and contributes to their elimination.

I would argue that the strongest support from the lay public will come when the forbs are a success. We must therefore

direct our experiments toward creating esthetic values which the prairie offers in such singular fashion. Through the appreciation and enjoyment of the beauty of the prairie people can be taught with relative ease what the environmental problems are about. The herbaceous character of the prairie permits observations from earliest spring growth to the decay at year's end, a whole cycle. The response of herbaceous plant communities to site variations is particularly clear, and it is easy to list other aspects of the prairie that can serve to enlighten the interested layman about the wonderful intricacies of nature and their significance for our survival. Perhaps the greatest art of all is the art of living, and in this, the prairie is one of our finest teachers, if only we give it a chance and are willing to learn.

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PRAIRIE PRESERVATION IN MISSOURI

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Abstract. Nearly 40 percent of Missouri was once tall grass prairies. About 75,000 acres remain of the original 15,000,000 acres of native prairies. A total of 3,160 acres of virgin prairie has been set aside for preservation in the past 12 years. The University of Missouri-Columbia acquired 140 acres; the Department of Conservation preserved two native prairies of 85 and 1,360 acres; The Missouri Prairie Foundation acquired three prairies of 40 acres, 260 acres, and 160 acres; and The Nature Conservancy purchased 1,115 acres of prairie. A goal of an additional 13,000 of native prairie to be preserved in the next 15 years has been set.

PRAIRIE PRESERVATION IN MISSOURI

Missouri is well known for its forested Ozark mountains, but few people today realize nearly 40 percent of the state was once magnificent tall-grass prairie, equal in quality to the Kansas, Iowa and Illinois prairies (Figure 1).

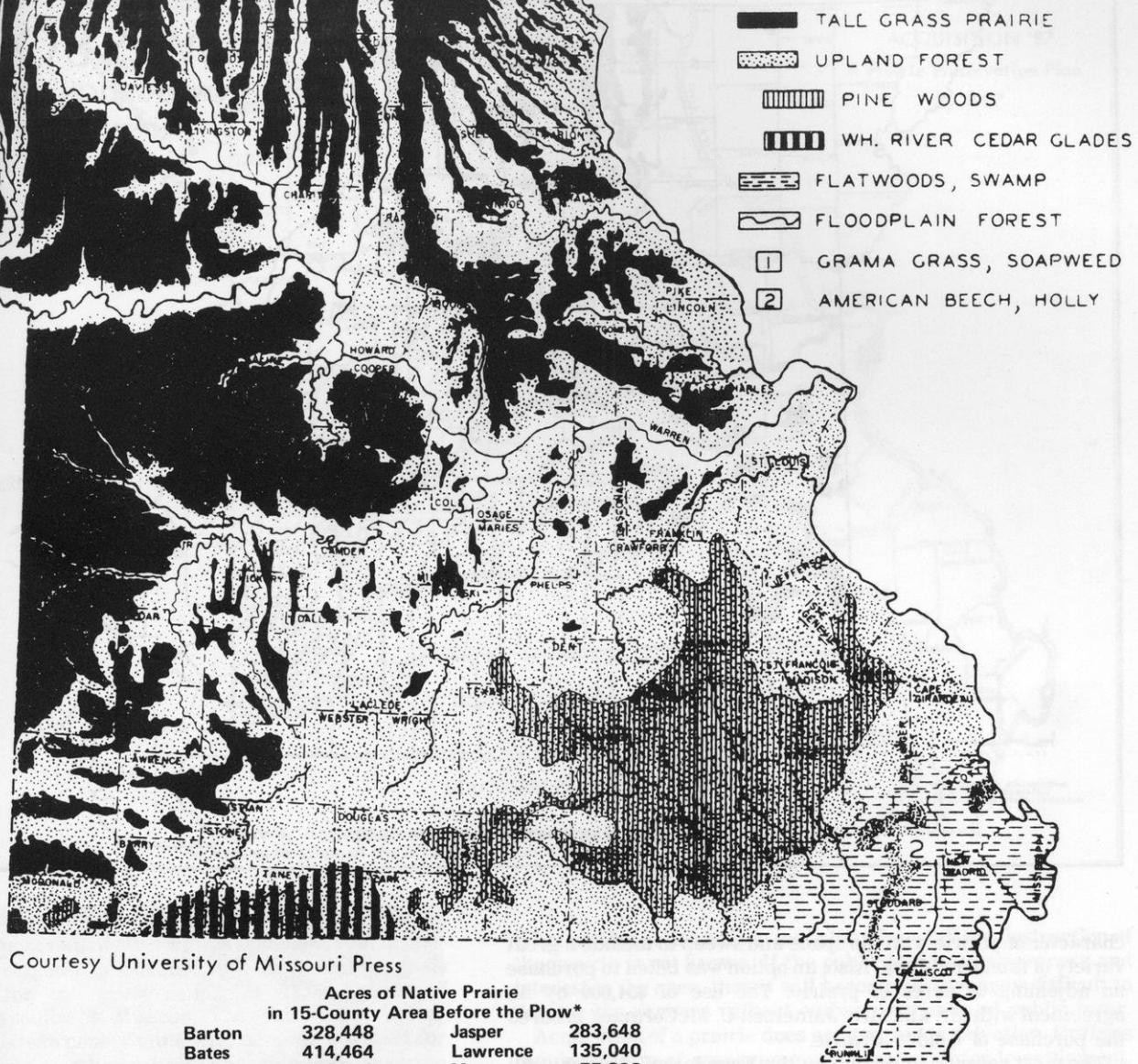
The prairie preservation movement in Missouri began with the concern for the greater prairie chicken. Studies by the Wildlife Research Unit at the University of Missouri in the late 1930's and the Missouri Conservation Commission in the mid 1940's attributed the decline of the prairie chickens to deteriorating habitat. Once numbering hundreds of thousands of birds throughout northern and western Missouri, the population dwindled to a few thousand. Land-use trends following World War II touched off a new era in agriculture to the detriment of grassland habitat. Irrigation and soil treatments made it possible to grow corn and soybeans on the poorest of lands. Localities once suitable for prairie chicken range soon became marginal when the proportion of permanent grass cover fell below 25 percent of the cropland. The full impact of land-use change struck north Missouri during the mid 1950's; several thousand birds disappeared within less than a decade. Almost overnight 1,600 square miles of the 2,500 square miles of prairie chicken range was lost (Figure 2).

Loss of habitat in north Missouri brought the realization that conceivably the prairie chicken could be extirpated in the state.

Further study of the situation revealed that the unplowed virgin prairie was the backbone of prairie chicken habitat. Some introduced grasses such as timothy and red top furnished acceptable grass cover for an interim of time but agriculturists turned to short term rotations, close cropping, and other types of grasses ill-suited for prairie chickens. Only southwest Missouri with remnants of tall grass prairies, offered much hope for the birds. The Commission decided in 1951 to acquire some native prairies, hopefully to insure the preservation of several flocks of prairie chickens. This marked the beginning of the prairie preservation movement although it was not apparent at the time.

Actually the first virgin prairie to be preserved in the state by public ownership was the 140-acre Tucker Prairie. This central Missouri prairie was acquired in 1957 by the University of Missouri-Columbia, with the help of the National Science Foundation, The Nature Conservancy, and the cooperation of the owners.

Eight years after a directive was issued, the Conservation Commission, in 1959, bought 1,680 acres of rolling farm land, of which 1,360 acres was virgin tall-grass prairie, for prairie chickens. This area, known as Taberville Prairie, is located in western St. Clair County just a few miles from the Osage River and north of El Dorado Springs (Figure 3). A second parcel of 85 acres of virgin prairie known as Milo, was purchased a year later in Vernon County, south of Nevada. Both areas are used by



Courtesy University of Missouri Press

Acres of Native Prairie in 15-County Area Before the Plow*			
Barton	328,448	Jasper	283,648
Bates	414,464	Lawrence	135,040
Benton	118,528	Morgan	75,392
Cedar	106,496	Newton	102,336
Dade	157,632	Pettis	323,456
Dallas	40,384	St. Clair	191,168
Henry	318,080	Vernon	396,736
Hickory	61,312		

*According to land office survey records, courtesy Walter A. Schroeder, Dept. of Geography, University of Missouri - Columbia.

Figure 1. Pre-settlement vegetation of Missouri, and acreage of native prairie in a 15-county area in southwestern Missouri before settlement.

prairie chickens and have been included as natural areas in a state preserves system.

The pure prairie preservation movement began with an article in the *Conservationist* magazine in 1965 and brought such good response that a meeting was held in Columbia, in May, 1966, to explore the possibility of forming an organization.

The group of 15 people decided a specialized conservation organization was necessary if significant amounts of native prairies were to be saved. An organizational meeting was held in October, 1966. The little group of some thirty people who organized the Foundation has grown to 450 on the membership roles and includes people from a broad spectrum of vocations and backgrounds.

The accomplishments of the Foundation in the first two years of life were mostly limited to organizational chores. The action began in 1969 with the purchase of a 40-acre prairie parcel in Pettis County south of Sedalia. Friendly Prairie may have been the most important of all prairies to The Foundation simply because it was the first. It assured the conservation watchers that The Foundation was not a "paper tiger" on prairie preservation. It instilled confidence in the board as to its purpose in meeting the challenge. It meant The Missouri Prairie Foundation was for real.

The Foundation, in 1970, bought Golden Prairie, a 260-acre tract in Barton County east of Lamar. This was a significant transaction because the area was large enough to show the true

MISSOURI

CONSERVATION COMMISSION

PRAIRIE CHICKEN RANGE 1940

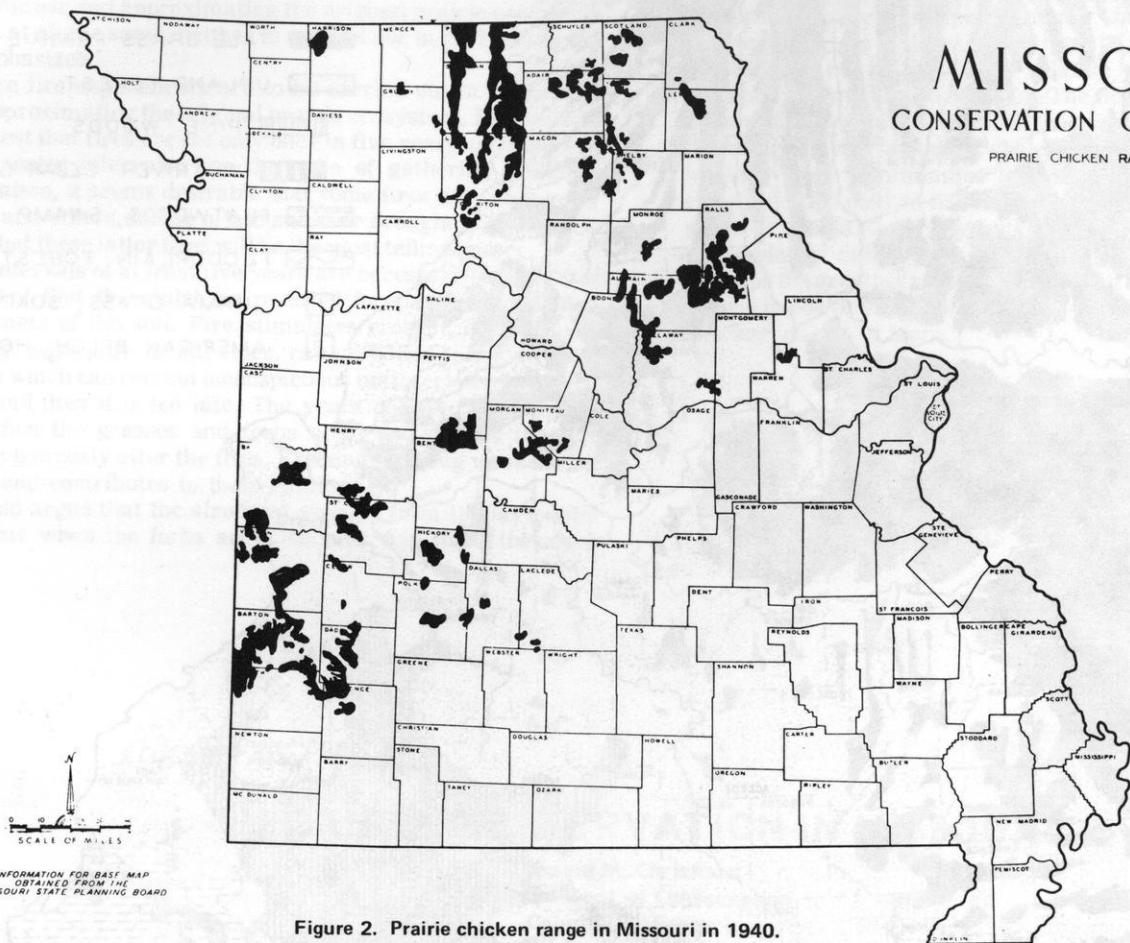


Figure 2. Prairie chicken range in Missouri in 1940.

character of prairie with the space and sweep to include a great variety of fauna and flora. Also, an option was taken to purchase an adjoining 60 acres of prairie. The use of \$54,000 by an agreement with Mr. and Mrs. Jamerson C. McCormack assured the purchase of Golden Prairie.

The most recent acquisition by the Foundation is a beautiful 160-acre native prairie with a rich variety of plant and animal life in western Dade County. Whereas, the Golden Prairie acquisition was largely the result of one source of money, Penn Sylvania Prairie exemplified broad-based financing, primarily by little people with big hearts. Encouragement was given potential contributors by the Natural Area Council who agreed to match any contribution of \$100 or more. As a result, about half of the purchase price of \$32,000 was matching funds from the Natural Area Council, a reflection of the sizeable gifts from little people. Presently negotiations have been initiated to add another 160 acres of prairie to this unit.

Early this year, The Nature Conservancy purchased 1,115 acres of native prairie in Vernon County bounding the Department-owned Milo Prairie on three sides. The acquisition of Osage Prairie represented the preservation of a significant tract of prairie arranged through The Missouri Prairie Foundation between the owners and the Conservancy.

This has been the extent of prairie preservation in Missouri to date but there is no room for complacency. Last November the Board of The Missouri Prairie Foundation adopted a set of goals for preserving Missouri's native prairie. No conservation agency or organization in the state, until then, had set forth objectives to encourage the preservation of this unique natural resource. The plan known as Acquisition 87, urges conservation agencies and organizations to preserve by acquisition, seven-



Figure 3. D. M. Christisen among indiangrass in Taberville Prairie, October, 1965. (Photograph by Don Wooldridge, Missouri Conservation Commission).

NORTHERN PRAIRIES - 1,000 ACRES

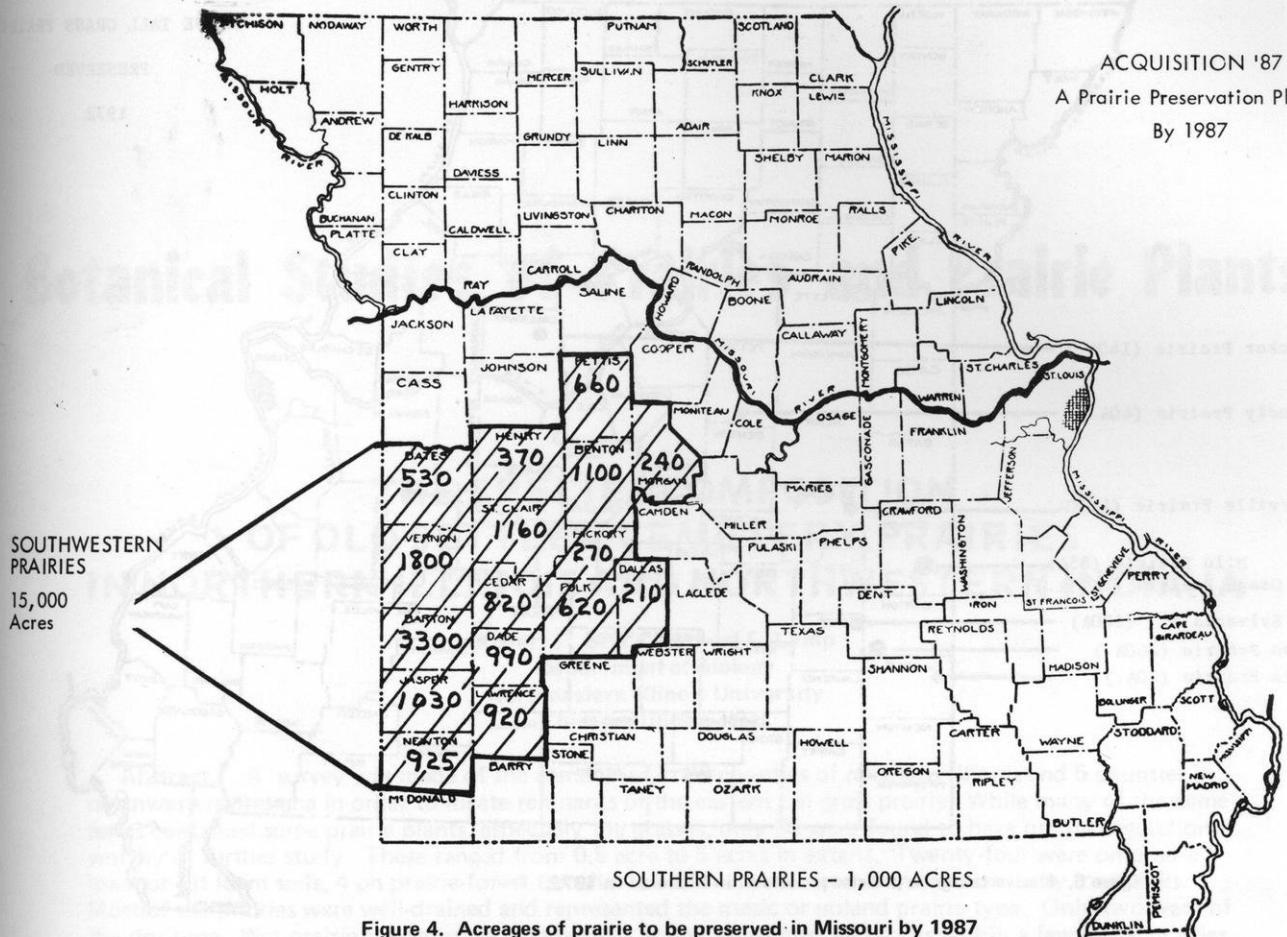


Figure 4. Acreages of prairie to be preserved in Missouri by 1987 according to plans of the Missouri Prairie Foundation.

teen-thousand acres of native prairie; less than one-tenth of one-percent of the original grassland, by 1987. These goals include a call for the preservation of 15,000 acres of residual prairie in southwest Missouri. The southwest is further sub-divided into sixteen county units with acreage goals set for each county (Figure 4). Obviously it is an ambitious program but not without promise providing conservationists can pool their talent and resources on the project. The one great fear is that the acreage of prairies now present in each county will shrink below the goals declared even before action can be taken to preserve it.

Prairies are destroyed in many different ways. Plowing and over-grazing are the foremost decimators of prairie. Unfortunately, Missouri has some extensive beds of soft coal, shallow enough for strip mining. Much of it is in the prairie region. Mining activity has destroyed an unknown acreage of prairies and continues to be a factor in the attrition rate as return from mineral rights exceeds agricultural values.

The Missouri Prairie Foundation has a relationship with a power plant which touches on the matter of strip mining. A steam-powered generator plant, using strip mine coal as a source of fuel, was constructed on an 80-acre native prairie. Representatives of the Foundation contacted the private utility company and learned that the officials were receptive to a management plan, setting aside the prairie as a preserve to be viewed by the public. A joint agreement to this effect was formalized in 1970.

Undoubtedly the company will reap some much needed good-will publicity from this agreement and The Foundation will have gained access privileges for the public to view a native prairie.

ACQUISITION '87
A Prairie Preservation Plan
By 1987

Whether this action will do more than forestall the destruction of the prairie is not known. If the public builds up awareness and interest in the area, then it will become increasingly difficult to destroy the prairies without embarrassment and public furor.

Acquisition of a prairie does not guarantee salvation. Prairies require a form of management to survive. Prior to settlement, periodic fires and intermittent grazing had a decided impact in determining the nature of the prairies. Today, over-grazing and protection from fire have degraded or even destroyed some prairies. Fire, grazing, and mowing (for hay) are valuable tools in retaining the character of the prairie and maintaining the prairie community. Both the Department and The Foundation use one or more of these tools to preserve their prairies.

Success in the preservation of prairies depends on reaching people and communicating with them. It requires education and publicity. The Missouri Prairie Foundation has been able to reach people by direct mail, newspaper stories, magazine articles, photo exhibits and a movie film. Radio and television have not been utilized to any extent as yet but hold great promise, not only for publicity but for education of the public in the preservation of prairies. Each prairie preserved, in itself generates community interest. Prairies are less spectacular to the public eye than a snow-capped mountain or a redwood forest, but we people are beginning to show maturity and depth of understanding with an awareness of the whole environment including deserts and prairies. The people of Missouri were ready to preserve prairies in 1966.

If the goals set forth in Missouri are to be achieved, it will mean acquiring over 13,000 acres of prairie in the next 15 years, about double that preserved to date. It will be no small chore. We can only hope there will be native prairie to preserve after

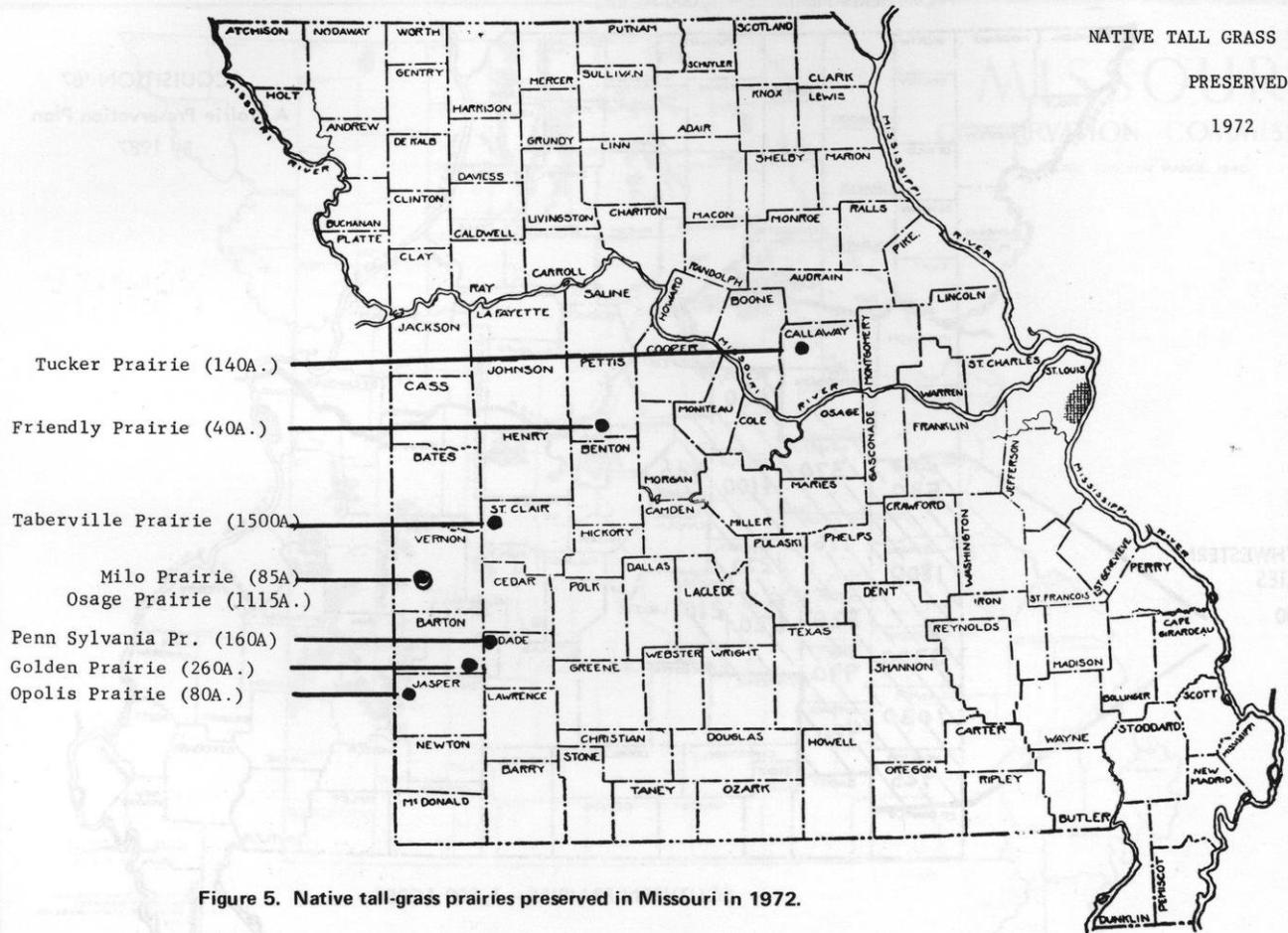


Figure 5. Native tall-grass prairies preserved in Missouri in 1972.

1980 in Missouri. Much will depend on the cooperation and awareness of the public to the impending loss of this natural resource.

If it were not for the elderly farm-owners who have maintained their prairies as valuable assets to their farms, few prairies would exist today. It is an interesting paradox. The new breed of farmers often are not appreciative of prairies, yet across the spectrum of conservation today, the younger generation is immensely concerned with environmental problems. The reason for this contradiction seems to be a matter of economics. The young farm owner, burdened with high overhead costs, plus the steep cost of land and loans, must be fiercely competitive to survive. He has virtually no cultural nor economic experiences with native prairies in an agribusiness world which promotes fertilizers, herbicides, insecticides, irrigation, and cash crops. As a result, more and more prairie is turned upside-down with little thought to heritage, esthetics, and destruction of an eco-system thousands of years old. These are the intangibles which escape our system of cash values. Fortunately, some beautiful prairies are being saved by concerned people.

In summary, the University of Missouri-Columbia, has acquired an invaluable prairie laboratory of 140 acres; the

Department of Conservation, with expenditures of nearly \$150,000, has preserved two native prairies of 85 and 1,360 acres. The Missouri Prairie Foundation has invested over one hundred thousand dollars in acquiring three virgin prairies of 40 acres, 260 acres and 160 acres. It has an option to purchase 60 acres and a joint agreement with a utility company to preserve nearly 80 acres of prairie. The Nature Conservancy has purchased 1,115 acres of prairie. This represents a total of 3,160 acres of virgin prairie (7 parcels) acquired in the past 12 years by the efforts of The State, The Foundation, and The Conservancy with the help of several other groups and many individuals (Figure 5).

The prairie national park concept came too late for Missouri to receive consideration as a potential site for a park. The great extensive prairies were broken into pieces a few years after Lewis and Clark pushed up the Big Missouri. This nation still has one last chance to set aside grassland parks in other states more fortunate than Missouri. No longer is it a matter of choice for Missouri; effort now must be confined to the preservation of the remnants, but even these prairies sparkle like jewels amidst the drab, mono-cultured landscape of corn and soybeans. Missouri people will continue to preserve a bit of their rich prairie heritage, for wherever there are prairies, there is fullness of life for those who see and enjoy.

Botanical Studies of Prairies and Prairie Plants

THE SPECIES COMPOSITION OF OLD SETTLER CEMETERY PRAIRIES IN NORTHERN ILLINOIS AND NORTHWESTERN INDIANA

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Abstract. A survey was made of the cemeteries in 36 counties of northern Illinois and 5 counties in northwestern Indiana in order to locate remnants of the eastern tall-grass prairie. While many of the cemeteries contained some prairie plants, especially the grasses, only 35 were found to have prairie vegetation worthy of further study. These ranged from 0.5 acre to 5 acres in extent. Twenty-four were on prairie loam or silt loam soils, 4 on prairie-forest transitional silt loam soils and 7 on sand or sandy loam soils. Most of the prairies were well-drained and represented the mesic or upland prairie type. Only two were of the dry type. Wet prairie species were occasionally found in isolated wet spots within a few mesic prairies. Over 130 species of prairie plants were found in these cemetery prairies, many of them rare within the state and the first to be recorded for their respective counties. In general, they contained over 40 different prairie species per acre. The richest cemetery prairie studied contained over 70 species per acre. The dominant grasses were prairie dropseed (*Sporobolus heterolepis*), big bluestem (*Andropogon gerardi*), little bluestem (*Andropogon scoparius*), prairie panic grass (*Panicum leibergii*), Indian grass (*Sorghastrum nutans*) and porcupine grass (*Stipa spartea*).

SOME STUDIES IN DAKOTA SANDSTONE PRAIRIES OF KANSAS

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One of the reasons for submitting this title was that these Dakota Sandstone Prairies of Kansas have never been studied to any extent and I have always wanted to study them. Another reason for submitting the title was to make sure that I did get some studies made but perhaps the most important reason was that they are some of our most beautiful and extensive grasslands in Kansas. We refer to them as the Dakota Sandstone Prairies because they are located on the Dakota formation which consists of old delta deposits of rivers that used to run through this area toward the central basin. Some of the iron-containing Dakota Sandstone is hard while some lacking iron is quite soft. The hard Dakota Sandstone is sometimes used as a building material and very frequently, especially recently, has been used as landscape material for rock gardens, backyard

fountains, etc. In certain places the Dakota Sandstone rock is covered with lichens which add to its decorativeness. The Dakota Sandstone prairies in Kansas lie just west of the Flint Hills area and just east of the Bluestem-Grama prairies of central Kansas.

You can stand on top of the hills in these prairies and look for miles and miles without seeing anything but native grassland interrupted only partially by trees in various locations or by livestock grazing upon it. The grasses grow beautifully in protected areas such as fenced out right-of-ways, ungrazed corners, cemeteries, and other remnant areas.

I have been traveling for several years on I-70 observing a fenced right-of-way and making mental notes to myself that some day I was going to stop and study the area. We studied two

prairie remnant areas in the summer of 1972. Several years ago F. W. Albertson and I made a study of 14 other undisturbed stands of Dakota Sandstone Prairies. Even though some of the data represents as many as 16 stands I still feel that we do not have sufficient data to fully understand the Dakota Sandstone Prairie.

Even though we must label these floristic studies preliminary, we found 142 separate species in 42 different families with the most important families being Gramineae, Asteraceae, and Fabaceae. Most grassland areas in the central U.S. have the same three important families.

The species nearest to each of 500 single points was recorded in each stand. Percent composition is the percent of the total points at which each species occurred in the 16 stands. Frequency, the percent of plots in which each species was found, was recorded in 100 0.25 m² (100 x 25 cm) plots in each of two stands.

Big bluestem is probably the most prevalent grass species, both from the standpoint of composition and frequency (Table I). However, little bluestem is also quite important as are switchgrass, sideoats grama, blue grama, and tall dropseed. Although not very important from the standpoint of composition fall panicgrass and fall witchgrass seem to be quite characteristic of these grasslands.

Table I. Dominant grasses in the Dakota Sandstone prairies of Kansas.

Species	% Composition (16 Stands)	% Frequency (2 Stands)
Big Bluestem	46.0	62
Little bluestem	15.1	43
Switchgrass	8.4	30
Sideoats grama	5.2	33
Blue grama	4.0	3
Tall dropseed	3.5	41
Buffalo grass	2.7	T
Fall panicgrass	1.9	26
Fall witchgrass	1.4	T
Plains muhly	1.0	1

This summer when we investigated these prairie remnants we found that the tops of the tall hills were not Dakota Sandstone but were limestone. As a matter of fact, this formation is a member of the greenhorn limestone from which fenceposts are made. One member of the greenhorn limestone is frequently referred to as fencepost limestone because of this use. About half way down from the top of the hill is a noticeable very dark green area. This dark green area lies above the Dakota Sandstone and is over a granerous shale material. The lower portion of hills in our study area was Dakota Sandstone.

The composition and fequency of the limestone areas, the transitional areas which are actually the shale areas and the sandstone areas are compared in Table II. Big bluestem is more common on the shale followed by the sandstone and least common on the limestone. On the other hand, little bluestem is more common on the limestone area. Sideoats grama is also more common on the limestone area but tall dropseed and indiangrass are more common on the sandstone. The presence of large amounts of big bluestem and switchgrass on the shale or transitional areas would indicate that there is considerably more water available in this area between the limestone and sandstone. There are a large number of springs found in the Dakota Sandstone area and it is assumed that many of them surface in this shale area. It is also interesting to note that Schribners' panicgrass and fall panicgrass were only found, to any extent at all, on the Dakota Sandstone.

Table II. Per cent composition and frequency of dominant grasses over three types of geological materials in the Dakota Sandstone prairies of Kansas.

Species	Limestone		Transition (shale)		Sandstone	
	% Comp.	% Freq.	% Comp.	% Freq.	% Comp.	% Freq.
Big bluestem	22.4	40	72.0	100	29.4	48
Little bluestem	23.0	100	T	T	19.1	68
Sideoats grama	11.2	100	5.0	24	7.4	56
Tall dropseed	2.9	36	1.0	36	8.1	48
Indian grass	5.3	48	1.0	4	4.4	48
Plains muhly	10.6	36	1.0	4	T	T
Switchgrass	9.4	68	16.0	48	T	12
Schribners' panicgrass	—	—	—	—	8.1	24
Fall panicgrass	—	—	—	—	14.0	44

In some of our earlier studies with Dr. Albertson, and in visiting with SCS technicians in the area, it seems that the Dakota Sandstone Prairie deteriorates more readily under grazing than the limestone prairies. The Dakota Sandstone prairies generally change from big bluestem-grama complex to a mixture of tall dropseed, little bluestem, and short grasses under moderate grazing and to a mixture of short grasses, weeds and less desirable panicgrasses under heavy grazing.

This beautiful natural prairie that we have in east-central Kansas, known as the Dakota Sandstone Hills, certainly needs to be studied much more thoroughly than it has been in the past. These few studies have sharpened my appetite and I hope that I have opportunity to study this type more in the future and perhaps encourage some other people to also make some studies.

SYSTEMS ANALYSIS OF A TALL-GRASS PRAIRIE¹

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DESCRIPTION OF THE STUDY AREA

The Osage Site represents the tall-grass prairie in the U.S. International Biological Program (IBP) Grasslands Biome. This research area is located on the Adams Ranch, 19 km north, and 5 km east of Shidler, Oklahoma, in Osage County, which is in the northeast corner of Oklahoma. The ranch (approximately 14,000 ha) is owned by Mr. K. S. Adams, and managed by Mr. Dick Whetsell. The Osage Site is located at an elevation of 375 m on predominately rolling topography. Long term climatic records are available from the U.S. Weather Bureau Station in Pawhuska, Oklahoma, which is 32 km southeast of the ranch.

For the past fifty years or so, the grasslands of the prairie-forest border region have been studied by numerous investigators. Although there are some exceptions, most of these previous studies have involved the analysis of only one trophic level at a time. This paper represents a preliminary attempt to evaluate simultaneously some information from various trophic levels as they operate in the movement of carbon through a tall-grass ecosystem.

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The average January temperature is 2.70°C and the average July temperature is 27.30°C. The average annual precipitation is 100 cm, with 60 cm occurring in the April-September warm season. The growing season is 205 days.

The soils of the Osage Site are Brunizems, and of the Labette-Summit-Sogan association. These are darkly colored soils with mostly clay-like sub-soils developed on shales, sandstones, and limestones under tall-grass. Specifically, the experimental area is on a Labette soil with a dark, silty clay, A horizon 30 to 45 cm in depth. The B₁ is dark brown, 45 to 90 cm; the B₂ is reddish brown, 60 to 90 cm; the B₃ is a brown, silty clay, 90 to 120 cm; and most of the bedrock is limestone at 1 to 2 m.

The vegetation on the study plot is a typical tall-grass prairie dominated by little bluestem (*Andropogon scoparius*), switchgrass (*Panicum virgatum*), and Indian grass (*Sorghastrum nutans*). This 5 ha area has been ungrazed for about fifteen years though it was mowed for prairie hay in 1965. During the 1970 growing season, the research area was studied intensively at several functional levels (Blocker and Reed, 1971; Harris, 1971; Hoffmann, Jones and Genoways, 1971; Risser, 1970, 1971; Wiens, 1971).

METHODS

A small micrometeorological station was established on the study site and the accumulated precipitation was measured either bi-weekly or monthly in a standard Weather Bureau raingauge, 76 cm above the soil surface. Wind was measured with a totalizing anemometer mounted 153 cm above the soil surface and solar radiation was recorded with a pyranometer located at a height of 76 cm. Air temperature and humidity were continuously measured with two recording hygrothermographs, 31 and 153 cm high, respectively. Continuous soil temperature was recorded at depths of 1 and 10 cm below the soil surface. Soil water was measured by the gravimetric technique from 6 sampling points each time the herbage data was collected.

The 5.0-ha ungrazed treatment was divided into two replicates of equal size, and a grid was established to coordinate sampling activities. Clipped quadrats, soil cores, insect traps, etc., were located within selected 18- and 30-m blocks on a given sample date. The location of each sample was recorded so that the same area would not be sampled repetitively. Each replicate was sampled once a month during April, May, September, October, and November and twice monthly during June, July, and August. Belowground biomass samples were collected in June, July, August, September, and November.

Primary producers. Herbage biomass was sampled with 0.25 m² quadrats. The number of quadrats was adjusted so that the standard error of the total biomass was estimated within 10 percent of the sample mean at the 80 percent confidence level. This represented between 3 and 10 quadrats per replicate per sample date. In each quadrat the major species were separated: *Andropogon scoparius*, *A. gerardi*, *Panicum virgatum*, *Sorghastrum nutans*, *Sporobolus asper*, *Bromus japonicus*, *Poa pratensis*, and *Ambrosia psilostachya*. The remainder of the plants were classified as miscellaneous grasses, forbs, or sedges. In each of these categories the material was harvested and divided into live standing crop, previous year's standing dead, and current year's standing dead. Each sample was dried at 600°C for 48 hr and weighed. Litter was collected from each of the quadrats, dried, weighed, ashed, reweighed, and was expressed as ash-free weight. Belowground biomass was collected with a hydraulic corer to a depth of 90 cm. Two cores were taken from each quadrat, and each core was divided into depth segments of 0 to 5, 5 to 10, 10 to 20, 20 to 30, 30 to 50, 50 to 70, and 70 to 90 cm. Root cores were analyzed separately from crowns and washed through a 30-mesh screen dried, weighed, ashed, reweighed, and were expressed as ash-free weight.

The rate of litter accumulation was measured by installing 36, 15 x 15 cm, 2-mm mesh screen wire quadrats on the soil surface.

These screen quadrats were nailed to the soil surface, and the material which fell on the screen was collected at five different sampling dates throughout the season.

The rate of litter decomposition was measured with 15 x 15 cm, 2-mm mesh screen wire litter bags which were established on May 26. The material placed in the bags was freshly fallen litter, and the amount coincided with that normally present on the soil surface at that time. Sub-samples of these bags were collected twice during the growing season, September 30 and November 14.

Invertebrates. Invertebrate sampling was conducted to obtain quantitative estimates of numbers and biomass of major groups. A 0.5-m² modified "quick trap" patterned after Turnbull and Nicholls (1966) was used. After the trap was dropped the enclosed vegetation was clipped and removed to a paper sack. The interior of the trap was then vacuumed with a "D-vac" collector and the material returned to the laboratory in ice chests for separation. A total of 20 samples, five samples from each of two replicates and for two treatments each, were taken adjacent to the herbage biomass samples at each collecting period. Samples were collected on July 3, July 16, August 3, August 17, September 27, October 25, and November 23. These dates correspond closely with the dates of vegetation sampling with the exception of the November collection, which was taken late and during sub-freezing temperature.

Laboratory separations were done in four stages:

- (1) Extraction of the D-vac collections into 70 percent isopropyl alcohol from Berlese funnels (48 hr).
- (2) Hand-sorting of the D-vac collections after removal from the funnels.
- (3) Extraction of vegetation clippings into 70 percent isopropyl alcohol from Berlese funnels (48 hr).
- (4) Hand-sorting of vegetation clippings after removal from funnels (when necessary).

Insects were then separated into families (when possible) and into life stages. Representatives of each taxon were removed and oven-dried at 600°C for 24 hr and weighed for biomass determinations.

Birds. Breeding bird populations were censused between June 12 and June 15 on one 8.4-ha plot located in the grazed treatment. Populations were censused using the territory flush technique (Wiens, 1969): singing individuals were approached and flushed from their display sites, and their movements were recorded on a scaled field map of the plot. Individuals tended to remain within clearly delimited areas during these flushings, and these areas corresponded closely with breeding territories. To estimate population densities, territories of all individuals present on the plot were mapped; and, for each species, the number of territories (by area) present in the 8.4-ha plot was determined. This number was then multiplied by a mating system conversion factor (generally 2.0, except for polygynous species) to account for the presence of females, and the estimate of plot population density was converted to individuals per/ha. Changes in population density throughout the season were not directly measured, but were estimated from phenological data presented by Sutton (1967) and Johnston (1964) using the mid-June census value as an estimate of the stable breeding population density. Recruitment rates were also estimated using information on clutch sizes and hatching success from the works of Sutton and Johnston, from the studies of Ryder (personal communication) and his students at Pawnee, and from Maher and Felske (personal communication) in the Canadian IBP Grassland studies at the Matador Site, Saskatchewan. Bird weights were recorded from specimens collected in other portions of the Adams Ranch and were converted to dry weight by assuming a water content of 70 percent. Dietary composition was estimated from a preliminary analysis of the stomach contents of specimens collected at Osage; and for the four species recorded in the census plot, these values were:

Upland Plover (<i>Bartramia longicauda</i>)	100	insect
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Eastern Meadowlark (<i>Sturnella magna</i>)	100 insect
Dickcissel (<i>Spiza americana</i>)	40 seed; 60 insect
Grasshopper Sparrow (<i>Ammodramus savannarum</i>)	30 seed; 70 insect

Small mammals. Populations were sampled by means of adjacent live-trap and snap-trap grids. Both grids were a square of 12 x 12 stations (144 total). The interval between each station in the rows and columns was 15 m, giving the grid a minimum area of 2.76 ha. The live-trap grid was located on the east end of the ungrazed treatment, except for rows 11 and 12, which were in an area that was cultivated 12 years ago. The snap-trap grid was located just west of the ungrazed treatment in an area which was lightly grazed during parts of the winter season.

Two Museum Special snap-traps were placed at each station on the snap-trap grid, and two aluminum Sherman live-traps were placed at each station on the live-trap grid. All traps were prebaited for 5 days before they were set to catch animals. Traps were baited with a mixture of oatmeal and peanut butter. After the prebaiting period all traps were set for 10 consecutive days unless rainy weather interfered.

Decomposers. Bacterial biomass was calculated by the plate-count method on samples taken from a soil depth of 0 to 50 cm. Plate counts were done using plate-count agar with incubation at 28°C for 5 days. Colonies counted included actinomycetes for biomass calculations. The average cell was assumed to be a sphere with an average volume of $1\mu^3$ and 80 percent water.

Fungal hyphae measurements were made on diluted water-soil (not homogenized) spread over an area of 1 cm² and stained with dilute methylene blue. With a calibrated ocular and camera lucida a map measurer was used to trace the total length of hyphae in 100 microscopic fields per dilution. Knowing the area counted, the total length per g of soil was calculated. The average fungal strand diameter was assumed to be 5 μ , had a specific gravity of 1.2 and a water content of 90 percent.

To estimate carbon dioxide evolution in the field, 10 ml of NaOH were exposed in a 100-ml beaker in a closed system of 10 cm in diameter for 24 hr. The absorption chamber was a metal cylinder enclosed in a tightly fitting plastic bag, and it was driven into the soil. These systems were shaded where necessary. Measurements were taken from both bare soil and chambers containing two to four crowns of *Andropogon scoparius*. The CO₂ absorbed was determined after barium chloride precipitation of the carbonates and titration of the residual alkali with standard HCl using phenolphthalein indicator.

ASSUMPTIONS AND CONDITIONS FOR THE OSAGE COMPARTMENT MODEL

The sampling procedures were designed to capture the dynamics of the system. For example, Figure 1 depicts the changes in biomass for each major producer component throughout the growing season (A, aboveground live material; B, belowground live plus dead material; C, standing dead aboveground material; D, litter). Between each of the state variables, there is a rate at which carbon is transferred from one compartment to the next (E, rate of transfer from live material to standing dead material; F, rate of annual litter accumulation; G, rate of litter decomposition beginning in June of the current season). Similar relationships can be determined in each trophic level. The following compartmental model is an attempt to examine the state variables and transfer rates in a number of functional groups of organisms.

In the preliminary calculations of this compartment model (Figure 2), when possible, all principal system variables were expressed as g/m² and rates were expressed as g/m²/day. The calculations could have been converted to energy (calories) to more easily express the respiration rates.

Eventually the model will be converted to a dynamic model with time-varying coefficients; in fact, the primary producer part of the model is already at this stage. However, during the

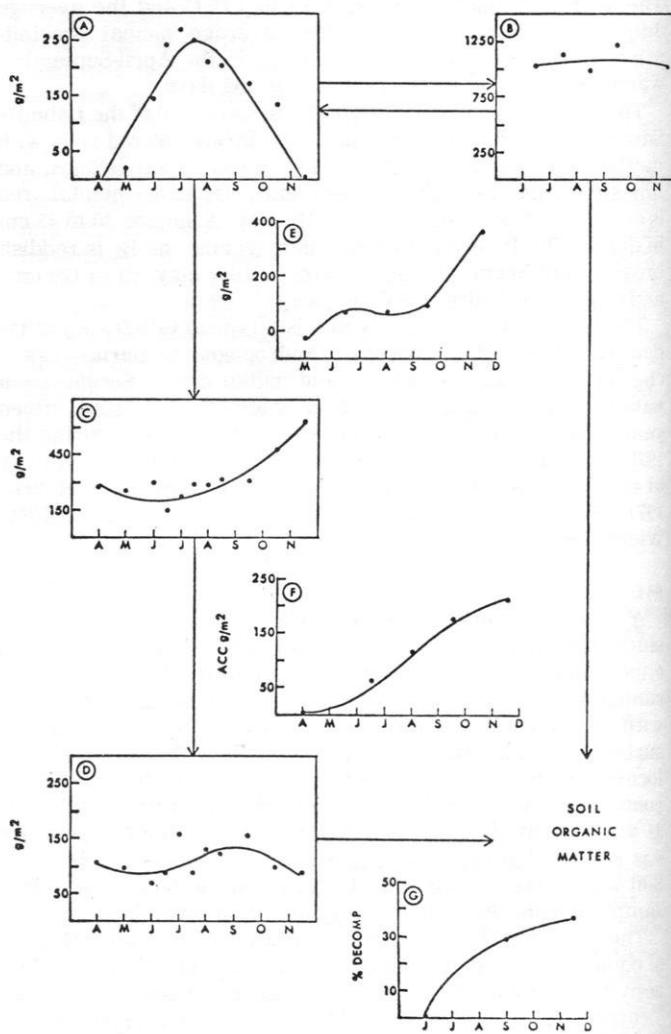


Figure 1. Producer dynamics of a tall-grass ecosystem. See text for explanation.

1970 season, small mammals were measured only twice and birds only once. Insect measurements were made throughout the year, but measurements were initiated fairly late in the growing season. Since time-series measurements were not available for all compartments, this model will employ the producer biomass values and rates which occurred nearest the date of peak live standing crop. For the other compartments data from the sample interval nearest this date (1 July 1970) have been utilized. Data for the microorganisms, primary producers, invertebrates, small mammals, and abiotic factors were obtained on the ungrazed treatment. The bird studies were performed on the grazed treatment adjacent to the ungrazed treatment.

Compartment Values and Transfer Rates

Primary producers. The value for the total incoming solar radiation is the amount of energy available on a clear day at the approximate date of the peak live standing crop. The highest radiation value was 1.3 cal/cm²/min, and the daily value was calculated from the solar radiation recorded on the strip chart of the pyranometer.

The photosynthesis rate [$\gamma(0,1)$] was calculated from gas exchange rates determined under laboratory conditions for 40-day-old seedlings of *Andropogon scoparius*, *A. gerardi*, *Sorghastrum nutans*, and *Panicum virgatum*. The measured values were 8.8, 6.3, 18.8, and 19.0 mg CO₂/g/hr, respectively. These rates were prorated among these four species, and the proportions were used to calculate daily photosynthesis for the

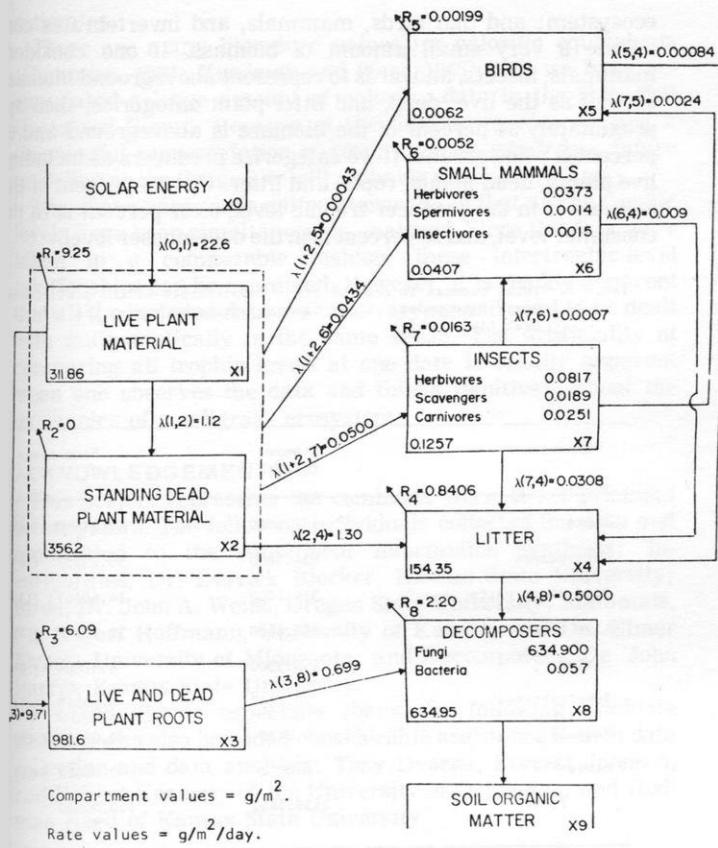


Figure 2. Osage compartment model.

total aboveground biomass. The final gas exchange values for each of the four species were summed to provide a value of 19.59 g CO₂/m²/day as the fixation rate at peak live standing crop.

Respiration was calculated in a similar manner using laboratory data for *Andropogon scoparius*, *A. gerardi*, *Sorghastrum nutans*, and *Panicum virgatum*. The respective respiration rates were 1.9, 1.6, 1.5 and 3.4 mg CO₂/g/hr. At peak standing crop the respiration component is 13.61 g CO₂/m²/day, and gross photosynthesis (respiration component is 13.61 g CO₂/m²/day, and gross photosynthesis (respiration plus net photosynthesis) is then assumed to be 33.20 g CO₂/m²/day.

This estimate of net photosynthesis [$\gamma(0,1)$] is probably an overestimate since the rate studies were conducted on 40-day-old seedlings which presumably have a higher proportion of photosynthetic tissue than older plants which constitute a majority at the stage of peak standing crop. Both photosynthesis and respiration rates were calculated at 27°C, and previous experimental work in our laboratory has shown that photosynthesis rates increase up to about 35°C. During July the average daily temperature is considerably above 27°C, so that respiration is probably higher than the laboratory conditions which may lead to an underestimate. Since net photosynthesis is probably an overestimate and respiration an underestimate, there may be a compensation in the final photosynthesis value.

The transfer rate from the live biomass compartment to the standing dead compartment was estimated from root turnover and root respiration. Root-turnover rate is calculated as 26 percent per year, root respiration was estimated at 0.5 g CO₂/g/hr, and it was assumed that 75 percent of the root biomass was respiring.

The above calculations suggest a net gain in biomass of 2.50 g/m²/day at the time of peak standing crop which conforms with the field data. If one assumes a caloric value of 4.1 cal/g, then the photosynthetic fixation of energy on a clear day (1 July 1970) is approximately 1.2 percent of the incoming solar radiation.

Birds. The calculations of the bird compartment were based upon procedures of bioenergetic estimation developed more fully elsewhere (Wiens and Innis, in prep.). Briefly, existence-energy demands per individual were calculated for each species using weight-dependent, temperature-dependent metabolic functions modified from Kendeigh (1963, 1970) and the temperature records for the Osage Site. This estimate was adjusted for activity by a factor of 1.4 (Schartz and Zimmerman, 1971) and was multiplied by population density to obtain the population energy demands for the species. The additional energy demands placed on the system by the production of young were considered by projecting changes in population density resulting from reproduction and adding the estimated existence and growth-energy requirements of young to those of the adults.

Bird populations were not censused at the time of peak standing crop of the vegetation components. The bioenergetic estimates used to obtain the values reported here were obtained by projection from the mid-June census estimate of adult population densities to values for July 1. Estimated avian immigration and emigration rates for the Osage populations are as follows:

Immigration Rates	
April 1-30	0.00017 g/m ² /day
May 1-15	0.00500 g/m ² /day
May 16-20	0.00026 g/m ² /day

Emigration Rates	
August 1-15	0.00029 g/m ² /day
August 16-31	0.00010 g/m ² /day

Estimates were not projected beyond August 31. These values are not included in the overall compartment model.

Compartment values for biomass flux through the bird populations were calculated from the bioenergetic estimates for July 1. The energy intake by each species was divided into seed and insect sources according to the dietary composition values given in the methods section of this report; these were then converted to grams dry weight by assuming that seeds had a mean caloric value of 5.2 cal/g dry weight and insects had a value of 5.6 cal/g dry weight. A digestive efficiency of 70 percent was assumed so that the contribution to the litter compartment via egestion of undigested food and excretion was 30 percent of the food-intake rate. Respiratory rate was calculated by the difference (Respiration = Gross Intake - Egestion). The estimated inputs for bird biomass were from plants (seeds—0.00043 g/m²/day) and invertebrates (0.0024 g/m²/day) and transfer to litter (0.00084 g/m²/day). Avian standing crop on July was estimated as 0.00620 g/m².

Small mammals. Small mammals were sampled on May 28 and August 27, so biomass measurements in the compartment model represent the mean of these two dates. Field measurements were in terms of liveweight and were converted to dry weights by assuming a water content of 70 percent (Golley, 1960). Nearly 90 percent of the biomass was contributed by *Microtus ochrogaster*. Consumption rates for the various species were derived from Golley (1960) for *Microtus*, McNab (1963) for *Reithrodontomys*, Pearson (1947) and Rood (1958) for *Blarina*, and Douglas (1969) for *Spermophilus*. The rate of food consumption for *Sigmodon* was assumed to be similar to that of *Microtus*. *Cryptotis* made negligible contributions to the total biomass and was simply estimated. Most of the material flow into the small mammal compartment was via the foliage-eating *M. ochrogaster*. The material transfer from the aboveground vegetation to the small mammal biomass was calculated as 0.107 m²/day from the literature. The vegetation at this date was approximately 60 percent water, so the consumption rate was converted to dry weight. Similarly, the material transfer from the invertebrate compartment was converted to dry weight by assuming a 30 percent dry weight of invertebrate material. The contribution of the small mammal compartment to the litter compartment was calculated on the basis of

estimates made by Golley (1960) concerning caloric losses in feces and urine and are thought to be on the order of 20 percent of the total energy intake into the small mammal compartment or 0.009 g/m²/day dry weight.

Respiratory losses were estimated by employing values from McNab (1963), Pearson (1947, 1948, 1960), and Weigert (1961). Overall, small mammal respiration was estimated to be about 5,000 cc oxygen/ha/hr or 11.8 cc O₂/m²/day. This may be converted to .057 cal/m²/day. For the compartment model, respiration (R₆) may also be estimated by the differences between inputs and outputs and is approximately 131 cal/m²/day; or may be converted and is (44 x 10⁻⁶) x cc O₂/m²/day = g/m²/day. These two estimates of respiration are of the same order of magnitude, and the discrepancies are probably due to the underestimation of rates of active metabolism by small mammals, failure to include any energy contribution to small mammal production rates, and/or overestimation of energy intake in food. Considering the many assumptions involved and their relative lack of quantitative precision, a two-fold discrepancy represents reasonably good agreement.

Invertebrates. The invertebrate biomass was partitioned among herbivores, scavengers, and carnivores. Of the total biomass in the invertebrate compartment (0.1257 g/m²) the herbivores contributed approximately 65 percent, the scavengers 15 percent, and the carnivores 20 percent. It was estimated that the invertebrates consumed approximately 10 g of primary productivity throughout the season, and assuming a 200-day growing season the daily rate is approximately 0.05 g/m²/day. The literature suggested that 50 percent or more of the material (0.0250 g/m² day) was transferred directly to the litter compartment. The remainder of the litter transfer (Figure 1) includes transfer through insect and other secondary consumers as well as carcass values of dead insects. The respiration was assumed to be approximately 65 percent of the assimilated biomass or 0.0163 g/m²/day. The amount of transfer from invertebrates to birds was estimated to be 0.0024 g/m² by Wiens and Innis (See Compartment Values and Transfer Rates; Birds).

Litter. The litter biomass at peak standing crop was 154.35 g/m². The litter screen experiments provided an approximate rate of 1.3 g/m²/day for material moved from the aboveground compartment to the litter compartment. At the time of peak standing crop of the aboveground components the litter biomass was essentially constant. Data from litter-bag experiments indicated that the rate of transfer from litter, through decomposers, to soil organic material was 0.5 g/m²/day. Inputs from the birds, mammals, and invertebrates are included as suggested from these compartments. No data were available for litter respiration, so the value of 0.8406 g/m²/day was calculated as the difference between the other output and the inputs.

Decomposers. The decomposer biomass was determined on June 19 and September 30, so the biomass estimates represent averages between these two dates. The amount of CO₂ released, recalculated as g C/m²/day, was obtained from cores in the laboratory and also represents a mean of the two sampling dates. The fungal biomass and bacterial counts represent values to a depth of 50 cm in the field. The inputs to this compartment are represented by the transfer of material from the litter (0.5 g/m²/day) and from the roots (0.699 g/m²/day), and are less than the measured output of respiration (2.20 g/m²/day). This would indicate that at the time of peak standing crop for the live material, the decomposers are working on stored organic material in the soil.

SUMMARY

Since all this information has been collected on one grassland at roughly the same time, a number of intriguing comparisons are possible. Table 1 shows the amount of biomass in each compartment. It is obvious that the greatest percentage of biomass (66 percent) is in the producer component of the

ecosystem; and that birds, mammals, and invertebrates contribute a very small amount of biomass. If one considers mammals, insects, and birds to represent aboveground biomass as well as the live, dead, and litter-plant categories, then approximately 34 percent of the biomass is aboveground and 66 percent is belowground. If we categorize producers as including live plants, dead plants, roots, and litter, then 74 percent of the biomass is in the producer-trophic level, 0.007 percent is in the consumer level, and 26 percent is in the decomposer level.

Table 1. Total biomass in each of eight compartments of the preliminary Osage Site model. These biomass estimates are at the time of peak live herbage.

Compartment	Biomass (g/m ²)	Percentage
Roots	981.6000	40.24360 (40)
Decomposers	634.9600	36.03207 (36)
Dead plant parts	356.2000	14.60347 (15)
Live plant parts	311.8600	12.78562 (13)
Litter	154.3500	6.32804 (6)
Invertebrates	0.1257	0.00515 (<1)
Mammals	0.0438	0.00180 (<1)
Birds	0.0062	0.00025 (<1)
Total	2439.1457	100.00000

At the time of peak live herbage standing crop, only the decomposer compartment shows a net loss in carbon. It should be recalled that litter "respiration" was calculated by differences since the net amount of litter showed very little change at this time of year. Clearly, then, the net change in the compartment model will be zero (Table 2).

Table 2. Summary of inputs and outputs of each compartment at the time of peak live herbage standing crop. All tabular values are in terms of g/m²/day.

Component	Inputs	Outputs	Net Change
Aboveground biomass	22.6000	19.0038	+3.5962
Belowground biomass	2.9200	6.7890	+2.9210
Birds	0.0028	0.0028	0.0000
Mammals	0.0441	0.0142	+0.0299
Insects	0.0500	0.0500	0.0000
Litter	1.3406	1.3406	0.0000
Decomposers	1.0990	2.2000	-1.0010

Throughout this data manipulation, estimates of respiration have proved to be difficult. Actual measurements were made in the laboratory for aboveground live material and in the field for the decomposer compartment. All other compartments have been estimated from literature values. The invertebrate section of this report has shown that because of substrate differences, laboratory techniques, etc., respiration should probably be included as caloric values. In fact, the estimates for small mammal respiration in this model are based on caloric

estimates.

There are many literature values for calorific equivalents (Cummins, 1967; Kendeigh and West, 1965), and we have accumulated a large amount of calorific data in the U.S. IBP Grassland Biome. Because of the difficulties of preparing a meaningful representation of respiration as g/m²/day, future modeling on the Osage Site will probably utilize cal/m²/day.

The above analysis is quite noteworthy in that all the trophic levels have been simultaneously analyzed. Since the data were taken in a comparable fashion, these intertrophic-level relationships can be examined. However, it is readily apparent that all the included data are time-varying and need to be dealt with mathematically in the same sense. The artificiality of comparing all trophic levels at one date is readily apparent when one observes the data and thinks intuitively about the mechanics of a tallgrass ecosystem.

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AZOTOBACTER OF THE KONZA PRAIRIE

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Abstract. A preliminary study of occurrence of *Azotobacter chroococcum* was made on Konza Prairie Research Natural Area, Geary County, Kansas, an area of native bluestem prairie, as a beginning of a study of nitrogen relationships in bluestem prairie. *Azotobacter* was abundant in soils near neutrality, and decreased in abundance with increasing acidity, being absent at pH values of 5.80 and below.

Although the nitrogen cycle has received extensive attention in cultivated soils (1), much less research has been centered on natural equilibrium situations such as the tall grass prairie. Because of the essential role of nitrogen in all biological processes and because much of the current data on the nitrogen cycle are derived from non-equilibrium plant and soil conditions of agricultural soils, considerable research on microbial nitrogen transformations has been under way in the various "biome" programs of the International Biological Programs (I.B.P.). The recent acquisition of Konza Prairie by the Kansas State University Endowment Association through financial aid from the Nature Conservancy has given ecologists in this area

the opportunity to initiate long-term studies in the typical bluestem grasslands. As part of the overall biological assessment of this area we have undertaken a limited study of the free-living nitrogen-fixing bacterium *Azotobacter* sp. with the intention of gradually accumulating data on all phases of the nitrogen cycle occurring in the Konza Prairie soils.

In considering the over-all nitrogen cycle of a grassland as compared with a cultivated soil, one immediately observes that the grassland much more closely resembles a closed-system than does the cultivated situation. Pasturing of grass with the subsequent removal of the nitrogen in animal protein gives a steady removal of a small amount of nitrogen. The influence of

fire also causes an increment of loss varying with the degree of leaching of the dead plant material prior to the burning. The loss of nitrogen through leaching would be expected to be small and likewise denitrification would also be minor. The summation of all nitrogen loss possibilities in the grassland would be of a much smaller magnitude than that removed in a high yielding crop. Just as the losses of nitrogen are low, so would be the inputs into the system. Practically the non-biologically fixed nitrogen from the air represents a low level but steady input into the soil.

The magnitude of biological fixation through the wild leguminous plants in symbiosis with root nodule bacteria very likely represents the major source of nitrogen in prairie soils. The plant ecologists are evaluating the productivity of the numerous Leguminosae. Most of these are nodulated during the growing season. The efficiency of this symbiotic relationship and the amount of nitrogen being added to the biological system each year represent an area of research being developed for the near future. The aerobic free-living *Azotobacter* may or may not play an important role in the nitrogen economy of the soil. Presently soil microbiologists do not agree as to the importance of this group of bacteria. If these *Azotobacter* are not present then, of course, they could fix no nitrogen. Since these bacteria may or may not be present in soils of this region our initial problem was to ascertain their presence or distribution in the Konza Prairie.

The methodology for isolating *Azotobacter* from soil is relatively simple yet accurate procedure. An agar medium devoid of fixed nitrogen is inoculated with crumbs of freshly collected soil. Following incubation at 30° C for five days *Azotobacter* colonies will be large gummy masses and other microbial development will be limited because of the lack of assimilable nitrogen. Purification and identification of the bacteria follow usual streak-plate methods.

The major factor limiting development of *Azotobacter* sp. in nature is the acidity of the soil or water. As early as 1918, Gainey (2) reported that these organisms were not found in soils below pH 6.0. Hence pH determinations were made on all soil samples collected in this study. The Konza prairie has a variety of soil conditions caused by the topography of the area. Fairly typical of the Flint Hills area of Kansas the highest elevations are extremely old, shallow and well-weathered soils. These lie above the Florence limestone and have been designated Florence cherty silt (or clay) loam. Since these have been weathering during the recent Pleistocene, they are low in exchangeable cations and generally acidic (pH 5.0-5.5). The Florence limestone plays a dominant role in maintaining the neutrality of the soil in its immediate area and in the soil zones developed at lower elevations. The soils of the Konza Prairie form a complex patchwork of types depending on slope, sedimentary accumulation, and drainage conditions. We have not attempted to characterize the area but rather have collected soil samples on various transects which gave a variety of pH conditions.

The results of the sampling and cultural studies are shown in

Table 1
Presence of *Azotobacter* in Konza Prairie soils is dependent on the pH of the soil. Results are shown after 5 days incubation on original soil-inoculated N-free mannitol agar. Abundant colony formation is indicated by 4+, and relatively less by the designations 3+, 2+, and 1+ while - indicates no *Azotobacter* in 1 gram soil.

pH of Soil	Relative abundance of <i>Azotobacter</i>	Number of samples with these results
7.31	4+	1
7.30	4+	3
7.2	3+	4
7.1	4+	8
7.0	4+ (2+)	6 (4)
6.6	3+	3
6.5	3+	5
6.45	4+	3
6.40	2+	4
6.35	3+	2
6.30	2+	3
6.15	1+	4
6.15	0	1
6.05	1+	3
5.95	2+	2
5.90	1+	1
5.80	0	4
5.65	0	3
5.55	0	2
5.40	0	5

Table 1. As expected the presence of *Azotobacter* depends on the pH of the soil. The zones where the soil is near neutrality have enormous numbers of these bacteria present. Each particle of soil on Petri dishes would be covered with developing colonies. Pure cultures were isolated and shown to be typical *Azotobacter chroococcum* by their morphology and pigmentation. The range of relative frequency of the isolations is seen on samples with the pH ranging from 6.0 to 6.4. On samples where the soils were most acid, no *Azotobacter* were cultured.

The results of this investigation show that *Azotobacter chroococcum* is present in soils in large numbers near the neutral point. The numbers decrease with increasing acidity. The mosaic-like nature of the various soils on this natural area will afford an unusual opportunity to attempt to correlate the presence and activity of *Azotobacter* with other characteristics such as organic matter content, nitrogen balances in soils and plants, and in general give information on the role of these bacteria in the nitrogen cycle of the prairie soils.

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THE DISTRIBUTION OF ENERGY INTO SEXUAL AND ASEXUAL REPRODUCTION IN WILD STRAWBERRIES (*FRAGARIA VIRGINIANA*)

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Abstract. The relative effort expended in sexual reproduction by flowers and fruit and in asexual reproduction by stolons by wild strawberries (*Fragaria virginiana*) was estimated throughout one growing season. Effort was estimated in terms of calories of tissue produced in sexual and asexual reproductive structures and was measured with a bomb calorimeter. Sexual reproductive effort is somewhere between 1 and 8 times the cost of asexual effort. Modification of the extent of interspecific competition did not appear to affect the ratio of the effort expended on sexual and asexual reproduction. The biological significance of relative energy expenditure on sexual and asexual reproduction is discussed.

Harper (1967) noted an unfortunate void in the ecological literature when he wrote, "I know of no attempts to compare the capital investment in seed and vegetative reproduction in any species that possesses both." The goal of this study was to start to fill that void. The wild strawberry (*Fragaria virginiana*) seemed like an ideal plant for the study because sexual reproduction in flowers and fruit is clearly distinguished from asexual reproduction in stolons (runners). In addition, the runners grow above the ground so that there would be none of the practical difficulties in isolating and measuring them that would be involved with subterranean rhizomes.

Another virtue of wild strawberries as organisms for study is that a large amount of general biological information about them is available because of their close relationship to domestic strawberries. Cytogenetically, *F. virginiana* is an octoploid species which readily interbreeds with two contiguous, but allopatric, North American octoploid species (*F. ovalis* and *F. chiloensis*). All three octoploids were probably derived from the wide ranging diploid *F. vesca* (Longley 1926, Ichijima 1926, Darrow 1966 and Senanayake and Bringhurst 1967). Watkins and Spangelo (1967) demonstrated the relative importance of additive, dominance, and epistatic genetic variation in some cultivated octoploid strawberries which are derived mainly from *F. virginiana* and *F. chiloensis*. Extensive studies of the genetics of the genus *Fragaria* have been performed recently in Russia (Fadeeva 1966 a, b, c, and d, Fadeeva and Narbut 1965, and Narbut and Fadeeva 1966). The two-way passage of chemicals through runners between parent runner plants has made *Fragaria* a particularly useful tool for physiological studies (Downs and Piringer 1955, Guttridge 1959 a and b, Norton and Wittwer 1963, Thompson 1963, Creasy and Sommer 1964, Leshem and Koller 1964 and 1965, Moore and Scott 1965, Collins 1966, Darrow 1966, Soczak 1966, Starck 1966, Antoszewski and Lis 1968, and Arney 1968). Plakidas (1964) has reviewed the literature on the diseases of strawberries. The control of the herbivorous two-spotted mite (*Tetranychus urticae*) by predacious mites has served as a good example of biological control of plant pests (Oatman, McMurtry, and Voth 1968). Finally, Free (1968 a and b) has studied the behavior of two species of bees pollinating strawberry flowers.

Energy distribution into sexual and asexual reproduction in strawberries is of general interest because of the difference in frequency of new genetic combinations resulting from the two forms of reproduction. The potential for new genetic combinations resulting from genetic recombinations in sex is far greater than the potential for new genetic combinations resulting from mutations during asexual reproduction. The formation of new genetic combinations is advantageous when placing offspring into a new or changing environment, but often disadvantageous to a plant that is placing offspring into the same environment that it has been successful in exploiting. Because of the difference in the advantage of sex in constant and changing environments, it seems that a

plant might adjust its relative effort into sexual and asexual reproduction in relation to the constancy of its environment. Plant species which are typically found in early successional stages of a sere of communities should experience new environments where areas are opened to their invasion. During succession, an established individual is experiencing an environment that is increasingly less like the one it invaded. It should be advantageous for the first successful invading individuals to make genetic replicas of themselves to fill the new environment. As the environment is invaded by species of later successional stages it should be increasingly important to make new genetic combinations to invade other areas. An individual in such an early successional species could use the degree of competition it is experiencing as a cue to the relative importance of sexual and asexual reproduction in leaving successful offspring.

The wild strawberry is an early successional species in the prairies of central Kansas. In order to test the above predictions about the changing relative advantage of sexual and asexual reproduction during succession, I measured the effect of experimental manipulations of competition on the relative energy expenditure on fruit and runners in wild strawberries.

One problem with studying an early successional species is that optimum distance for dispersing offspring also differs during the life of an individual as it experiences increasing competition from species of later successional stages. Short range dispersal is adaptive when competition is low and long range dispersal when competition is high. For strawberries, seeds in fruit have a potential for long range dispersal and runners a potential only for short range dispersal. Thus a shift in energy expenditure from runners to berries as competition increases should be adaptive for its effect on both genetic recombination and dispersal. Therefore, strawberries cannot serve as an effective organism in sorting between the advantages accruing from genetic recombination and dispersal as a result of shifts in the relative amount of effort spent in sexual and asexual reproduction.

There is relatively little difference between asexual reproduction by runners in strawberries and the vegetative growth of plants by lateral branches. Both processes increase the horizontal area covered by the leaves of a genetic individual. The main difference between the two growth patterns is that runners only maintain connection between active terminal meristems for one growing season, while the branches of a bush or tree maintain a permanent connection between all active meristems and allow some coordination of growth between all parts of the genetic individual. One consequence of separating different active meristems into different physiological individuals by the death of runners over winter is that each runner plant must develop its own root system. This separation could cause more competition between leaves of the same genotype than occurs on trees which can coordinate their leafing pattern to maximize light interception (Horn 1971). However, plants on

either end of a runner are seldom close enough to shade each other. Horizontal spreading of a genetic individual by runners has the potential of covering an indefinite area because there are none of the support problems experienced by the lateral branches of a tree (Horn 1971). On the other hand, by using the solid substrate of the ground for support of its lateral growth strawberry plants cannot attain enough height to avoid shading by other vegetation and can only succeed in early successional stages or in periodically disturbed areas such as stream banks or the strand habitats where the genus is thought to have evolved (Darrow 1966). The similarity between asexual reproduction in strawberries and vegetative growth in other plants creates a strong similarity between this study and the study of the ratio of reproductive effort to total plant growth by Harper and Ogden (1970).

I am grateful for the numerous hours of help in gathering data that I received from Phillip Elliott and T. J. Socolofsky. Michael Johnson and Stephen Fretwell offered helpful criticisms of the manuscript. My wife Ann provided help in preparation of the manuscript. This research was supported by a grant from the Bureau of General Research at Kansas State University. Some of the data on the digestive efficiency of squirrels was gathered while I was supported by NSF Research Grant GB-8480. Additional support came from the NIH Biomedical Sciences Support Grant FR7036 to Kansas State University.

METHODS

An acre of prairie in Section 29 of Range 8 East and Township 8 South in Pottawatomie County, Kansas was the source of all the data gathered in this study with the exception of the feeding efficiency of squirrels which was measured in Columbia, Missouri. The acre, which had been part of a 1000-acre pasture for grazing cattle, was fenced off during October 1970 to prevent further disturbance by cattle for the 6 months before the start of the data gathering in May 1971. Both the vegetation and the soils were quite variable along the steep northwest facing slope of the acre which was chosen for its dense strawberry population. Because of the variability of the environment for the strawberry plants, I wanted to determine if past experience would affect the patterns of distribution of energy into sexual and asexual reproduction upon which I was experimenting. I therefore divided the acre along a line that would separate it into two parts having very obvious differences in their vegetation, slope, and amount of disturbance by cattle. The experiment was performed separately in the two parts of the acre. The western part of the acre had a more gentle slope and was disturbed by numerous cattle trails and a stream cut, all of which were surrounded by numerous forbs. The steep slope of the eastern part of the acre was covered mainly by tall grasses, especially big blue stem (*Andropogon gerardi*).

The experimental design for testing the effects of reduced competition on the distribution of energy into sexual and asexual reproduction is illustrated in Figure 1. I used 2 experimental and 2 control plots with the like plots diagonal from each other in order to reduce the possibility that some unnoticed environmental variable might differ between a single experimental and a single control plot.

A sketch was made of each of the plants under study to indicate the position of its leaves, flowers, runners and the leaves of its runner plants (Figure 2). The plants were revisited at about weekly intervals and new structures added to the drawings. Each of the plant's structures was given a coded number on the drawing and the status of the structure was recorded on a tally sheet at each visit. Flowers were tallied as to whether they formed fruits or not, and the fruits were tallied as to whether they disappeared or dried on the parent plant. The length of each runner was measured to the nearest cm at each successive visit until it stopped growing and then it was checked as alive or dead. Leaves were also checked as alive or dead during each visit.

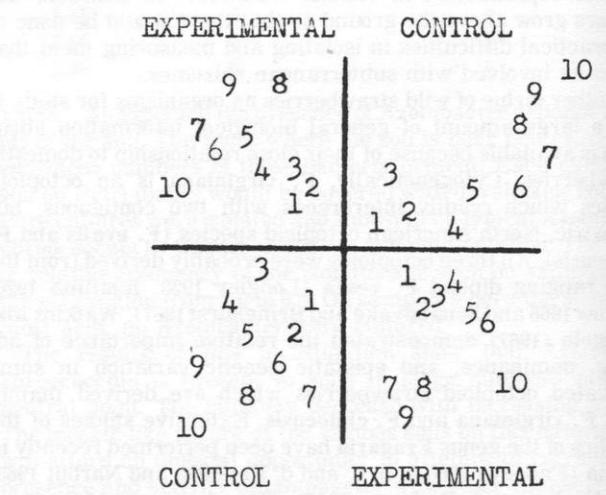
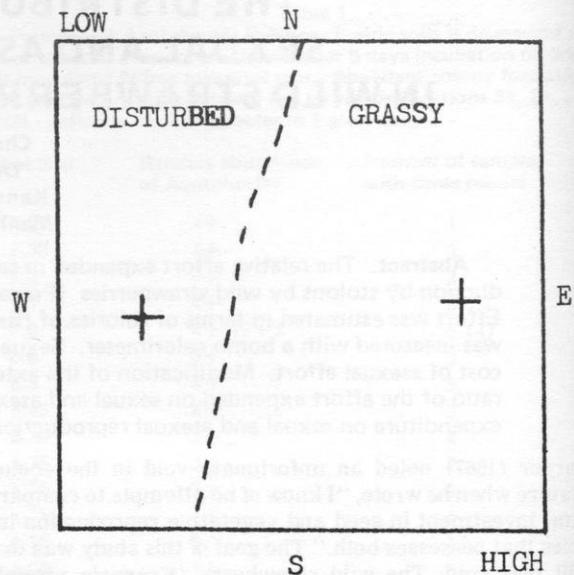


Figure 1. Outline of the acre used for the two experimental plots (crosses) and an example of the positioning of the 20 experimental and 20 control plants as they were found at the beginning of the study for each of the two experiments.

The materials burned for calorimetric measurements were first dried to a constant weight at 60°C. The methods of Paine (1964) for a Parr Semimicro Oxygen Bomb Calorimeter were used in making all the calorimetric measurements.

The methods used to determine assimilation and metabolizing efficiencies of squirrels eating strawberries are the same as those of Smith and Follmer (1972). Means of the series of measurements given in the results are followed by \pm one standard error.

RESULTS

In Table 1 are listed the caloric values for the various plant tissues that are part of sexual and asexual reproduction. These caloric values, multiplied by the weight of plant tissues, give values of energy expended in sexual and asexual reproduction (Table 2). It appears from Table 2 that the effect of reducing competition by weeding away all other species of plants is an increase in the proportion of energy expended on asexual reproduction as predicted. However, this experimental result may actually be only an artifact of the way the experiment was conducted. The plots were weeded in early May 1971, at about

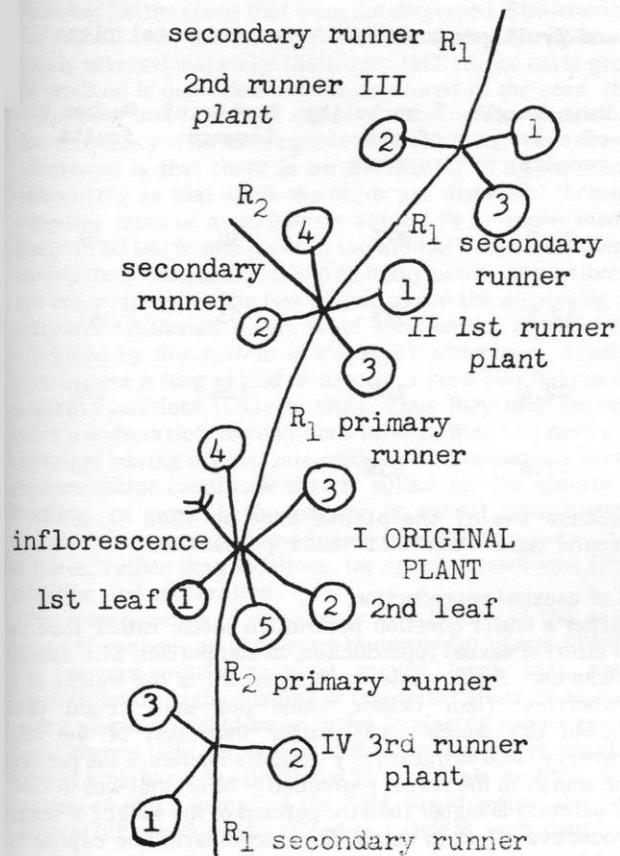


Figure 2. An example of the type of diagram used to keep track of the growth of each of the 40 plants in each of the two experiments.

the time the plants were flowering, so there was little chance for the plants to modify their energy output in flowers and fruit that year. There were no new flowers initiated after the weeding while most of the runners were initiated after the weeding. Therefore, the effect of weeding was felt mainly in the differential production of runners between weeded and unweeded areas. I was able to return to the study area once the following spring of 1972 in order to check the degree of flowering between the weeded and unweeded areas (Table 3). The flowers were just being initiated and the growth in the unweeded areas was somewhat behind those in the weeded areas so that a few more flowers may have been initiated in the unweeded area at a later date. The effect of weeding was to nearly triple the flower production by these plants in comparison with the previous year. A comparison of the runner production in the weeded and unweeded plots in 1971 shows that the effect of weeding was to about triple runner production. Thus the effect of reducing competition by weeding is to increase sexual and asexual reproduction at about the same rate and there is no change in the ratio of energy expended on the two forms of reproduction.

Table 1. Caloric values of different parts of the reproductive effort of strawberry plants in calories/gram dry weight.

Structure	Number of measurements	Caloric value	Standard error
runner	2	4182 \pm 20.9	
whole fruit	5	4456 \pm 141.6	
whole seeds	2	5396 \pm 56.6	

Table 2. The ratio of sexual and asexual reproductive effort of wild strawberries under weeded and unweeded conditions in two natural habitats.

A: Ratios calculated from asexual reproduction in primary runners only			
Area and Treatment	Mean caloric content of runners per plant (calories of asexual reproductive effort)	Mean caloric content of fruit per plant (calories of sexual reproductive effort)	sexual effort/sexual effort
Grassy area: control = unweeded	468	968	2.07
Grassy area: experimental = weeded	1415	1569	1.11
Ratio of experimental over control			1.86
Disturbed area: control = unweeded	744	4490	6.03
Disturbed area: experimental = weeded	2130	1670	0.78
Ratio of experimental over control			7.73

B: Ratios calculated from asexual reproduction in primary and secondary runners			
Area and Treatment	Mean caloric content of runners per plant (calories of asexual reproductive effort)	Mean caloric content of fruit per plant (calories of sexual reproductive effort)	sexual effort/sexual effort
Grassy area: control = unweeded	1078	968	0.90
Grassy area: experimental = weeded	2601	1569	0.60
Ratio of experimental over control			1.50
Disturbed area: control = unweeded	1764	4490	2.55
Disturbed area: experimental = weeded	5956	1670	0.28
Ratio of experimental over control			9.11

Table 3. Comparison of numbers of flowers produced in 1971 and 1972 in the experimental plots.

Area and treatment	Number of flowers in 1971	Number of flowers in 1972	Numbers in 1972/Numbers in 1971
Grassy area: control = unweeded	36	0	0.00
Grassy area: experimental = weeded	53	130	2.45
Disturbed area: control = unweeded	126	12	0.10
Disturbed area: experimental = weeded	53	199	3.75

A comparison of the ratios of sexual effort to asexual effort from grassy and disturbed areas in Table 2 shows that the ratio was greater in the disturbed area for unweeded controls, but is reversed to being greater in the grassy areas for weeded experimental plots. This reversal in the relative size of the ratios of sexual effort to asexual effort for control and experimental treatments in grassy and disturbed areas causes the ratio of experimental over control to be much higher in the disturbed area than in the grassy area. Most of these differences in ratios are a result of lack of control in the experimental design and can be traced to the number of flowers that were initiated in weeded and unweeded parts of grassy and disturbed areas in 1971 (Table 4). In the grassy area there were more flowers and fruits in the weeded plots while in the disturbed area there were more flowers and fruits in the unweeded plots. Since the weeding had nothing to do with flower initiation in 1971, the differences in flower number are a chance result of the positioning of the plots, and the effects of these differences on the ratios between experimental and control and between grassy and disturbed areas have no causal connection to the experimental reduction of competition.

A second factor that was not properly controlled was the effect of herbivores on the growth of runners. Table 4 shows that herbivores killed a higher percent of the runners in the grassy area than in the disturbed area. Because many runners were

Table 4. Numbers and length of runners and number of flowers and fruit produced in the experimental plots during 1971.

Area and treatment	Number of primary runners	Mean length of primary runners (cm)	Total number of runners	Mean length of all runners	% mortality of all runners	Number of flowers	Number of fruits
Grassy area: control = unweeded	19	34.4	68	22.2	39%	36	29
Grassy area: experimental = weeded	142	13.9	286	12.7	57%	53	47
Disturbed area: control = unweeded	36	26.0	99	22.4	46%	126	121
Disturbed area: experimental = weeded	130	22.9	479	17.4	45%	53	50

*The totals for this area are for 18 rather than 20 plants because two of the plants were on the edge of the weeded area and were freed from competition around more than half their perimeter.

killed when they were only a small fraction of the average length of completed runners, the mean runner length in the grassy area was lowered. Therefore, while the number of runners initiated in the grassy and disturbed areas was similar (Table 4), the energy expended in producing runners was considerably higher in the disturbed area (Table 2). In order to insure accuracy of measurements of the types of ratios shown in Table 2, both feeding by herbivores and the size of the plants at the start of the experiment must be under control. However, the ratio of sexual effort to asexual effort in weeded plots are probably more representative of the ratios of natural populations under varying environmental conditions than would be a uniform, highly controlled experiment.

The ratio of the energy in the tissues of berries and runners (Table 2) can give only a rough estimate of the metabolic cost of growing these two types of reproductive structures. The chemical composition of woody runners and fleshy fruits with their embedded seeds are undoubtedly very different. The metabolic cost of building the different types of chemicals may also differ considerably. An additional problem in estimating the energy expenditure in asexual reproduction comes from determining the extent to which runners and runner plants photosynthesize their own energy supply. It is probable that the original plant produces most of the energy for synthesis of the primary runners which start at the original plant. The original plant probably also produces the energy for the initial leaves and roots for the first runner plants. Usually secondary runners grow from the first runner plant shortly after it initiates its first leaves and roots. Much of the energy for these secondary runners probably also comes from the original plant. However, as runner plants grow and add leaves, they send out other runners for which they probably assume all the energy expense. Thus, in considering the annual energy expense for asexual reproduction for a plant, the real expense probably lies somewhere between the cost of all the primary runners and the cost of all the runners growing from the original plant and its runner plants. The values in Table 2 for unweeded plants indicate that the cost of sexual reproduction is somewhere between 1 and 6 times the cost of asexual reproduction.

Not all the tissues involved in sexual reproduction were weighed. Although the fruits that were weighed were cut off below the receptacle and sepals, much of the pollen and the petals of the flower were missing. Much of the stalk that supports the fruit and flower was also missing. Because these stalks also support modified leaves, they cannot be considered to be wholly an expense associated with sexual reproduction. If these missing tissues are taken into consideration, sexual reproduction is probably somewhere between 1 and 8 times the

cost of asexual reproduction.

Harper's (1967) question pertains to seeds, rather than the total effort of sexual reproduction, in comparison with asexual reproduction. Seeds made up 26.2 percent of the weight of 10 strawberries. Their caloric value per unit weight (5396 cal/gram dry weight) was higher than that of the total strawberry (4456 cal/gram dry weight). Therefore the per cent of the energy in the sexual reproductive effort that was in seeds (31.7 percent) is higher than the percent of the weight of sexual reproductive effort in seeds. If one compares the capital invested in seeds and asexual reproduction, the ratio should be close to unity.

The parts of the strawberry fruit other than the seeds appear to function in attracting vertebrate dispersal agents for the seeds. Feeding experiments with gray squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*) indicated that they were quite successful in digesting the fleshy parts of strawberries (Table 5). The feces of squirrels feeding on strawberries consist mainly of undigested seeds. The fact that most of the seeds, which have a higher caloric value than the fleshy parts of the strawberry (Table 1), are passed through the gut leads to a higher assimilation of weight of strawberries than calories of strawberries (Table 5). If none of the seeds are digested then about two-thirds of the fleshy material is being digested. Although it is highly unlikely that tree squirrels are dispersing strawberry seeds on prairies, I have observed tree squirrels in the genus *Tamiasciurus* feed on strawberries and the pattern of digestion of strawberries by squirrels is probably similar to that of other small mammals that might eat them on the prairies.

Table 5. The digestive efficiencies of squirrels feeding on strawberry fruits, with standard error.

Squirrel species	Percentage of ingested dry weight assimilated	Percentage of ingested calories assimilated	Percentage of ingested calories metabolized
Gray squirrel	54.2% \pm 3.7%	49.6% \pm 4.5%	42.0% \pm 4.7%
Fox squirrel	46.0% \pm 2.4%	40.1% \pm 2.7%	33.6% \pm 1.2%

Asexual reproduction in the strawberry appears to have a much higher frequency of success than sexual reproduction. Fifty-two percent of the runners that were initiated in the two experimental plots were successful in forming runner plants. Those that failed were killed by some form of herbivore; probably an insect with sucking mouth parts in most cases. There was no way to measure the exact success of sexual reproduction, but over half of the berries dried on the plant and were probably not dispersed. I noticed no new strawberry seedlings in the weeded areas which would indicate a very low

success for the seeds that were not dispersed. Strawberry seeds are small (0.53 milligrams), which is typical for species of an early successional stage (Salisbury 1942). Since early growth of a seedling is dependent on energy stored in the seed, it is not surprising that the small seeds of strawberries should have a low frequency of developing into mature plants. What does seem surprising is that there is an average of 77.8 ± 5.8 seeds per strawberry so that when the seeds are dispersed through the digestive tract of a vertebrate animal 78 or more seeds are likely to be left in one place in the animal's feces. Rather than having the seeds scattered into as many places as possible, they are concentrated in the few places where the dispersing agent defecates. Although diversity of location for germination is sacrificed by this system of dispersal, strawberry seeds germinate over a long period of time in a seed bed having fairly uniform conditions (Darrow 1966). Thus they may germinate under a wide variety of conditions through time and have a good chance of having at least one seed germinate under a series of environmental conditions that is suited for the growth of a seedling. In general, the pattern of sexual reproduction in strawberries appears to be adapted to sampling a large variety of times, rather than locations, for optimal conditions for germination and maturation.

One consequence of weeding is a reduction in the average length of runners as compared to unweeded plants (Table 6). The runners, which grow at ground level, may respond physiologically to the shading of unweeded areas by etiolation. Such a response would be adaptive in placing runner plants in more intense light, especially if the growing tip of the runner formed a plant when stimulated by more intense light. Such a process of patch sampling for light would insure the runner plants of high productivity (Gordon H. Orians, pers. com.).

Table 6. Comparison of the length (cm) of fully-grown runners growing in weeded and unweeded areas.

Type of runners	Number	Mean length of runners from weeded areas	Number	Mean length of runners from unweeded areas	"t" value for difference
Primary runners only	69	29.4 ± 1.24	85	38.5 ± 0.93	3.90^{**} d. f. = 152
All types of runners	108	23.0 ± 0.70	44	30.3 ± 1.35	3.69^{**} d. f. = 150

** significant at the 0.01 level.

DISCUSSION

My original prediction that the relative distribution of energy into sexual and asexual reproduction would be adjusted in response to competition was not borne out. Instead, a reduction in the competition experienced by a plant leads to proportional increases in the energy expended on both asexual and sexual reproduction. The difference in the seasonal patterns of energy expenditure on sexual and asexual reproduction may be the adaptive basis for the constancy in the proportion of energy expended on the two forms of reproduction. The initiation of all the flowers occurs in early May, while the runners involved in asexual reproduction may be initiated at any time from May through September. The bud that initiates a single inflorescence may commit the parent plant to the production of as many as 15 or 20 flowers and fruits, whereas a plant commits itself to one runner at a time. Once a flower is initiated, the parent plant can gain no rewarding increase in fitness until the resulting fruit is mature. It has been demonstrated that some plants adjust the number of carpels they initiate to the number of fruits they are most likely to be able to mature (Johnson and Cook 1968). Natural selection for efficient use of energy dictates that other species of plants, including strawberries, should do the same. A large commitment of energy into sexual reproduction is best made when the amount of energy available for reproduction is greatest and most predictable.

In prairies, where midsummer droughts are common and unpredictable (Dix 1964), the spring should be the best time for

strawberries to commit energy to sexual reproduction. For strawberries, productivity should be highest in the spring because the dominant vegetation of grasses and fall blooming composites will not be shading them yet, and moisture stress will be minimal. The predictability of productivity will also be highest in the spring because the rate of the plant's early growth can be predicted from the energy reserves stored in its roots from the previous growing season and moisture conditions are most predictable in the spring. Synchronous flowering in the spring may have added advantages in allowing efficient pollination (Free 1968, a and b, and Heinrich and Raven 1972) and effective seed dispersal by providing a large enough food supply to attract animals as dispersing agents.

In contrast to sexual reproduction, runners can grow at varying rates and in varying numbers in response to the unpredictable changes in the physical environment throughout the growing season. Single runners, of the average length, contain less energy than the average strawberry, and therefore, would be less of an energy commitment to the parent plant than a single flower and fruit. If runners do indeed form runner plants in response to high light intensity (patch sampling), then they could be most effective in patch sampling when the dominant vegetation had reached its full height in the later part of the growing season.

With sexual and asexual forms of reproduction having their most efficient season of growth at different times of the year, any adjustment in the relative energy expenditure on the two forms of reproduction would have to incorporate information between different seasons. In order for my prediction to be true, that a reduction in competition should lead to an increase in the relative amount of reproductive effort going into asexual reproduction, then low competition and high productivity in the summer should lead to high levels of asexual reproduction in the summer and low levels of sexual reproduction the following spring. This response to low levels of competition should present no problems, but the reverse response to high levels of competition would present problems. High levels of competition in the summer would give the plant little energy reserve for either asexual reproduction during the summer or sexual reproduction the following spring. Since sexual reproduction requires the greater total energy commitment per unit time, it would have relatively little chance of success after periods of intense competition and very little sexual reproduction would result. Thus it is the separation of the two forms of reproduction into different seasons that would appear to preclude a functional adjustment of the relative energy expenditure on sexual and asexual reproduction in response to competition.

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ECOLOGY OF THE PRAIRIE SPECIES OF THE GENUS LIATRIS

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Abstract. *Liatris punctata*, *L. mucronata*, *L. pycnostachya*, *L. aspera*, *L. squarrosa*, *L. cylindracea*, *L. ligulistylis* and *L. spicata* occur in the prairie areas of North America. The first five occur in greater frequency throughout the central and western prairies and are discussed in greater detail as to the ecology including hybridization, speciation, and evolution within this complex group of composites.

The genus *Liatris* is a perennial composite native to North America. The genus was monographed by Gaiser (1946) who recognized 32 species and 10 hybrids in 10 series. There are many additional categories of varieties, forms and hybrids; several of these differ only slightly from the species type and appear to represent ecological variations. Several species are broadly sympatric but ecologically distinct.

All species of *Liatris* are herbaceous perennials with erect, leafy, usually slender stems with branching only occasionally in the terminal inflorescence. Most species develop a globose or ovoid corm from which fibrous roots spread to anchor the plant; in some species underground food storage occurs in an elongated and branched tuberous root and rhizome. Most of the diagnostic characters of the species are to be found in the heads, especially in the characteristics of the phyllaries, the number of flowers contained in each head, the presence or absence of pubescence inside the corolla tube, and the degree and type of plumosity of the pappus hairs.

Prairie species of the genus include *Liatris punctata* Hook. which occurs on dry prairies and plains from Canada to Mexico and from western Iowa and Missouri to the foothills of the Rocky Mountains; *L. mucronata* DC. occurs in dry soil in open areas from eastern and central Texas northeastward to Kansas and Missouri; *L. pycnostachya* Michx. occurs in damp prairies from Indiana to South Dakota across the Great Plains southward to Louisiana, Texas and Oklahoma; *L. aspera* Michx. occurs on dry sandy soil in open areas from North Dakota southward to East Texas and eastward to North Carolina and Florida, *L. squarrosa* occurs on rocky sandy soil most often along bluffs or bluff escarpments or in dry open woods and clearings from Canada to Florida and Texas and west to the Rocky Mountains; *L. cylindracea* Michx., *L. ligulistylis* (A. Nels.) K. Schum., and *L. spicata* (L.) Willd. occur in moist marshy lands and damp meadows in eastern prairies of Wisconsin, Illinois, and Missouri.

HYBRIDIZATION

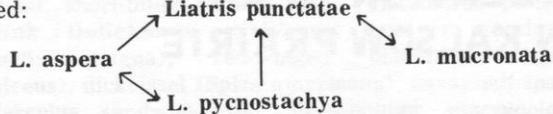
The haploid chromosome number for the genus is $n=10$ with ploidy reported in the genus, and according to Gaiser (1950a, 1950b, and 1951), occurs frequently in the Punctatae series which includes *Liatris punctatae* and *L. mucronata*. Natural and artificial hybrids have been reported by Gaiser (1946, 1950a, 1950b, and 1951), Hadley and Levin (1967), Cruise (1964), and Menhusen (1963b).

As a result of extensive areas of distribution, areas of sympatry occur. Hadley and Levin (1967) reported on a study in Lake County, Illinois, in which they found three species, *Liatris aspera*, *L. cylindracea*, and *L. spicata* growing in a series of old dunal sand ridges and interdunal depressions with highly variable texture and organic matter content. The three species are distributed in a mosaic pattern reflecting subtle microenvironmental differences found within the prairie. The species intermix creating broad transition zones or ecotones. Densities of species were found to be a function of soil moisture and soil organic matter. *Liatris aspera* grew on drier upland sites with low soil moisture and matter and good internal drainage. *Liatris cylindracea* occurred downslope in areas of increased soil moisture and organic matter content with less internal drainage. *Liatris spicata* occurred on the lower slopes and lowland depressions which were high in soil moisture and organic matter but poor internal drainage. In the ecotonal areas they reported <0.09 percent hybrids. The paucity cannot be attributed solely to internal reproductive barriers for these have been readily surmounted by experimental studies. Flowering periods overlap and plants were within pollination range.

Levin (1967) reported sympatric populations of *Liatris aspera* and *L. spicata* in Cook County, Illinois, in which seasonal and ecological barriers were surmounted and resulted in extensive hybridization to produce an heterogenous assemblage containing F_1 , advanced generation and backcrossed hybrids. A large proportion of hybrids were backcross derivatives with *Liatris spicata* being the predominant recurrent parent.

In the prairies of Kansas, Nebraska, and Oklahoma, I have found a few colonies of sympatric species of *Liatris punctata* and *L. aspera*, *L. mucronata* and *L. pycnostachya*, *L. mucronata* and *L. aspera*, and *L. punctata* and *L. pycnostachya*. I have not found any patterns of distribution except for soil types. *Liatris squarrosa* and *L. pycnostachya* occur in prairies chiefly in sandy soil; the first occurs in well-drained areas while the latter occurs in less well-drained areas. The latter three occur principally in areas of limestone deposits. Herbarium specimens of population samples of 25 or more plants have been collected from the three state area and studied carefully for morphological evidences of hybridization but none have been found that could be identified as hybrids.

Artificial hybrids are comparatively easy to produce; Gaiser (1950a and b, 1951), Cruise (1964), and Menhusen (1963b) have all reported this. In the University of Kansas Experimental Gardens, I found that the following putative hybrids could be produced:



The percentage of seed set was less than 25 with less than 50 percent germination. The survival rate of the seedlings was above 90 percent for the first growing season. *Liatris* plants are perennial and do not produce flowers and fruits during the first growing season. Construction work in the experimental garden area necessitated transplanting the seedlings; climatic conditions were unfavorable and all seedlings died.

Within the Punctatae Series of the genus, however, the species *Liatris mucronata* and *L. punctatae* hybridize freely in the experimental garden and apparently do so in the field. One of the most reliable distinguishing characteristics between the two species is the type of root or rhizome. *Liatris mucronata* plants of the eastern one-third of the three states produce a globose or

ovoid root or corm while *L. punctata* plants of the western one-half to two-thirds of the states produce elongated tuberous roots and rhizomes, especially in loose sandy soils. Gaiser (1946) described *L. densispicata* from sandy soils in Minnesota. I found the same in the Sand Hills in Nebraska. In the experimental gardens *L. punctata* plants develop adventitious buds and new shoots along the rhizome in soft soil that had not done so in the prairies in uncultivated soils with competition from other plants. This seems to be an "ecotype" species or ecospecies. Across the Flint Hill area and the area to the west for approximately 30 to 60 miles the two species hybridize and it is nearly impossible to find a colony of either parent that can be classified as either *L. mucronata* or *L. punctata*. The characteristics of the root system is about the only character that remains stable and not overlapping. In the apparent hybrids often a globose root structure develops which becomes much elongated as the plant matures. No adventitious growth ever occurs from roots of *Liatris mucronata*, even as a result of experimental cuts which produce stems in *L. punctata*.

Much morphological variation occurs within a population in the field with the original collections or in the experimental garden. Variation of phyllary shape and size within a population was great (Menhusen, 1963b). The height of plants, number of heads, leaf length, corolla and style length, also, vary within populations in the experimental garden as well as yearly growth patterns. The most important factor in determining mean plant heights across the state was the amount of rainfall. The phenology seemed to be genetically controlled. Flowering dates in the experimental garden correlated with those in the field. Though some would designate these populations as races or varieties, I consider these to be a cline across the area from east to west. On the eastern side, I feel that *Liatris mucronata* is a well-defined taxon and on the western side of the distribution area that *L. punctata* is a well-defined taxon but that through the Flint Hills there is an ecotone area in which the two taxa hybridize freely. Endler (1973) indicates that gene flow may be unimportant in the differentiation of populations along such environmental gradients.

ECOLOGY

The genus is able to adapt to many factors and survive. Weaver (1958) listed *Liatris punctata* as a plant of the true prairie and mixed prairie hard lands and stated that their effect upon grasses is not marked except where they occur in unusually dense clumps. He found that in clay soil with sandy subsoil roots penetrated only about 6.5 feet with a scarcity of absorbing laterals.

Weaver and Albertson (1943) found that during periods of drought, that *Liatris punctata* decreased in abundance and height. Examination of root systems of *L. punctata* near the end of the drought showed normal root conditions in every respect and no modification that could be attributed to drought. The forbs probably survived because of the moderately moist soil at 5 to 16 feet. In a study of vegetation on two prairies in western Kansas, Tomanek and Albertson (1957) list *Liatris punctata* as a common forb at the Atwood site with an abundance of 1.5 plants per 100 square feet. At the Ashland station *Liatris punctata* was one of the five most abundant forbs on the upland; there were 3.2 plants per 100 square feet, where it is listed as one of the most common decreasers at these two stations.

Few diseases or insects appear to harm *Liatris* plants. Ants appear to be some of the most frequent visitors of the *Liatris* plants during the growing season. Lady beetles and bees are attracted to the plants. Grant (1950) attributes an important evolutionary role to the flower constancy of bees.

A Texas horned lizard, *Phrynosoma cornutum*, was collected in a rocky hillside area with many plants of *Liatris punctata*; the lizard had apparently been feeding upon the ants around the plants.

Weaver and Fitzpatrick (1934) state that young *Liatris* plants are eaten by rodents. Kennicott (Jameson, 1947) reports finding

five or six quarts of roots of two species of *Liatris* among food stored in a cache for winter use in Illinois of *Microtus ochrogaster*. In an investigation of the feeding habits of *Microtus ochrogaster*, *Signodon hispidus*, *Reithrodontomys megalotis*, and *Peromyscus maniculatus*, Menhusen (1963a) found the animals to feed freely and eagerly upon the buds, seedlings, and new leaf growth of the *Liatris* plants. The animals all ate the starchy material from the centers of the large tuberous roots when these were split. The seeds were eaten eventually, but only as a tertiary choice of food.

Evans and Dahl (1955) reported that a herd of white-tailed deer, *Odocoileus virginianus*, fed on forbs including *Liatris* on a reserve in southeastern Michigan. Martin, Zim and Nelson (1951) list *Liatris* as one of the plants composing 1/2 to 2 percent of the diet of the pronghorn antelope, *Antilocapra americana*, in New Mexico.

Hetzer and McGregor (1951) list *Liatris pycnostachya* as one of the prairie forbs that decreases under grazing. I have seen cattle graze on the plants and have seen damage caused from livestock grazing.

From observation it seems that burning by a fast fire or mowing the prairies, especially in the Flint Hills, does not damage the *Liatris* plants; this, in fact, may be advantageous to the plants for it prevents the build up of deep litter and promotes earlier emergence. Most *Liatris* plants cannot seem to tolerate deep litter or shading; grasses do provide competition, especially those tall enough to shade the *Liatris* plants.

SUMMARY

Gaiser (1946, 1950, 1951), Leven (1967), Endler (1973), and others report that *Liatris aspera*, *L. pycnostachya*, *L. squarrosa* are chiefly diploid plants with little ploidy found; these plants are much more limited by their ecological environmental tolerances, while in *L. mucronata* and *L. punctata* much ploidy and hybridization occurs. These latter two species are widely distributed with broad ecological tolerances and a wide transition zone across the middle one-third to one-fourth of the states of Kansas, Nebraska, and Oklahoma.

The results of the hybridization experiments demonstrate the close genetic relationship which exists among the *Liatris* species of *L. aspera*, *L. squarrosa*, *L. pycnostachya*, *L. mucronata*, and *L. punctata*. It appears that differences in ecological adaptation are the most significant barriers in preventing partial or complete fusion of taxa. Since hybrid progeny develop in most crosses these may be defined by the biosystematist as ecospecies and *L. aspera*, *L. pycnostachya*, *L. squarrosa*, *L. mucronata*, and *L. punctata* are ecotypes of the same species. Morphological and ecological criteria permit a separation of these five into species. We are faced then with the situation in which populations have one and at the same time the status of species, and the biosystematic status of ecotypes.

This situation is encountered in cases of gradual speciation where morphological and physiological differences between species arise ahead of genetic differences whose accumulation would lead to intersterility. Evolutionary changes are occurring among these five at very different rates; either the rate is more advanced by *L. punctata* and *L. mucronata* than the other three or the reverse with these two being the least rapid to change. Through such vast geographic areas as the prairies it seems these evolutionary changes will be a long, slow process.

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SPECIES PATTERNS IN RELATION TO SOIL MOISTURE GRADIENTS IN KALSWO PRAIRIE

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Abstract. Species presence was determined for vascular plants in 968 contiguous 30 by 30 foot quadrats in Kalsow Prairie, an original remnant of the tall-grass prairie in central Iowa preserved by the State of Iowa. Soil series and elevations were determined for each plot so that species distributions could be correlated with changes in soils and microrelief. Cover estimates showed that *Sporobolus heterolepis* and *Andropogon gerardi* were dominants of the upland prairie. Strong zonation occurred around shallow prairie potholes. Dominants of zones from upland prairie to the center of potholes consisted of *Helianthus grosseserratus*, *Calamagrostis canadensis*, *Carex atherodes*, *Scirpus fluviatilis*, and *Polygonum coccineum*, respectively.

Zoological Studies of Prairies and Prairie Animals

HABITAT RELATIONSHIPS OF GRASSLAND BIRDS AT GOOSE LAKE PRAIRIE NATURE PRESERVE

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Abstract. Goose Lake Prairie was purchased by the Illinois Department of Conservation in 1969 to preserve one of the largest remaining tracts of native prairie in the state. The 1500-acre area that was dedicated as a nature preserve contains a mosaic of habitats ranging from potholes and marshes to upland ridges. Degradation from over-grazing and attempts at cultivation, especially on the better drained portions, has resulted in extensive invasion by crab, hawthorne, bluegrass, and miscellaneous forbs, so that shrub inhabiting species now rank high in dominancy. The most abundant species are red-winged blackbird, eastern meadowlark, field sparrow, short-billed marsh wren, henslow's sparrow, traill's flycatcher, yellow warbler, bell's vireo, and brown thrasher. One group of grassland species, upland plover, bobolink, and grasshopper sparrow, are restricted to the bluegrass and have not been found in the tall grasses. Dickcissels inhabit only weedy fields outside the preserve. Future management should result in a reduction of shrub-inhabiting species and perhaps the bluegrass inhabiting species and thus reduce the diversity of the breeding bird population.

The tall grass prairies that once covered most of Illinois have practically disappeared. Most were plowed before any basic information about their composition and the animals that inhabited them were recorded. Today, most of the tracts of prairie that remain in the state are either degraded or are so small that true faunal relationships are difficult to evaluate. All of the grassland birds, except the prairie chicken (*Tympanuchus cupido*) have now adapted to pastures and hayfields. Thus, the exact habitats that the grassland species occupied in Illinois native prairie are not known.

Thirteen species of grassland birds nest in the vicinity of Goose Lake Prairie. These are the marsh hawk (*Circus cyaneus*), ring-necked pheasant (*Phasianus colchicus*), upland sandpiper (*Bartramia longicauda*), horned lark (*Eremophila alpestris*), short-billed marsh wren (*Cistothorus platensis*), bobolink (*Dolichonyx oryzivorus*), eastern meadowlark (*Sturnella magna*), red-winged blackbird (*Agelaius phoeniceus*), dickcissel (*Spiza americana*), savannah sparrow (*Passerculus sandwichensis*), grasshopper sparrow (*Ammodramus savannarum*), Henslow's sparrow (*Passerherbulus henslowii*), and vesper sparrow (*Pooecetes gramineus*). These appear to represent all of the grassland species found here when prairies covered the area except that the pheasant has replaced the prairie chicken. Goose Lake Prairie is large enough and possesses diverse associations so that the specific habitats that these species occupy may be measured and the relationships among the species may also be studied.

Goose Lake Prairie was purchased by the Illinois Department of Conservation in 1969 to preserve one of the largest remaining tracts of native prairie remaining in the state. A total of about 2200 acres of land have been purchased, 1523 acres have been dedicated as a prairie nature preserve. The remainder, mostly

farmland, will be developed as a state park to furnish supportive facilities for interpretation and recreation. Much of this land eventually will be planted to native grasses.

The prairie is located on till plain near the Illinois River about 50 miles southwest of Chicago and 6 miles east of Morris, in Grundy County. The topography is level to rolling. Soils are shallow silt and clay loams underlain by Pennsylvanian sandstone (Pottsville Formation) and Ordovician limestone (Maquoketa Formation). This bedrock, the many glacial erratics on and near the surface, and poor drainage have saved most of the prairie from cultivation although it has been grazed for many years. Overgrazing and attempts to cultivate parts of the area, especially on the ridges, have allowed extensive invasion by woody species, primarily hawthorn (*Crataegus sp.*) and crabapple (*Malus ioensis*). Plans for managing the preserve call for removal of much of this shrubbery, but at present extensive areas are overgrown, and shrublands are one of the major habitat types.

The habitat ranges from hydric to mesic. Marshlands, potholes, and swales are abundant, especially in the southern and eastern parts of the tract (Fig. 1). Much of the remainder of the prairie is poorly drained. These areas contain meadows of bluejoint (*Calamagrostis canadensis*) and sometimes sedges and rushes. Such meadows are often extensive and presently are the most abundant association. On the ridges and other better drained sites big bluestem (*Andropogon gerardii*), little bluestem (*A. scoparius*), indiangrass (*Sorghastrum nutans*), prairie dropseed (*Sporobolus heterolepis*), and switchgrass (*Panicum virgatum*) predominate. One small tract in the northeast part of the prairie contains the above and side-oats grama (*Bouteloua curtipendula*). Because of overgrazing many of these areas now contain extensive stands of the woody

species, miscellaneous weeds, and bluegrass (*Poa pratensis*) in addition to the native prairie species. Many are now unsuitable for grassland birds. One nearly pure 20-acre stand of bluegrass is located in the northwest corner of the preserve. It extends northward onto adjacent private land. The prairie does provide by far, however, the largest contiguous tract of native prairie remaining in Illinois and probably this part of the midwest.

The prairie furnishes a habitat that has been increasingly restricted in Illinois in recent years. Grassland habitats are now furnished almost entirely by pastureland and hayfields. Both of these types often are temporary, being grazed or cut regularly, hence permanent grassland is scarce. Even hayfields and pasture have annually constituted less than 2 percent of the total land area in much of east central Illinois since 1964 (Joselyn 1968).

The purpose of this study was to document the bird fauna of the preserve. A bird list will be helpful to visitors to the area. Also, knowledge of present bird populations will provide a basis for assessing management efforts in the future and documenting other changes that may occur in bird populations. When habitat associations of the grassland species were examined I noticed that some of the species did not appear to fit either the vegetation type to which they have usually been associated or did not take advantage of the native prairie to which they presumably formerly inhabited. Thus, it seems appropriate to report upon these relationships. Goose Lake Prairie will be known as the prairie preserve in a prairie state, yet many of the common grassland birds of the area apparently will tolerate only very small and specific sites on the preserve.

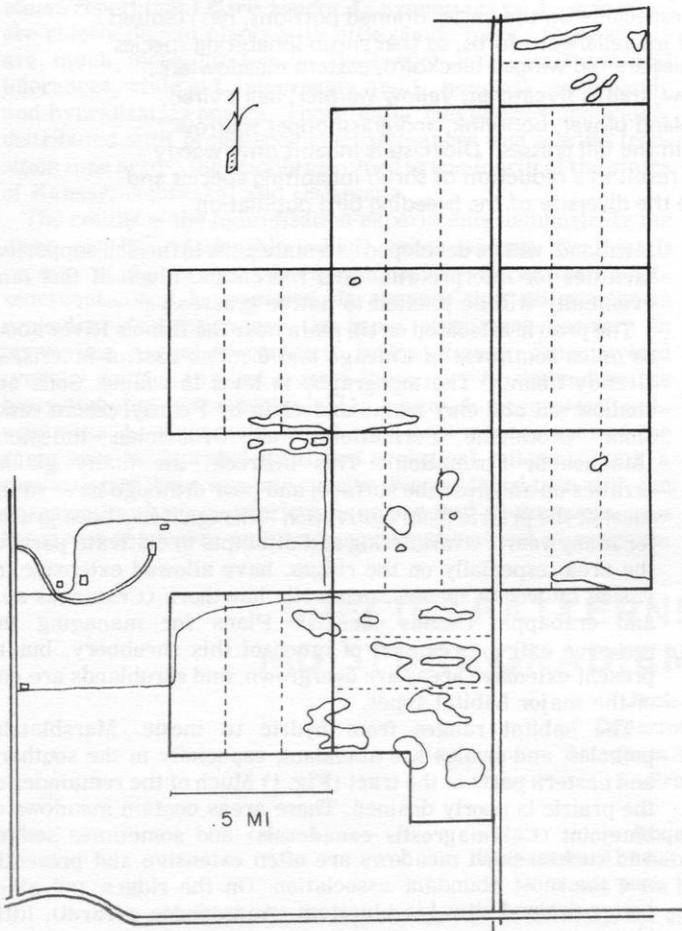


Fig. 1 Location of census transects on Goose Lake Prairie Nature Preserve. In some cases transects were detoured slightly to avoid dense thickets. Each block is 0.5 mile across, or approximately 160 acres.

METHODS

Bird populations were determined simply by searching the entire area thoroughly throughout the breeding season. In addition records were kept when the prairie was visited at other seasons. Censuses were made during June of 1971 and 1972. The area was divided into blocks of 160 acres each, and two transects were established across each block (Fig. 1). These were walked beginning at dawn on clear, calm mornings. All birds seen or heard 100 yards on either side of the transect were recorded. A total of 88 hours was spent censusing and otherwise searching for birds in the summer of 1971, 95 hours in 1972.

RESULTS

In 1971 and 1972 a total of 81 species of birds was recorded at Goose Lake Prairie. Four species; marsh hawk, sora (*Porzana carolina*), Virginia rail (*Rallus limicola*), and warbling vireo (*Vireo gilvus*) were recorded in only one of the two years. A total of 65 species probably nested; 28 species were inhabitants of grasslands or marshlands.

The results of the census lines are shown for the ten most abundant species in Table 1. Only three species restricted to grasslands are in the top ten. The red-winged blackbird nested in a variety of habitats, being most abundant in the marshes, and the other species occupied shrubland. The remaining grassland species were so scarce or restricted in their distribution that they did not appear in large numbers on the census.

TABLE 1. Number of individuals censused in June, 1971 and 1972, as described in text, of ten most important summer birds at Goose Lake Prairie Nature Preserve.

Block	Redwing		Eastern meadowlark		S. b. marsh wren		Henslow's sparrow		Yellow-throat		Field sparrow		Yellow warbler		Traill's flycatcher		Brown thrasher		Bell's vireo			
	71	72	71	72	71	72	71	72	71	72	71	72	71	72	71	72	71	72	71	72	71	72
1	12	16	5	7	1	0	0	0	2	1	4	1	1	1	2	3	1	1	0	2		
2	15	17	18	16	0	0	5	8	4	7	7	3	1	0	0	0	1	0	0	0		
3	14	21	8	9	2	1	2	5	5	5	8	9	0	1	4	2	1	0	2	5		
4	18	20	15	16	4	9	8	12	3	4	4	1	0	0	2	0	1	2	0	1	2	0
5	22	27	7	11	6	2	4	8	6	11	3	5	3	5	3	4	1	3	1	2		
6	40	46	5	11	4	1	4	7	3	10	0	4	0	0	1	0	1	0	1	0	1	0
7	24	18	4	6	7	9	4	6	5	2	0	1	0	2	3	1	1	0	0	1		
8	39	48	6	5	2	1	5	8	4	6	5	1	2	1	3	0	1	0	2	1		
9	12	16	2	4	1	0	0	0	8	6	11	7	5	5	2	5	4	2	4	5		
10	36	45	2	3	2	0	2	0	4	6	1	0	6	3	4	2	1	0	4	2		
Total	232	274	72	88	29	23	34	54	44	58	43	32	18	18	24	17	13	8	14	19		

Most species inhabited specific associations on the preserve. The most striking feature about the distribution of grassland species was the restriction of several species to the bluegrass association, found in the northwest corner of the preserve and on private land to the north. This distribution raised questions about the habitats provided by native prairie in this area or about the behavior of some of the species found on it.

Of the 13 species of grassland birds that nest on Goose Lake Prairie or in its vicinity, the habitats of only 7 can be commented upon. Only one pair of marsh hawks occupied the entire area in 1971 and none was there in 1972. The cover was too dense or tall for the horned larks and Vesper sparrow, and they occurred only in adjacent fields. The red-winged blackbirds and ring-necked pheasant nested in a variety of habitats in addition to the grasses. The short-billed marsh wren was restricted to the sedge and bluejoint meadows. The remaining species are discussed below.

The eastern meadow lark was the only nearly ubiquitous grassland species appearing on the prairie. It was found in nearly equal densities in all associations if they were adequately drained. Most individuals were found in those areas such as

blocks 2 and 4 which had the highest percentage of prairie vegetation (see Table 1).

Henslow's sparrow was the most abundant grassland fringillid, being found in all blocks except 1 and 9. These areas consisted mostly of shrubland. This species was most abundant in meadows of bluejoint, little bluestem, and prairie dropseed in which the grassy cover was dense and less than 24 inches tall. On sites where tall grasses predominated this species was not found.

Three species, upland sandpiper, bobolink, and grasshopper sparrow, were confined to stands of bluegrass. At the northwest corner of block 4, in the northwest part of the preserve, a little bluestem-prairie dropseed mixture was replaced abruptly by a nearly pure stand of bluegrass. Bluegrass then extended to the north onto private land. These three species were found only in this area. These two adjacent stands were studied in some detail to ascertain the environmental conditions that might account for the differences in the bird populations (Figure 2). Coefficient of association between grasshopper sparrow and Henslow's sparrow in these two associations was -.80, which indicates a

fields containing forbs that were adjacent to these tracts. One pair of savannah sparrows nested in the same area in both years. It occupied a territory containing the native prairie described above and bluegrass. This would be somewhat intermediate to the areas occupied by grasshopper and Henslow's sparrow.

DISCUSSION

In spite of the simple nature of the habitat few community studies have been made of grassland birds (Wiens, 1969). In Illinois descriptions of habitats used by grassland birds (e.g. Gruber and Gruber 1963) have necessarily been limited mostly to pastures and hayfield because these are the only extensive grassland habitats left. Wiens (1969), in a detailed study of ecological relationships among grassland birds, studied an area containing mostly introduced and forage grasses. The associations of native, tallgrass prairie used by birds in Illinois were not studied before the prairies were plowed.

Nearly all of the birds formerly found on Illinois prairies survive here today. All, however, have adapted to pastures and hayfields. The preservation of Goose Lake Prairie provided an opportunity to measure grassland bird populations on tall grass native prairie.

Grassland habitats on the prairie were inhabited primarily by eastern meadowlarks and Henslow's sparrow. Both species occupied nearly all of the native grassland associations and the latter species was restricted to them. Three species of common Illinois grassland species, upland sandpiper, bobolink, and grasshopper sparrow, were found only in bluegrass associations which bordered the prairie. In one area, where a bluegrass area was compared with an adjacent native grass association, the only difference in the two habitats was the more dense nature of the latter vegetation, particularly at ground level. Grasshopper and Henslow's sparrows were nearly completely exclusive of each other in these two areas. Smith (1963) reported grasshopper sparrows as using cultivated grasslands or bunch-forming grasses, but in less vigorous growth than that which supports Henslow's sparrows. In contrast Kendeigh (1941) reported from northwest Iowa that grasshopper sparrows were found where prairie grasses were better developed, and none was found where bluegrass predominated on his study area. Henslow's sparrows inhabit the denser prairie grasses or low, moist depressions in upland prairie (Bent, 1968). Wiens (1969) arranged the species found on his Wisconsin study area in the following sequence, based on an increasing "richness" of the habitat (vegetation density and height, litter coverage and depth): western meadowlark—vesper sparrow—savannah sparrow—grasshopper sparrow—eastern meadowlark—bobolink—Henslow's sparrow. The richness of the Goose Lake Prairie grasslands, coupled with the available adjacent sparser bluegrass may provide two distinct habitats not connected by intermediate habitats, thus the nearly complete habitat separation of the two sparrows. Gruber and Gruber (1963), however, reported grasshopper sparrows from all grassland and hay habitats in Illinois, and they noted highest populations in mixed hay and alfalfa. The latter cover would appear to provide a habitat similar to the little bluestem-prairie dropseed mixtures, except that the litter is missing in hayfields.

The absence of bobolinks and upland sandpipers in the native prairie associations is more difficult to explain. Gruber and Gruber (1963) reported that bobolinks formerly used ungrazed grassland, but that now highest populations are found in mixed hay. Kendeigh (1941) found five nests in *Andropogon* sp. and four in *Poa* in northwest Iowa. Wiens (1969) places the bobolink next to the Henslow's sparrow regarding richness of the grasslands that it utilized. Bent (1958), however, reported that the bird "apparently never liked to nest on the virgin prairie" and that it followed civilization westward.

Surprisingly, upland sandpipers were also restricted to bluegrass associations at Goose Lake Prairie. Stout (1968) reported the species as nesting in rank grasses, but that it

BLUEGRASS	NATIVE GRASSES
G G G	H H H
G G G	H H H
G G H	H H
G G	
U U	
M M M	M M M
M M M	M M M
M M M	M M M
M M M	M M
H H H	
H H	
G G	

Fig. 2 Census of grassland birds along sharp boundary between bluegrass and little bluestem-prairie dropseed association. Letters denote presence of birds, not relative location. Transect was 0.25 miles in length and is represented by the vertical line. Symbols in center at bottom represent small area of bluegrass-native grass mixture described in text. Symbols are: U-upland sandpiper, M-eastern meadowlark, H-Henslow's sparrow, and G-grasshopper sparrow.

strong negative association. Chi square for fidelity of the two species to separate habitats was 12.7 (d.f. 19) which is significant at the .90 level. One small area of about 5 acres contained a mixture of the two associations. In this area I counted 5 Henslow's and 2 grasshopper sparrows. It appears from this limited occurrence that Henslow's sparrow is more tolerant of a slightly different vegetation than grasshopper sparrow. In the 20 acres that were selected, 10 acres contained a nearly pure stand of bluegrass and 10 acres consisted of a mixture of mostly little bluestem and prairie dropseed. Two parallel transects, each 100 meters long, were laid across each tract. Height of grass, depth of litter, foliage cover, ground cover, and soil moisture were measured every 2 meters along the transects. Height (average of 20 inches), litter depth (average 4 inches), and ground cover (100 percent) were the same on both areas. Foliage cover at 12 inches was higher (average of 60 percent) in the native prairie than in the bluegrass (an average of 30 percent). Soil moisture was slightly higher in the native prairie (60 percent versus 40 percent). The variation in height was greater, however, in the native prairie (S.D. 5.5) than in the bluegrass associations (S.D. 3.4).

Dickcissels inhabited neither the native prairie nor the bluegrass associations. They were common, however, in idle

THE REGULATION OF PRAIRIE SWIFT (LIZARD) POPULATIONS—A PROGRESS REPORT¹

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Abstract. Using demographic techniques the seasonal and sexual variations in mortality rate in an isolated Kansas population of the lizard *Sceloporus undulatus* were measured over a single year-long generation. The effects of density and relatively larger size on probability of survival and of female density on fecundity were evaluated also.

Mortality rates were variable. Mortality rates per day were highest for the 1971-1972 generation in early and late spring 1972 for maturing males and in late spring 1972 for adult females. The fall and winter preceding this period had the lowest mortality rate for both sexes. The late summer 1971 hatchling and juvenile period had a mortality rate intermediate to that of the fall-winter and spring 1972 periods for both sexes. Greater mortality rates among males than among females in spring resulted in a sex ratio skewed toward males by late spring 1972.

The effect of density on survivorship was variable. Survivorship rates were strongly and negatively correlated with density in early spring, 1972 for males and late spring, 1972 for females. Density was only weakly and negatively correlated with survivorship in the winter for the entire population and not at all in the late summer 1971 hatchling and juvenile period.

The effect of density on density change was not always correlated with that on survivorship. Density dropped at a higher rate in high density areas than in low density areas during the late summer 1971 hatchling and juvenile periods, but survival rates were not correlated with initial density. Also, for adult females in late spring and in the winter for the entire population, density change rates were not negatively correlated with initial density but survivorship rates were. The meaning of these disparities was discussed.

Larger males survived significantly better than smaller males from early to late spring 1971. This was considered as preliminary evidence for social regulation among males.

Density of breeding females was negatively correlated with number of young per female added to the population.

Hypotheses of environmental regulating and limiting factors and concerning the role of social behavior in regulation of numbers were presented with suggestions of experimental tests of these hypotheses.

Modern population regulation theory suggests that, for most natural species, environmental limiting factors regulate population size via behavioral and physiological mechanisms operating in a density dependent fashion. Presumably, reproduction is curtailed and mortality rates increase until the environmental limits are reached. But, details of this regulation process are poorly understood. Aggressive behavior is coming to be regarded more and more as an important mediator of survival and reproduction, but only indirect data are available to support this contention or to explain how aggression operates in a natural population to change age structures, sex ratios or recruitment rates or, from an evolutionary point of view, to alter the fitness of individuals. Basic questions such as, "during what season or life history stage is a population regulated" or "at what life history stage does aggression play its most important role in regulating survival and fecundity" or "does experience significantly influence later aggression, reproduction and survival success" have been thoroughly investigated in only a few species (see Smith, 1968; Brown and Orians, 1970; Fretwell, 1972).

Behavioral ecologists seek species with the following advantages: 1) survivorship, fecundity easily monitored throughout a generation by marking all individuals in a population and recovering all survivors through periodic censusing, 2) individuals easily watched, not disturbed by close approach and extensive observation of social behavior, 3) individuals adaptable to captivity; space requirements small enough to maintain normal social structures in experimental

enclosures. Iguanid lizards satisfy these objectives much better than most birds and mammals studied to date. These lizards are conspicuous, sedentary, easily approached, captured, observed; they have short life spans and make hardy captives. Intensive study of their ecology should contribute greatly to the development of ecological theory.

In Kansas, lizards comprise a conspicuous part of prairie and riparian ecosystems. Cursory preliminary analyses of stomach contents indicate that several species feed on insects known to be important agricultural pests (Smith 1950; Fitch 1956; Hardy 1962). The impact of these species on the population density of their insect prey species and vice versa is unknown. Understanding of these impacts would help evaluate the potential of lizards as biological control agents. Although insect specialists, such as parasitic wasps, are thought to exert a stronger control on a particular pest species than opportunistic predators, like lizards, the importance of opportunistic predators in stabilizing biological control systems has been emphasized (Huffaker, 1970). Furthermore, lizards are more likely to regulate insect populations in summer than birds for the following reason. Most birds that breed in Kansas migrate south in the winter. Studies suggest that the size of breeding bird populations are regulated on the wintering grounds (Fretwell, 1972). Lizard populations which hibernate in winter are regulated in Kansas, and are more likely to increase in response to increases in insect populations. Clearly an understanding of the interactions of lizard and insect populations could have economic importance.

Considering the preceding justifications, the senior author has undertaken a long-term study of the regulation of mortality and fecundity in lizard populations in Kansas. Because the prairie

¹Contribution No. 1189, Division of Biology and Kansas Agricultural Experiment Station.

swift *Sceloporus undulatus garmani* is easy to study and demographic research has been conducted on this species in other parts of its geographic range (see Tinkle and Ballinger 1972; Tinkle 1972) we have chosen this species for initial studies. Immediate goals were to answer the following questions: 1) When are the critical periods of mortality, and when are these negatively density dependent; 2) is fecundity negatively density dependent; 3) does aggressive behavior mediate lower survivorship and reproduction during critical periods or are the density dependent effects of environmental limiting factors direct, 4) What are the important limiting factors?

Answers to these questions will come only after 1) several years of demographic monitoring of lizards and insect populations; 2) assessment of correlations between variations of survival and reproduction of lizards with other potential limiting factors such as weather and predator populations. 3) experimental manipulations of lizard populations and potential limiting factors. This paper presents findings available after one generation of demographic monitoring of a *Sceloporus* population.

MATERIALS AND METHODS

The prairie swift *Sceloporus undulatus garmani* is a small lizard of the family Iguanidae and adults measure about 55 mm from the tip of the snout to the cloacal opening. They inhabit a variety of habitats in Kansas from sandy river bottoms in the south and central part of the state to sandstone and limestone outcroppings in the western prairies. This race is part of a geographically widespread species that occurs from New Jersey to Florida in the eastern U.S., where it is primarily a forest-edge tree-dweller, to southern Utah in the west, where it is primarily a canyon-rock dweller. The demographic patterns have been well studied by Tinkle and Ballinger (1972) in Ohio, Georgia, Texas, Colorado and Utah. Longevity and reproductive rates vary geographically. Individuals in northern populations mature late in their second season, produce a single clutch of eggs in subsequent seasons and survive several seasons. Those in southern populations mature late in their hatching season, produce several clutches of eggs the following season, and rarely survive more than one breeding season. In Kansas, lizards mature in the spring following hatching. Eggs are laid in May and June, young hatch from mid-July to mid-September. They feed on a variety of arthropods including arachnids, coleopterans, hymenopterans, dipterans, orthopterans and hemipterans.

In spring 1971 an isolated population was located in the Kansas River bottom near Belvue, Pottawatomie County, Kansas. An area including about 4 acres was selected and gridded into forty-foot quadrats to facilitate the recording of locations and movements of individual lizards.

The habitat of the area included a loose sand and gravel substrate, sparsely vegetated with grasses and other annual weeds. Small cottonwood, mulberry and elm trees were scattered across the area, occasionally in small groves. The study area was bordered on the north by a pond, on the south by a riparian forest and ditch; and on the east and west by plastic drift fences. Thus, the population was relatively confined.

Several other vertebrates occurred on the area. Some of these who are potential lizard predators were: birds—bluejays, brown thrashers, catbirds, shrikes, cuckoos, sparrow hawks, kingbirds; mammals—deer mice, shrews, voles, raccoons, opossums, skunks, badgers and coyotes; amphibians—toads, bullfrogs, leopard frogs; lizards—racerunners, prairie skinks and plains skinks. No snakes known to prey on lizards occurred on the area.

Census of the population began in May 1971 and for most purposes of this progress report, terminated July 10, 1972. Recruitment data from late summer 1972 is included. Census methods were identical to those reported by Tinkle (1967). Processing of individual lizards included capturing, measuring

and recording snout-vent length, clipping toes of lizards and recording toe-clip numbers for future identification of individuals, recording location, recording habitat, painting tail base, and releasing at point of capture. The area was searched systematically. On the first search all lizards seen were captured and processed. On subsequent searches all lizards lacking a paint mark were captured and processed while those with a paint mark were merely tallied. After 6-8 sweeps the proportion of "new" lizards was usually less than 10 percent and the census was considered complete. Then, population sizes were estimated using the Haynes index (Hayne 1949). Due to the high rate of hatching in the period from July 23, 1971 through September 7, 1971, and the low manpower available during that time, that entire 47 day period was considered a single census. Subsequent census periods were shorter and included September 27 through October 10, 1971; March 23 through April 10, 1972; May 13 through May 19, 1972; July 10 through July 17, 1972.

RESULTS

Mortality rate per day (M), was calculated on the basis of disappearance of marked individuals between two census periods as follows: $M = (1 - N_1/N_0n)/d$, where "N_{0n}" equals the number of lizards marked during the first census on a particular quadrat, "N₁" equals the number of those lizards recaptured during the second census somewhere on the study area and "d" equals the number of days from the end of the first census to that of the second census.

The period between the end of the May census and the end of the July 1972 census was that of greatest mortality rate for the 1971-72 generation (Table 1). The fall-winter period from October to March imposed the least mortality on the population. Mortality was greater for males than for females in the March through May period and this resulted in a skewed sex ratio in the May census.

TABLE 1. Mortality rate per day (M), densities and sex ratios of the 1971-1972 generation of prairie swifts on the Belvue study area.

	M during period		density at beginning of the period	♂ : ♀ at beginning of period
	males	females		
July, 1971 - October	.0085	.0105	159/acre	1.00 : 1.01
October - March	.0030	.0028	85/acre	1.00 : 1.01
March - May	.0102	.0075	44/acre	1.00 : 1.01 ¹
May - July	.0130	.0117	26/acre	1.00 : 1.50
July, 1972	----	----	8/acre	1.00 : 1.65

¹Actual sex ratio measured during March census was 1.00 : 0.60. But, for reasons discussed in the text, we believe that many females were dormant during the March census and thus not recorded. Thus, we assumed that sex ratio did not change over the winter. The density estimate was adjusted to a 1.00 : 1.01 sex ratio. Winter mortality rates might be over estimated for females, because females alive but not active during the March census might have died after emergence but before the May census. Thus, on the data cards they were recorded as disappeared (died) in winter when they actually died in spring. Spring mortality rates for females were calculated only on the basis of females active and captured during the March census. So, they hold for only about 60% of the female populations.

We define "regulation" as negative feedback of current density on future density or survivorship. The effect of density on survivorship was assessed by calculating linear regressions of survivorship ($S = N_1/N_0n$) on initial density (N_0n) for each of the 24 quadrats of the study area. A quadrat size of 640 square feet was chosen as a compromise between that large enough to encompass the home ranges of several lizards and that small enough to yield a large enough sample size of quadrats for the regression analyses. We considered a statistically significant negative linear regression of survivorship on initial density to indicate survival regulation. Where a significant regression was not detected, the study area was subdivided according to habitat uniqueness, eg. sandhill, young cottonwood, gravel, open sand, etc. subareas, and regressions were calculated using quadrats within each subarea.

The above technique for assessing "regulation" has been criticized (see Brockleman and Fagan 1972). It has been argued that a significant negative slope can be due to statistical artifact rather than the biological reality of feedback. We utilized the regression analysis technique to obtain a first approximation of regulation. We admit for the time being to the possibility of statistical artifact in our data.

Table 2 (part A) suggests that regulation occurred at some but not all of the periods and that different patterns existed for males and females. Regulation seemed present but slight in winter for both sexes. Regulation was stronger in males during the March through May period but only in the sand-hill sub-area which included over one-half of the population and about one-third of the area. Regulation was strong in the females but not until the May through July 1972 period. The relatively low survivorship among juveniles in the July 1971 through October period and adult males in the May through July, 1972 period were not negatively correlated with density. Adult males were well spaced by May and variations of density across quadrats was low.

TABLE 2. Effects of density on survivorship and density change during the 1971-1972 generation of prairie swifts. Double asterisk (**) indicates negative regression of survivorship or density change on initial density significant at 0.01 level; (*) indicates significant at 0.05 level; (-) indicates not significant.

	A. Survivorship (S)			B. Density change (C)		
	males	females	total	males	females	total
July, 1971						
October	-	-	-	-	**	*
October - March	-	-	*	-	-	-
March - May	** ¹	-	-	*	-	-
May - July, 1972	-	**	-	-	-	-

¹Significant only for sand-hill sub area, not for entire study area. Sand-hill sub area included about 1/3 of the area and 1/2 of the population in March.

Let us define density change as $C = N_{1n}/N_{0n}$, where " N_{1n} " equals the number of lizards residing on a particular quadrat during the second census regardless of whether or where they were marked during the first census. In other words " C " merely monitors density changes on a particular quadrat without following the fate of marked individuals. Although survivorship (S) was not regulated among juveniles in the July 1971 through October period, density changes (C) among the quadrats was (Table 2, part B). Density change was also strongly regulated for males during the March through May period, when survivorship also was regulated. During some other periods S was density dependent but C was not.

Another question asked was, "is future survival dependent on size?" We attempted to answer this as follows: We divided the lizards alive at a particular time (A) into two groups: future survivors and future nonsurvivors. Membership in the first group required a lizard to be recaptured during a future census (A+1). Those never captured during future censuses were relegated to the nonsurvivor group. The snout-vent length of the lizards, taken at time A, were compared for the two groups. A significant "t" value was assumed to indicate a dependence of future survivorship on size. Survivorship was size-dependent only among males during the March through May period (Table 3). The survivors were larger than the nonsurvivors.

TABLE 3. Mean snout-vent lengths ($\bar{x} \pm s.e.$) at beginning of period, of lizards surviving or not surviving to end of period. Asterisk (*) indicates lengths of survivors significantly different at the 0.05 level (t-test) from that of nonsurvivors.

period	MEAN SNOUT-VENT LENGTH			
	males survivors	nonsurvivors	females survivors	nonsurvivors
October - March	40.6 \pm 0.9	39.6 \pm 0.9	38.5 \pm 0.9	39.2 \pm 0.9
March - May	46.7 \pm 0.9	* 44.2 \pm 0.7	43.5 \pm 1.2	42.5 \pm 0.9
May - July	47.4 \pm 1.6	48.0 \pm 0.8	49.1 \pm 1.5	49.3 \pm 0.9

Table 4 suggests that a high female breeding density in 1972 resulted in a much lower summer recruitment of young than did the low female breeding density in 1971.

TABLE 4. Numbers of adult females and juveniles on the study area in 1971 and 1972. Asterisk (*) indicates beginning of egg laying season; (**) indicates end of egg laying season.

1971	adult females	juveniles	1972	adult females	juveniles
May*	40	0	May*	67	0
July**	25	0	July**	21	0
August	--	232	August	--	98
October	16	374	October	15	106

DISCUSSION

In our preliminary demographic analysis we have stressed certain aspects of mortality and recruitment of lizard populations that have not been previously stressed by Fitch (1940, 1956), Blair (1960), Tinkle (1967) and others. Significant periods of both density dependent and density independent mortality occurred. Males and females differed in both the severity and timing of their most critical period of mortality and regulation and this resulted in a skewed sex ratio during the breeding season.

We argue that the following factor was primarily responsible for the sex difference in mortality rate (M) in our study. Females emerged from dormancy later than males in the spring and thus were less subject than males to spring mortality factors. The following facts support this contention. Of all lizards captured during the March census the sex ratio was strongly skewed towards males (see footnote, Table 1), which would suggest that either more females than males had died since the October census or that more females than males were still dormant. More females (40 percent) recaptured in the May census were absent in the March and April census than males (20 percent). At other times these types of figures were always below 10 percent, e.g. figures comparing those present in summer and the following March but not the intervening October census. The absolute number of females was about the same in both the March and April (64) and the May (67) census but disappearance of marked individuals from April to May suggested that mortality was occurring among females.

We have tentatively identified several factors that could have operated as significant density independent mortality factors on the hatchlings during the July 1971, to October period. 1) Unsuitable physical habitat. About 20 percent of the hatchlings that were recaptured migrated long distances across the area; distances much longer than the diameter of a normal home range. Open sandy areas reached surface temperatures fatal to juvenile lizards. On one occasion, a hatchling, carelessly released onto open sand, died before our eyes. One particularly productive hatch area included predominantly open sand with little vegetation and litter. The many hatchlings marked here certainly had the opportunity to be exposed to dangerous temperatures as would any long distance migrants who were not careful in their direction of movement. 2) Opportunistic predator. Plains toads *Bufo woodhousei* were extremely abundant on the study area. They feed primarily at night, when lizards are not available. But, on warm overcast days, during which lizards were active, they sat quietly at the base of large plants. Juvenile lizards tethered by a noose and introduced near a toad by the investigators were readily eaten. It seems unlikely that toads "sought out" high density lizard areas. At least there seemed no correlation between daytime toad density and lizard density. But, the overall density of toads seemed high enough to influence the chance of survival of lizards on the study area. 3) A possible but hard to assess mortality factor could have been handling or stepping on lizards by the investigators. In practically all cases, considerable care was exercised in capturing, handling and releasing hatchling lizards. Released lizards seemed to behave normally. It is difficult to control for the

mortality effect we might have had through handling or inadvertently stepping on juveniles. This effect certainly would have been density independent since nearly all lizards were caught.

Although juvenile survivorship was not density dependent in late summer, 1971 (Table 2A), densities did equalize across the area (Table 2B). Thus, juveniles (particularly females) moved from higher to lower density areas between the late summer hatch period and October. Juveniles were observed to be aggressive at this time. This suggests that aggression may have influenced spacing without significantly affecting survivorship. At two periods there was a significant regulation of survivorship but no apparent regulation of density (October through March period for the entire population and May through July, 1972 period for adult females). This can be interpreted as follows: In winter, "good hibernating sites" are scattered. In late fall and early spring we often observed four or five lizards basking peacefully next to a particularly "good" hole. Lizards tended to congregate at these sites and were selectively removed from these areas either by predation, starvation or both. Those who, initially, were in the high density areas had a higher chance of dying before spring than those who came in later due to longer exposure to "site-selective" predators or food depletion. The densities in these areas were not regulated by aggression. Those removed were quickly replaced by immigrants. In the second example, adult females were moving to "good" egg laying sites. Again, selective predators or starvation could be selectively removing those from the high density areas. Those who started in high density areas had a higher chance of being removed than the later immigrants. Although aggression was observed among females in high density areas at this time, it apparently did not regulate the density of the area. However, female aggression could have regulated the reproductive success of losers of aggressive encounters (Table 4). By contrast, the aggression observed among the adult males in the March through May period did spouse the males, some of whom were driven out and then died due to predators or starvation. Both survivorship and density change were negatively density dependent.

The following data strongly implicate male territorial behavior as a regulating factor during the March through May period. Evans (1938) and Rand (1967) correlated relative size with winning an encounter in male iguanid lizards. Large lizards defeated smaller lizards with more than 90 percent predictability. Thus, since larger males in our study survived the heavy density dependent mortality period from March through May better than the smaller males (Table 3), larger more aggressive dominants must have successfully chased smaller lizards from their territories (Table 2B) and indirectly resulted in their death by starvation or predation (Table 2A). Fights among males were observed during this time and these never resulted directly in bodily injury or death to the loser. In contrast to males, females did not show size dependent survivorship during their period of heaviest mortality, May to July 1972. So the aggression observed during that time seemed less likely to be involved in the regulation of their survivorship than that of males.

The drastic lowering of recruitment in the season of high breeding density (Table 4) suggests three alternative causal explanations: 1) females, due to stress from aggression, starvation or both failed to produce as many eggs; 2) they produced as many eggs but they were of low quality and failed to hatch; 3) egg predators (small mammals) were at a higher density in 1972 and decimated the egg crop. Experiments are underway to determine the effects of nutrition and crowding of females on egg numbers and quality.

The returns on two seasons' collection of demographic data have proven quite rewarding. The following studies seem feasible and pertinent to the four questions outlined in the introduction. We plan to investigate these for several more years.

1) Continue monthly censuses to assess survival and recruitment of lizards.

2) Intensify censusing of female lizards during the breeding season to assess clutch size and number through weight-loss data (see Turner et al. 1970, for technique description).

3) Assess length weight ratios and juvenile growth rates to determine if starvation is an important direct or indirect mortality factor. Correlations of mortality and recruitment, length-weight or growth indices, and quantitative levels of available insects will be sought. Insects will be censused using fly paper and sweep net techniques.

4) Assess seasonal abundance of small mammal populations through live-trapping mark-and-recapture techniques.

5) Assess toad densities in fall through mark-and-recapture techniques.

6) Assess seasonal vegetation cover using point sampling techniques.

7) Each spring, determine bird breeding density through nest counts.

8) Determine seasonal variations in bird foraging activity on the study area through time-budget observation.

9) Observe lizards in field to assess frequency of aggressive encounters, to identify the winners and losers of aggressive encounters and determine the later survival, growth and reproduction of each.

10) Conduct field enclosure experiments increasing densities on parts of the area and comparing high and low density plots regarding survival and reproduction of lizards, density and movement of mammals, foraging frequency of birds.

11) Conduct laboratory experiments to assess crowding and food supply effects on behavior, survival and fecundity of adult females; hatching success of their eggs; vigor of their young. Conduct similar experiments testing crowding and food supply effects on survival and behavior of adult males.

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THE REGULATION OF BIRD POPULATIONS ON KONZA PRAIRIE. THE EFFECTS OF EVENTS OFF OF THE PRAIRIE

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Abstract. It is likely that most bird species populations are regulated, at least in part, on the wintering grounds. The birds that breed on a piece of native prairie such as Konza Prairie are known to winter on prairies from Konza Prairie south to Argentina. Thus, the bird populations breeding on Konza Prairie might be determined by events on nearly all the prairie regions in the Western Hemisphere. For example, dickcissels that breed on Konza Prairie may have been raised in Texas, and the females may have bred in Texas prior to coming to Kansas. Their nesting success may be seriously reduced by cowbirds and red-wing blackbirds, species that may be more numerous because there is more sorghum being planted in Texas where these birds winter. Thus, the dickcissel populations on Konza Prairie may be largely determined by events in the northern South American Llanos and in the Texas prairie.

I wish to consider the problem of managing a piece of native prairie so that the bird life is "natural," or similar to what existed prior to the disturbances of agriculture or development. I will attempt to apply what is known about the regulation of bird populations to this problem, and will provide an example for one species. I will show, I believe, that the bird life on a single piece of native prairie cannot be managed without deep consideration of events on grasslands all over the western hemisphere.

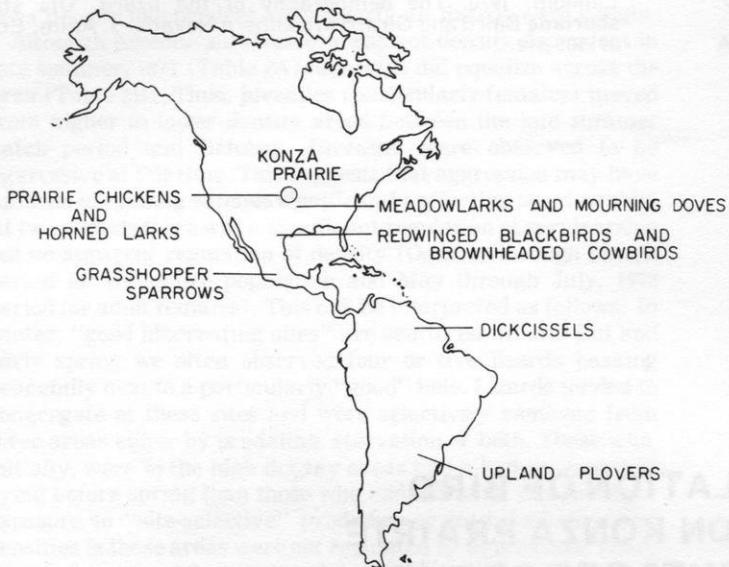
SEASONAL REGULATION IN THE BIRDS OF KANSAS BLUESTEM PRAIRIE

The single most important generalization derived from bird population research, is that populations are at least partly regulated in the non-breeding or winter season (Lack, 1966). This means that the resources available in winter typically are limited so that not all birds of a population that begin the winter can survive. It often means that breeding resources do not determine population size at all: an increase in breeding resources will often have no effect on population size. An increase in winter food, however, will presumably lead to a population increase (but see Krebs, 1971).

This generalization is not proven. It has been considered the most plausible explanation in a half-dozen studies of population regulation in temperate resident bird species (Lack 1966 provides a review, my own work, 1972 is complimentary.) Some recent research by myself and colleagues suggests that the generalization is more applicable to some bird species than to others. Most of the species that have been studied and appear to

be winter limited are year-round residents. There are few studies of migrants: they may have all the resources that they can eat in winter. So, I cannot claim that my application of this generalization to song-bird management will be altogether appropriate.

MacArthur (1959) claimed that the prairie was largely occupied by resident bird species, compared to deciduous forests in which most breeding birds are migrants. This claim has some validity on a continental scale, but it appears that almost all the birds that breed on a small 1000 acre piece of prairie such as Konza Prairie will winter elsewhere. Robel's work (1970) with prairie chickens suggests that prairie chickens will be year-round residents on the upland prairies and the same may be true of horned larks, and red-tailed hawks. Bob-white quail, mourning doves, and some owls might also appear on such an area year-round. But most of the small song birds that breed on a piece of prairie such as Konza Prairie will move away in winter. Every prairie south of Kansas harbors in winter some of the most common or conspicuous breeding birds of Konza Prairie (Fig. 1). This includes Mexican, Venezuelan, and Argentine prairies, as well as those of Texas and Oklahoma. The birds that breed together on Konza Prairie in spring represent an annual American Prairie Conference rather broader in scope than the present meeting of scientists. To the person sensitive to bird life, and aware of the life history of most of these species, a visit to the midwestern prairies in May is a way of putting one's finger on the pulse of all the grasslands of the Americas. It is an exhilarating experience.



WINTER RANGES OF SOME CENTRAL KANSAS GRASSLAND BIRDS

Figure 1. Winter ranges of some central Kansas grassland birds. The lines point to a region close to the center of the species' winter range.

My point is: if most bird's population are limited on the wintering grounds and if most of Konza Prairie breeding birds migrate elsewhere to winter, then it follows that the breeding birds of Konza Prairie are significantly, perhaps entirely, determined by events at other areas. Thus, a bird species of Konza Prairie could well disappear independently of management efforts on the nearly 1000 acres that have been set aside. If the species' wintering grounds have been seriously affected, the species could suffer a population crash so that the bird would find itself too few in numbers to populate broad areas of the country.

PROGRESS REPORT ON POPULATION STUDIES WITH THE DICKCISSEL

Realizing the above problem for several years and wanting to make the case clearer by providing an example, I have been bothered by the fact that no population study of migrant birds has been thorough enough to show the presence or absence of winter limitation. It is a gap that needs to be filled before we can confidently assert that the non-breeding season is so significant to the migrant birds of conserved areas. So, in 1964 I undertook a long-term study of the dickcissel (*Spiza americana*), named in Latin, the American sparrow. The dickcissel is a bird of the prairie, that breeds throughout the midwest and winters on the Llanos in northern South America, in Venezuela and Columbia. The males are yellow, black and grey, and appear to be patterned somewhat like a little meadowlark. Dickcissels are conspicuous, widespread, and well-known, even to non-bird watchers. The persistent, emphatic singing of the males in summer burns an impression of the bird into the mind and memory. Like the night-jars that call at night in bottomland forests, the monotonous repeated statement lulls the naturalist into reflecting upon the wilderness of himself, finding the mixture of peace and insight that is, I believe, the natural prairies' most important product.

What I will present now is a condensed review of what I have found out about the dickcissel since 1964, a statement of some of my current working hypotheses, and some predictions about the future for the species.

This research is still very much "in progress" and incomplete, despite five trips to the tropics and 40,000 miles of traveling in the midwest. While there is little direct evidence that dickcissels are winter limited, the indirect observations that I have been able to make are consistent with that hypothesis.

In late summer and early fall, dickcissels end their breeding activities in the midwestern U.S., and migrate south to Venezuela. They travel in large flocks, and are a nuisance to rice growers throughout Central America. They pass by a given area slowly, off and on for several months, up into October. At the end of October, however, most seem to be somewhere in southeast Venezuela. I have never traveled to South America this early in winter, so we know very little about exactly where. Then, in December or January (my own observation plus talks with farmers) (Fig. 2), there is an outward migration, east to Trinidad (ffrench, 1967), or west to the Andes.



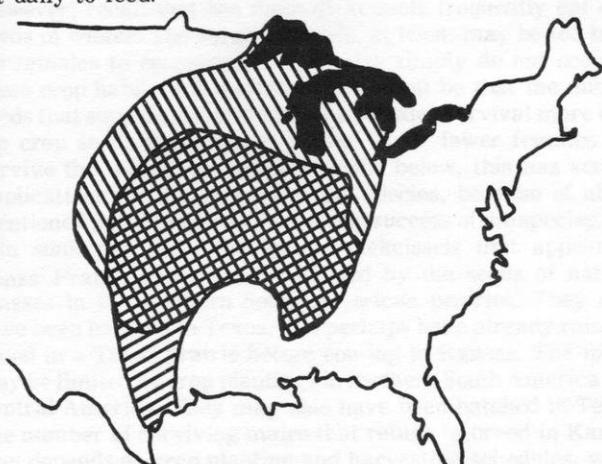
Figure 2. Winter range of the dickcissel. The species is localized until mid-December somewhere in eastern Venezuela. From this region, it spreads out as winter progresses with reports from as far north as Mexico. Most of the information is anecdotal, and refers to major population movements. Isolated dickcissels are reported from all regions north of Venezuela into the United States all winter long (AOU 1957).

I believe that this is a response to natural food shortages, and have found (unpublished report) that the members of the population that move are the ones that should be most severely affected by natural food shortages. For example, in the banding data of ffrench on Trinidad (1967), we found that large males move sooner than small males, juveniles move sooner than adults and females move least of all. Large males need more to eat than the smaller males or females, and so they should be more stressed by a food shortage. Juveniles (both large and small, male or female) tend to be subordinant and inexperienced and so they also suffer when food is short. Thus, females should have the greatest competitive advantage under food stress on natural foods.

This picture is muddied by the occurrence of crop seeds that are preferred by the larger males. Thus, in a sorghum field, mostly very large males were found eating the seeds. I think that this further reflects the food stress of the males, but it appears that these sorghum plantings might "save" the large males from starvation.

The time of the midwinter movement varies, and late movements, which suggest less food shortages seem to be associated with population increases in the U.S., especially of females. There are some remarkable tales associated with these midwinter movements. A farmer of German descent in Colombia talked of hordes of birds invading his rice fields in January and being so hungry that they could not be driven from the fields, and could be killed with sticks.

The midwinter movements apparently continue through March (Zimmerman 1963, Hespenheide letter). Some birds, mostly small males and females, seem not to move at all, but other birds, mostly very large males and some large females will probably move all the way back to Mexico. The emigrating birds are almost always found in crop habitats, sorghum and rice. Wherever the dickcissel occurs in the winter, they spend the night in large roosts of millions of birds, from which they fly out daily to feed.



SEASONAL CHANGES IN DISTRIBUTION OF MALE DICKCISSELS

MAY

JUNE - JULY

Figure 3. Breeding range changes of male dickcissels. The spread of dickcissels across the U.S. starts in Texas in late April and males appear in Kansas in early May. Males do not appear to arrive in the northern states and on the east or west fringes of the range until mid-June, however.

In mid-April, the birds fatten considerably in preparation for a return to the U.S. to breed. I'm quite puzzled at how they can fatten, if food is so limited, but they often nearly double their weight in just a few days. Richard ffrench (1967) in Trinidad describes the birds leaving the roost at dusk around April 15, probably to fly non-stop to Texas. They arrive in Texas in mid-to late-April. Apparently many males (Figure 3), and a very few females migrate on to Kansas and the more northern mid-western states. Most females appear to stay in Texas (Figure 4), and we have hypothesized that most attempt to breed there. Later on, in June, females begin to arrive in numbers in the central and northern prairie (Zimmerman, 1966). We suspect that many females arriving in Kansas in June have already successfully fledged a brood in Texas.



SEASONAL CHANGES IN BREEDING DISTRIBUTION OF FEMALE DICKCISSELS

MAY

JUNE - JULY

Figure 4. Breeding range changes of female dickcissels. The females arrive in Texas a week after the males, but do not appear in Kansas in numbers until June. A few females can be found in Kansas and more northern regions in May, but most males in central Kansas are unmated for 3 weeks or longer after they arrive.

There are two issues in regard to the summer changes in distribution that require elaboration. I propose first that dickcissels normally attempt two broods and second that they move from Texas to some northern state for their two attempts. The evidence regarding two broods is meagre, but is as follows. In North Carolina (1967) I studied one mated female that had to stay in one place all summer. Dickcissels are very rare in North Carolina and she had no other males to move to. This female attempted a second brood after she had been successful with her first. If this North Carolina female was typical dickcissels may well all rear second broods. But John Zimmerman (personal communication) is convinced that in Kansas only one brood is reared, and Margaret Francis found this to be true in Texas, also. If dickcissels do raise two broods, it appears that they must move to do so.

Why should female dickcissels make this mid-summer migration? John Zimmerman has brilliantly shown that in an area where dickcissels breed, there is a very special time for

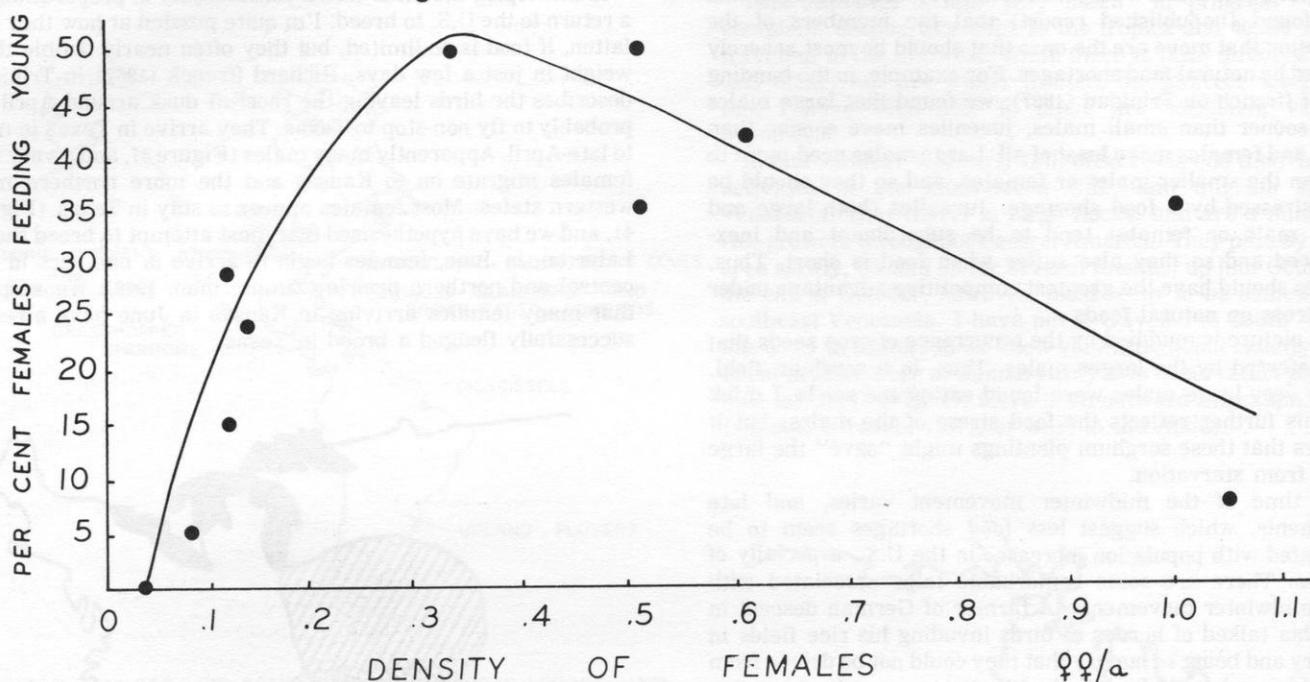


Figure 5. Visits to breeding areas were made three weeks after the females had arrived and had started nesting. Each female seen was scored for the stage of the nesting cycle that she had reached. Females were scored either as feeding nestlings or fledglings, or being in some other stage of nesting. The density was estimated from the number of females seen per acre. The percent females that were sufficiently successful to be feeding young was computed, and compared to the density. Females at low densities appeared to be least successful in rearing young.

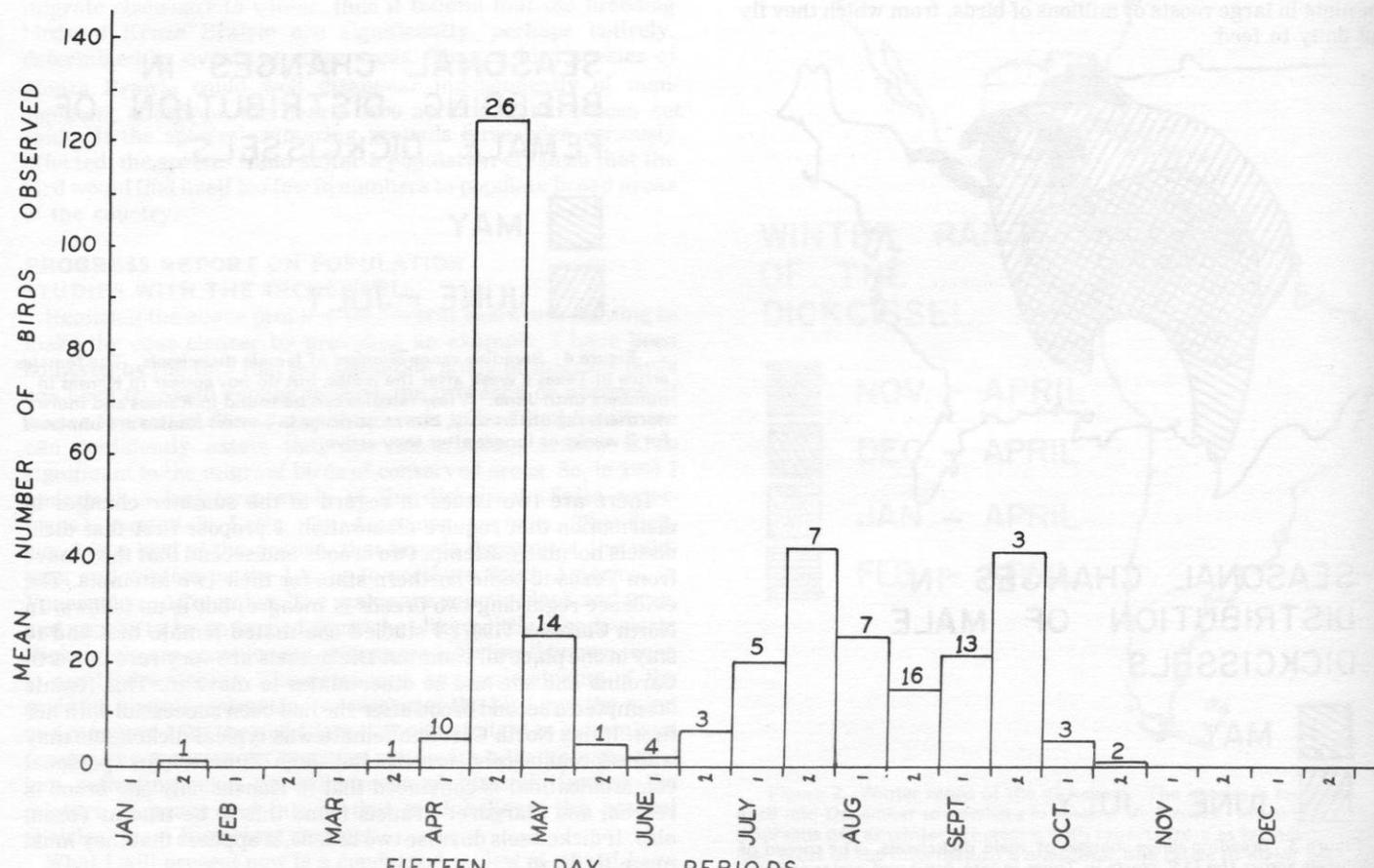


Figure 6. Census data from south Texas shows a spring migration peak as the dickcissels arrive and two late summer and fall peaks as the birds return to the Llanos to winter.

dickcissel reproduction. Zimmerman, in a presentation at the American Ornithological Union meetings in 1969 presented evidence showing that dickcissel nests in Kansas in May are so seriously parasitized by cowbirds that they are not successful. July nests, on the other hand, are heavily preyed upon. So, June is the best time for breeding in Kansas because neither cowbirds nor predators are such a serious problem. Probably May is the best time in Texas, and perhaps, July in the Dakotas. Also, I have found (Figure 5) that female dickcissels seem to be more successful when nesting at higher densities. Apparently cowbird parasitism is not so serious when the density of hosts is high because there are too many nests for the cowbirds to lay eggs in them all.

I think that the special timing and density requirements of female dickcissels has led most of them to stay in Texas for their first broods in May. By staying together, they raise the density to optimal values and they all get to breed when the time is right (May). Then in June, they move to Kansas for second broods, raised at high densities and when the time is right.

There is, in Texas, a migration in late July and another one in September (Figure 6). I have hypothesized that these are the young of the first and second broods migrating at different times. The second peak also should contain more females. This hypothesis needs testing.

There do not seem to be enough dickcissel females to go around. Sex ratios in winter always favor males, and in summer many males go unmated. Only one male in three across the northern tier of midwestern states has a mate at any one time, even in July when there are no females breeding in Texas. In Texas in May, there are a few more females than males in good habitats, but dickcissels are polygynous and males in good areas get more than one mate, while males in poor areas go unmated (Zimmerman, 1966).

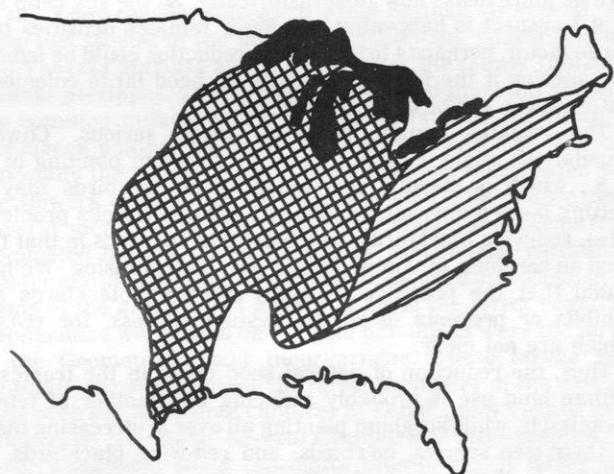
This shortage of females is puzzling since it seems that females have a competitive advantage on natural seeds. However, recall that the male dickcissels frequently eat crop seeds in winter. The sorghum seeds, at least, may be too large for females to consume, and females simply do not occur in these crop habitats in winter. It may well be that the natural seeds that support females limit the females survival more than the crop seeds that support males. Thus, fewer females can survive the winter. As I will describe below, this has serious implications for the success of the species, because of above mentioned peculiarities in the nesting success of the species.

In summary then, the female dickcissels that appear on Konza Prairie appear to be limited by the seeds of natural grasses in the northern South American prairies. They may have been hatched in Texas, and perhaps have already raised a brood in a Texas prairie before coming to Kansas. The males may be limited by crop plantings in northern South America and Central America. They may also have been hatched in Texas. The number of surviving males that return to breed in Kansas then depends on crop planting and harvesting schedules, while the number of surviving females depends on the seed production of wild grasses. We should be able to correlate the population fluctuations of female dickcissels (and, so, of males in later years) with rainfall and grazing pressure on these Venezuelan grasslands. Male numbers should be more stable, but should depend on levels of sorghum plantings and success at harvesting in these tropical countries.

To properly interpret these scattered observations, consider what happens when dickcissel numbers increase. Zimmerman and I both observed increased rates of nesting success in 1967 when female dickcissels were especially common (Zimmerman 1971, 1966). Thus, the population experiences positive feedback on its breeding grounds, which cannot limit population growth.

Further verification of some of these ideas comes in an observation on the historical population trends in the dickcissel (Figure 7). Dickcissels once ranged from the midwest to the Atlantic coast, but the species became extinct in the east in 1870-

1880. (Rhoads 1903). This extinction does not appear to have been caused by a failure of dickcissels to breed successfully in the East, because I have found that they can rear young there (Fretwell, 1967). Instead, I have found that there was a major expansion of the cattle industry on the Venezuelan Llanos from 1873-1884. (Wilgus 1941, p. 527). The number of head of cattle increased from 1.4 million to nearly 10 million, more than are now present. Dickcissels winter strictly in lush, high grass, and avoid grazed habitats (personal observation). Therefore, it is likely that the increased number of cattle decreased the acreage of suitable wintering habitats, and so, the overall population size of the dickcissel. Without crops available as an alternative food, this affected males as much as females so the males became simply too scarce to inhabit areas as far from the center of the range as the Atlantic coast. I looked at museum specimens from that period and found that it was the larger males that suffered most in the population crash, consistent with the food stress ideas present above (See Table 1).



HISTORICAL CHANGES IN THE BREEDING RANGE OF THE DICKCISSEL

PRIOR 1870
POST 1880

Figure 7. Reduction in the breeding range of dickcissels about a century ago.

Table I

Changes in average wing length in male Dickcissels collected over the period 1873 - 1884.

Date	Sample Size	Mean Wing Length mm
Prior 1873	28	83.50
1874 - 1884	45	82.62*
1884 - 1900	58	82.79*

*in both later periods, the wing length of males was shorter than prior to 1873, and the difference was statistically significant.

PROGNOSIS FOR THE FUTURE OF DICKCISSELS

I suspect that the dickcissel might be an endangered species. The natural seeds limiting females appear to be in short supply and getting scarcer, especially as human population pressure puts greater grazing or land use pressure on habitats now used by females for feeding. Conversely, the crop habitats used by males for feeding are increasing, for the same reasons. As a result we have already observed a sex ratio favoring males and we predict that the sex ratio will change to favor males more and more. On the breeding grounds, females apparently must occur at high densities in colonies to successfully reproduce (Figure 5). However, the females may not have any ability to congregate. They may depend on male colonies to pull them together. Historically, it seems likely that before man's influence, there were two or three times as many females as males in any given habitat. The trend now is for females to be one-third as dense as the males in any given habitat. The males set their density by territorial behavior (Zimmerman 1971), and are no more dense now than historically. So the sex ratio shift that I suspect is happening will lower females densities by a large factor, perhaps 4 to 9 fold. This reduction could be lethal to the species if the females actually do need large colonies to saturate the cowbird parasitism.

The situation might even be more serious. Cowbird populations might well be limited by sorghum planting in the U.S., which is steadily increasing. Thus, cowbirds may be getting more numerous, to intensify the dickcissel's problems. Also, red-wing blackbirds, which are like cowbirds in that they feed on sorghum in winter, might also be increasing. We have found that the presence of many red-wing blackbirds also inhibits or prevents dickcissel nesting success, for reasons which are not clear.

Thus, the reduction of natural seed crops in the tropics by human land use is probably reducing the number of female dickcissels, while sorghum planting all over is increasing males of their own species, cowbirds, and red-wing blackbirds. Increases in their own males threaten to reduce the females' breeding density, so that the cowbirds exploit them more efficiently. Increases in cowbirds intensify the cowbirds' exploitation, and an increase in red-wing blackbirds causes other problems.

Obviously, all bird species have problems, but few besides the dickcissel have such low nesting success in so many studies (e.g. Zimmerman 1966). If my fears are correct, the dickcissel is in trouble. What is especially ominous is this: the year when the species becomes doomed to extinction will be a year when males are most numerous and widespread. Observers will all report that dickcissels are "up," because bird watchers mostly count males and males will be numerous and widespread. But, that would be the year that females were too few relative to males to achieve many effective colonies. Females will be so thinned out that they will not reproduce enough to replace their losses due to death. Males will probably survive better than females, because of the constantly increasing availability of crops, so that once females are too thinned out to breed successfully, their numbers relative to males will continually decrease. Then they will become more and more thinned out as time passes, and will be less and less successful in breeding. Like the passenger pigeon, the dickcissel could become effectively extinct while still very numerous. It will be endangered without first becoming rare.

I hope I am wrong, and I may well be. We have much to learn about the dickcissel, and later information could well change my prediction. Perhaps the females will always collect in south Texas in sufficient numbers to maintain high breeding densities there.

My research on the dickcissel shows, I hope, how much the biology of migrant birds on a piece of restored prairie could depend on events off of the natural area. Each of these species carries with it a record of circumstances in other prairie regions, including the results of droughts, floods, over-grazing and crop plantings. So, as far as the birds are concerned, a natural area can never be altogether natural, and certainly cannot be regarded as self-contained.

Scientific Names of Birds Mentioned in the Text

Red-tailed Hawk	Buteo jamaicensis
Upland Plover	Bartramia longicauda
Bob-white	Colinus virginianus
Prairie Chicken	Tympanuchus cupido
Passenger Pigeon	Ectopistes migratorius
Mourning Dove	Zenaidura macroura
Horned Lark	Eremophila alpestris
Cowbird	Molothrus ater
Red-winged Blackbird	Agelaius phoeniceus
Meadowlark	Sturnella magna
Grasshopper Sparrow	Ammodramus savannarum
Dickcissel	Spiza americana

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INSECT DIVERSITY AND ASSOCIATIONS IN A RESTORED PRAIRIE

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Abstract. From mid-June to mid-August 1972, a survey of insects in a restored prairie was carried out on the Knox College Biological Field Station located twenty miles east of Galesburg, Knox County in west central Illinois. Of special interest were the insect-plant associations, particularly involving native insects and certain prairie forbs. The restored prairie was not uniform, but offered a variety of different grass-forb combinations and prairie-forest ecotones. This habitat diversity was coupled with a diverse insect population which ranged from natives to more cosmopolitan species. Some insect associations found on some common weedy plant species are also included in this study.

This paper reports on the various insect families and insect-plant associations observed on the restored prairie habitats of the Knox College Biological Field Station from mid-June to mid-August of 1972. The Knox Field Station is located twenty miles east of Galesburg, Knox County, in west central Illinois.

Due to the settlement of the prairies and the eventual development of metropolitan areas, a great many of the life forms, both plant and animal, were forced to redistribute or adapt to their new environments. Those which could adapt and survive were the organisms which had the shortest generation periods and could make these adaptations the quickest. The insects are both persistent and highly adaptable and are therefore likely to exhibit many of the same families today that were evident 150 to 200 years ago.

The original vegetation of the area consisted of tall grass prairie interfingered with oak-hickory forests. Prior to 1955, this area had been devoted to crop raising. From 1955 to the present, the area has undergone extensive restoration which has resulted in a well established tall grass prairie with some of the most important prairie forbs well represented.

This somewhat recent prairie restoration has provided habitat for an aggregation of native and cosmopolitan descendants of the original prairie insects. Using this idea as a starting point, we assumed that, for the most part, the families found in the restored prairie have not undergone too great an evolutionary change and would provide a sound basis for our study and others to follow.

MATERIALS AND METHODS

The daytime collecting was done with air nets and beating nets. The night trapping was done with a light trap which was moved throughout the various sectors of the prairie. The prairie at the field station can be subdivided into three sections: an east, west, and a south prairie. The east prairie is characterized by a close proximity to the lake and the forest. The west prairie also has a perimeter bordered with forest, but is further removed from the lake. The south prairie is the furthest from the lake and includes a one-acre plot of a commercial switchgrass from which insects were also collected. These three sections all contain a wide variety of plants ranging from the best prairie plants to introduced weedy types. Two of the weedy plants which were of note were *Pastinaca sativa*, the wild parsnip and *Asclepias syriaca*, the common milkweed. Although these two plants are not climax prairie plants, they did provide a great number of insects included in this study.

From mid-June to mid-August of 1972, a concentrated series of collections were taken at the field station. Trappings were conducted at a variety of times and under a variety of weather conditions. Although a superficial population study was conducted, not enough evidence could be compiled to substantiate presentation of our results at this time. The bulk of our study will be concerned with the presentation of the various families collected and, wherever possible, the plants with which they were associated. (Table 1).

OBSERVATIONS AND CONCLUSIONS

The Lepidoptera were common throughout all of the prairies at the Knox College Biological Field Station. Of special note were two species of the family Nymphalidae, *Speyeria cybele* and *Vanessa atalanta* and one species of the family Danaidae, *Danaus plexippus*. These three species feed upon the nectar of the common milkweed. The Satyridae favored the flower of *Echinacea pallida*, the pale purple coneflower. The Pieridae, especially the species *Colias eurytheme*, were associated with the flowers of *Silphium terebinthinaceum*, the prairie dock. Several members of the families Arctiidae and Ctenuchidae frequented the flowers of *Eryngium yuccifolium*, rattlesnake master and prairie dock. The Hesperiidae were noted among the stems of the grasses and forbs and along the forest edge. The Papilionidae were found on the wild parsnip as were the larvae of the Geometridae and Incurvariidae. These larvae were especially prominent along the forest perimeter of the east and west prairies. Nighttime captures of Lepidoptera yielded great numbers of Noctuidae. Several Geometridae were trapped, the genus *Caberodes* being especially prominent. Of lesser note were the captures of four other families (Ceratocampidae, Lithosiidae, Sphingidae, and Yponomeutidae).

The Coleoptera were well represented in all the habitats of the prairies. An important introduced family, the Coccinellidae, and the Carabidae were effective predators and were found nearly everywhere. These two families are predaceous in their larval and adult stages (Frost 1959). The Meloidae are predaceous on grasshopper eggs as larvae while the adults are plant eaters. The Cerambycidae frequented the leaves and flowers of the common milkweed. The Chrysomelidae were widely represented on *Amorpha canescens*, leadplant, *Silphium laciniatum*, compassplant, wild parsnip, and among the switchgrass of the south prairie. A genus of this family, *Orsodacne*, was collected in great numbers on the flowers and leaves of the common milkweed. The adults of these plant feeding beetles that hibernate had disappeared by mid-July (Chauvin 1967). The Curculionidae were frequenting *Baptisia leucantha*, the white false indigo and the wild parsnip. The Mordellidae, Lampyridae, and Cantharidae were found in great numbers on rattlesnake master. The Doscillidae were collected on the prairie dock. Four other families were found in the litter layer of the prairies (Mycetidae, Elateridae, Scarabaeidae, Melandryidae). Nighttime collections yielded the families Lampyridae, Elateridae, Carabidae, Coccinellidae, Cerambycidae, Curculionidae, and Scarabaeidae. The Scarabaeidae were the most common at night in both species and number.

The Hymenoptera were undoubtedly the most active insects during the day. They exhibited the greatest number of species and individuals of any of the orders despite the cool, wet summer. In the early summer, the larvae of the family Tenthredinidae were quite abundant in the big bluestem along the forest edge. The Bombidae, Formicidae, Halictidae, and Apidae all favored the wild parsnip and pale purple coneflower. The Apidae are one of the most important introduced insects found

Table 1. Association of insect families with selected plant species.

	WEEDS				PRAIRIE PLANTS				
	<i>Asclepias syriaca</i>	<i>Pastinaca sativa</i>	<i>Amorpha canescens</i>	<i>Andropogon gerardii</i>	<i>Baptisia leucantha</i>	<i>Echinacea pallida</i>	<i>Eryngium yuccifolium</i>	<i>Petalostemum purpureum</i>	<i>Silene laciniata</i>
Coleoptera:									
Cantharidae								abundant	
Carabidae	common								
Cerambycidae	abundant								
Chrysomelidae		common	abundant						
Coccinellidae	common								abundant
Curculionidae		common			common				
Doscillidae									
Lampyridae									
Meloidae		abundant			common			abundant	
Mordellidae								abundant	
Diptera									
Asilidae						abundant			
Mydidae							rare		
Syrphidae		abundant					abundant		
Tachinidae		common					common		
Hemiptera									
Coreidae					common				
Reduviidae		abundant	abundant	abundant					
Homoptera									
Aphididae	common								
Cercopidae								common	
Cicadellidae	common								
Fulgoridae	common								
Membracidae									
Hymenoptera									
Andrenidae									
Apidae		abundant				abundant		abundant	
Bombidae		abundant				abundant			
Chrysidae			abundant			abundant			
Formicidae		abundant				abundant		abundant	
Halictidae		abundant				abundant			
Ichneumonidae		abundant				abundant			
Megachilidae						common			
Sphecidae		abundant							
Tenthredinidae					common				
Tiphidae							abundant		
Vespidae		common	abundant					common	common
Lepidoptera									
Arctiidae									
Ctenuchidae									
Danaidae		abundant							
Geometridae *			abundant						
Incurvariidae *			abundant						
Nymphalidae		abundant							
Papilionidae		abundant							
Pieridae									common
Satyridae									
*larvae									

at the field station. The Ichneumonidae were common among the wild parsnip as they parasitize the Lepidoptera larvae which frequent it. The Tiphidae, which frequented the wild parsnip and rattlesnake master, are noted for their predation upon a variety of beetle grubs (Frost 1959). The Tiphids, along with the Braconidae and the Ichneumonidae, are the more important Hymenopteran families from a standpoint of biological control. The Andrenidae and Chrysidae were common on all the major forbs, especially leadplant, *Petalostemum purpureum* purple prairie clover, and pale purple coneflower. The Megachilidae were associated with leadplant and pale purple coneflower. The Andrenidae and Megachilidae are native solitary bees. The Sphecidae and Vespidae frequented the wild parsnip. The Vespids were also found on purple prairie clover, and a nest was found on a leaf of prairie dock. Some members of the Chalcididae were taken in the dense plot of switchgrass in the

south prairie. Other families noted were the Pelecinidae, Colletidae, and the Pompilidae. The Pompilidae, the spider wasps, are of note because of their parasitoid nature. They construct a nest in which they place the host to feed their larvae. Nighttime collecting yielded three families of Hymenoptera. There were the Formicidae (winged sexual forms), Braconidae, and the Ichneumonidae. The last of these was the most common.

The Diptera nearly equalled the Hymenoptera, both in variety and number. The Syrphidae, which frequented the wild parsnip and rattlesnake master, did double duty as predators and pollinators. The Tabanidae and Culicidae were common throughout the prairies at the field station as would be expected. The Asilidae, which are extremely predaceous, were observed ovipositing on pale purple coneflower. The Tachinidae, which are found on the wild parsnip and rattlesnake master, are important parasitoids of Lepidoptera larvae (Frost 1959). The

Sarcophagidae are parasitoids of a number of other orders and were taken in the switchgrass plot. Nine other families were captured in some number. A species of Mydidae, *Mydas clavatus*, was taken from a flower of rattlesnake master. Night trapping yielded a large number of families in about equal number and frequency. Among those noted were the Cecidomyiidae, Mycetophilidae, Dolichopidae, Trupaneidae, Agromyzidae, and Ephyrinidae. The most common family captured was the Chironomidae of which several species were noted.

Many members of the Hemiptera are predaceous. Most notable of these in the restored prairies at the field station were the Reduviidae and certain species of Pentatomidae. The Reduviidae were omnipresent but especially so in the stands of big bluestem, wild parsnip, and leadplant. Two families were found in shallow temporary ponds in the prairie. These were the Hydrometridae and the Gerridae. Both of these families are extremely predaceous. Some of the less prominent families noted were the Pyrrhocoridae and the Scutelleridae. The Coreidae were found on the white false indigo. Only two families of Hemiptera were taken at night, the Lygaeidae and the Miridae of which the Miridae were more common.

The Homoptera, which are wholly phytophagous, have the dubious distinction of supplying the prey and hosts for a variety of other orders. The Fulgoridae, Cicadellidae, and the Aphididae were especially common along the forest, but were found in some number on nearly all the plants in the prairies. The Cercopidae were taken from the south prairie switchgrass plot and on the flowers of the compassplant. The Membracidae were collected on the white false indigo. The Fulgoridae and Cicadellidae were especially common and trapped in great numbers at night.

Although more numerous in the parts of the prairies closest to water, the Odonata would have to be considered common throughout the prairies at the field station. Two species of Libellulidae were prevalent. *Libellula luctuosa* was common flying above the level of the prairie while *Erythemis simpliciollis* flew through the grass. The Coenagrionidae, and all the other Odonata collected were noted for employing the stems of big bluestem and some forbs as resting sites.

Four families of Orthoptera were taken from the litter layer of the prairies. The Locustidae, Tettigoniidae, Blattidae, and Gryllidae were all evidenced in great numbers. The Locustidae and Gryllidae were most prevalent along the forest edge.

The Ephemeroptera were represented by several members of the Ephemeridae. As with the Odonata, they were more frequent close to the lake.

One order of insects was taken at night only. These were the Trichoptera, the family Limnephilidae, the caddis flies.

As stated earlier, this project is to serve as the basis for more specialized studies to follow. By further study of the associations of the introduced and native insect species with the flora of restored prairies, a broader concept of relationships, adjustments, and interdependencies in the prairie community can be developed.

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A COMPARATIVE SURVEY OF SMALL MAMMAL POPULATIONS IN VARIOUS GRASSLAND HABITATS WITH EMPHASIS ON RESTORED PRAIRIE

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Abstract. During the spring and summer of 1972, a survey of small mammal populations was conducted in restored prairie and other grassland habitats of the Knox College Biological Field Station in Knox County, west central Illinois. A total of eleven different plots were divided into groups and live-trapped in order to determine the comparative densities and species composition of the small mammal populations present. Several of the plots were burned during the spring and some data on the immediate effects of fire on the populations were obtained. *Microtus pennsylvanicus*, *Peromyscus maniculatus*, and *Peromyscus leucopus* were the most common species present on the plots. We concluded that restored prairie vegetation supports higher and more diversified populations than do other grassland habitats such as orchard grass and other cool-season pasture grasses. Fire had a short-term detrimental effect on the densities of the small mammal populations with the possible exception of *P. leucopus* which invaded from woodland habitats. The results also indicated that litter accumulation and vegetational density may be key factors in determining the numbers of small mammals present.

The Knox College Biological Field Station, located in Knox County, west central Illinois, offers an opportunity to study the relationship between various grassland habitats and small mammal populations. The field station offers a variety of habitats within a relatively small area ranging from areas of cool-season pasture grasses to stands of restored prairie grasses and prairie forbs.

During the spring and summer of 1972, a survey of small mammal populations was conducted on eleven study plots of varying plant composition. This survey would determine which

small mammals species were present in the grassy habitats of the station and whether they showed a preference between restored prairie plots and pasture grass plots. A burn is conducted annually on portions of the prairie and some results from the immediate, short-term effects of fire on the small mammal populations were obtained from several plots located in the burn areas.

METHODS

Each area was surveyed by trapping with Sherman and

Longworth live traps. Two parallel lines of traps which were approximately thirty feet apart were placed in each area surveyed. Sherman traps were used for one line and Longworth's for the other. The traps were spaced fifteen feet apart in each line. The length of the lines were adjusted according to the size of the plot with the longest lines consisting of fifteen traps and the shortest, seven traps.

Sunflower seeds were used for bait. The traps were prebaited for one night before being set. The traps were then set continuously for two days during the trapping periods in the spring, and for four days during the summer trapping periods. All captured animals were toe-clipped for identification and then released. Pertinent data was recorded on IBM mark sense cards.

Descriptions of the Survey Plots

The following is a list of the plots surveyed with descriptions of their vegetational composition and other pertinent information. All prairie grass species were of local ecotypes (Knox County) except the commercial switchgrass plots which were from Wilson Seed Farms (Blackwell switchgrass), Polk, Nebraska. The number in parentheses following the name of the plot coincides with a location indicated on the map of the Field Station in Figure 1.

Indiangrass (1): Indiangrass (*Sorghastrum nutans*) was the dominant grass, with some big bluestem (*Andropogon gerardi*) present. The dominant forbs were yellow cone flower (*Ratibida pinnata*), whorled milkweed (*Asclepias verticillata*), and some tall goldenrod (*Solidago altissima*). This plot was a very narrow strip approximately fifty feet wide bounded by a gravel road and a strip of bluegrass. Patches of bluegrass were scattered throughout the stands of prairie grasses. This plot had a one-year accumulation of litter. Each trap line consisted of fifteen traps.

Switchgrass (2): This plot was dominated by very thick native switchgrass (*Panicum virgatum*) with black-eyed susan (*Rudbeckia hirta*) the only forb present. This plot ran parallel to the preceding plot with a distance of twenty feet separating the two plots. It also had a one-year accumulation of litter and fifteen traps in each line.

Burned Big Bluestem (3): Big bluestem dominated this plot, but a good representation of compass plant (*Silphium laciniatum*) and rattlesnake master (*Eryngium yuccifolium*) were present. Fifteen traps were in each line on this plot and there was no litter accumulation as this was one of the burned plots.

Weedy Big Bluestem and Indiangrass (4): The vegetation was an equal mixture of indiangrass and big bluestem. The dominant forbs were yellow cone flower and ashy sunflower (*Helianthus mollis*). Only half of this plot was burned. The unburned half had a one-year accumulation of litter. Eight of the fifteen traps in each line were on the burned portion of the plot with the other seven on the unburned portion.

Forby Big Bluestem and Indiangrass (5): This plot was a very pure prairie stand with big bluestem and indiangrass predominating. Prairie cone flower, rattlesnake master, prairie dock (*Silphium terebinthinaceum*), compass plant, pale purple cone flower (*Echinacea pallida*), rosinweed (*Silphium integrifolium*), and spiderwort (*Tradescantia ohiensis*) were the most common forbs. This plot was isolated for much of the study period by bare plowed ground. During the end of the study this ground became overgrown with annual weeds. Due to the size of the plot, only ten traps were used in each line. This plot was burned on the same day as were plots 3 and 4 (April 18).

Unburned Big Bluestem (6): Big bluestem dominated this plot which also had a very good representation of the forbs prairie dock, compass plant, prairie cone flower, and rosinweed. This plot had a two-year accumulation of litter. This small plot had only seven traps per line.

Commercial Switchgrass I (7): This plot was a two-year old planting of commercial Nebraska Blackwell Switchgrass seed

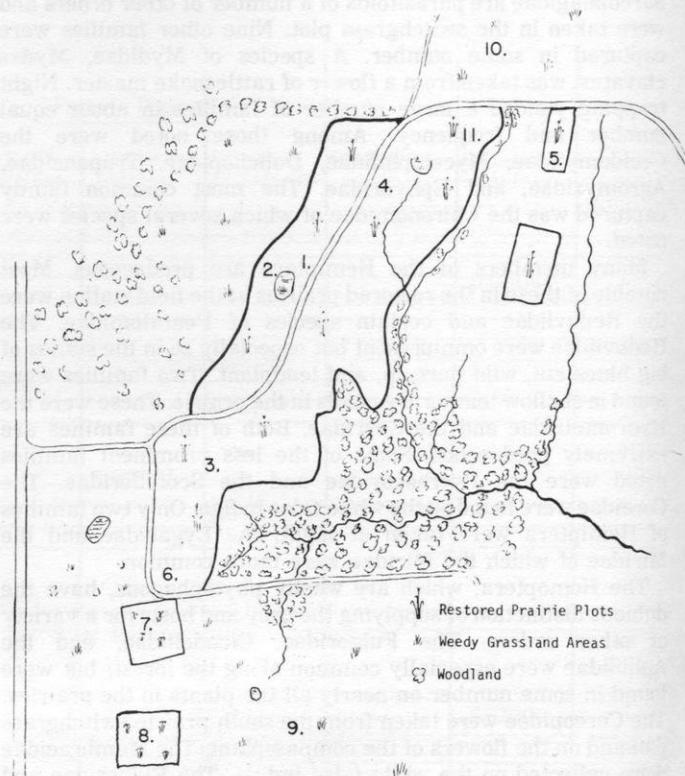


Figure 1. Map of Knox College Field Station showing the different grassland plots (numbered).

that was completely dominated by this species to the virtual exclusion of anything else. The grass was short but very dense. In spite of the fact that there was a one-year accumulation of litter, the ground was almost bare. There were seven traps in each line.

Commercial Switchgrass II (8): This plot was a similar planting of the same variety as plot 7, but it was planted three weeks later (summer of 1970) and not hand-weeded as Plot 7 was. There was a noticeable difference in the height of the switchgrass of the two plots. This plot was almost one foot shorter than that of Plot 7. It also had a one-year accumulation of litter and seven traps per line.

Orchard Grass (9): This plot was located in an extensive tract of grassland dominated by orchard grass and patches of smooth brome. The predominant forb was tall goldenrod. This plot had a minimum of a four-year accumulation of litter. There were seven traps per line.

Bluegrass (10): This very weedy bluegrass-dominated plot was heavily infested with tall goldenrod, curly dock and sweet clover. Tree invasion had also started. This plot had a minimum of a four-year accumulation of litter. There were fifteen traps in each line.

Unburned Big Bluestem and Indiangrass (11): This plot was very similar to Weedy Big Bluestem and Indiangrass (4) Plot. The grass present consisted of an almost equal amount of big bluestem and indiangrass with some dense stands of switchgrass at one end of the plot. The dominant forb was ashy sunflower and there were scattered concentrations of sweet clover. Fifteen traps per line were used and the plot had a one-year accumulation of litter.

Comparison Groups

The plots were divided into groups for comparison and the survey was conducted in such a way that all the plots of one group were trapped simultaneously. The plots were divided into the following groups:

- 1) Sudangrass (1) and Switchgrass (2)

2) Unburned Big Bluestem (6) Commercial Switchgrass I (7), Commercial Switchgrass II (8), and Orchard Grass (9).

3) Bluegrass (10) and Unburned Big Bluestem and Indiangrass (11).

4) Burned Big Bluestem (3), Weedy Big Bluestem and Indiangrass (4) and Forby Big Bluestem and Indiangrass (5).

Groups 1 and 2 were trapped during three different periods. Group 3 was trapped only once. Group 4 contains the plots that were burned. This group was trapped six different times, but several of these trapping periods were conducted during succeeding weeks. The burn was conducted on April 18 using methods described by Schramm (1970).

RESULTS AND DISCUSSION

During the course of this survey, nine different species of small mammals were captured on the various plots. The species represented were the meadow vole, *Microtus pennsylvanicus*; prairie vole, *M. ochrogaster*; white-footed mouse, *Peromyscus leucopus*; meadow jumping mouse, *Zapus hudsonius*; western harvest mouse, *Reithrodontomys megalotus*; house mouse, *Mus musculus*; short-tailed shrew, *Blarina brevicauda*; and the masked shrew, *Sorex cinereus*. Several of the species were present in such low numbers that not enough captures were made to determine their preferred habitats. These species were *Zapus hudsonius*, *Reithrodontomys megalotus*, *Mus musculus*, *Sorex cinerus*, and, in some cases, *Microtus ochrogaster* and *Blarina brevicauda*.

Group I—Indiangrass (1) and Switchgrass (2) Plots: Three species were present in enough numbers to warrant consideration (Figure 2). *Microtus pennsylvanicus* was the most common species. Both plots had equal numbers of individuals during early April, but during the interval between early April and the latter part of June the population of the Indiangrass Plot decreased while that of the Switchgrass Plot increased. Since both plots had a one-year accumulation of litter, this difference would appear to be related to the better protection afforded by the denser vegetation of the Switchgrass Plot. No reason is known for the marked decline in population between June and late July, especially on the Switchgrass Plot. A similar decline of almost all *M. pennsylvanicus* populations of the plots surveyed occurred during the month of July.

Peromyscus leucopus numbers were low on these two plots throughout the course of the study (Figure 2). Both of these plots were isolated from optimum habitat for this species which is primarily a woodland animal. This would account for the low numbers.

Peromyscus maniculatus bairdii, considered by many to be a prairie species, was present on both plots but in very low numbers. The population of the Switchgrass Plot remained constant during the survey (Figure 2). The population of the Indiangrass Plot was higher during June and July and it increased between April and June. However, the burned half of the Weedy Big Bluestem and Indiangrass Plot was separated from this plot by only a gravel road. After the burn, several individuals that were captured on the burned plot ran to the Indiangrass Plot after being released. It appeared that they were residing in the Indiangrass Plot, but for the most part foraging on the burned plot.

Several individuals of *M. ochrogaster* were captured on the Indian Grass Plot. One individual was captured during early April and three during late July. Two individuals of *Sorex* were also captured on the Switch Grass Plot during early April.

Group 2—Unburned Big Bluestem (6), Commercial Switch Grass I (7), Commercial Switch Grass II (8) and Orchard Grass (9) Plots. The unburned Big Bluestem Plot maintained the most stable population of *M. pennsylvanicus* during the course of the survey (Figure 3). This plot had a two-year litter accumulation, and the standing vegetation, including abundant prairie forbs, provided good cover and a diversity of plant species.

The standing vegetation of Commercial Switchgrass I and II was much denser than that of the Unburned Big Bluestem Plot,

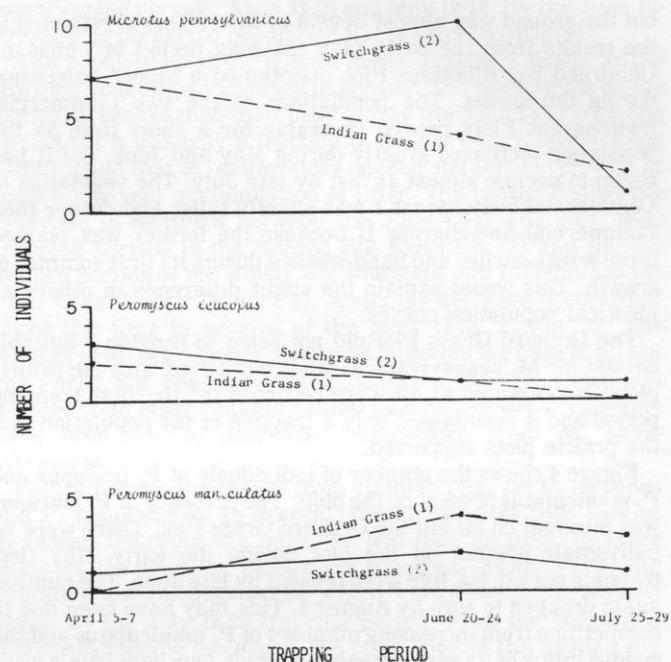


Figure 2. Comparisons of numbers of the three most common species of small mammals in Group 1 plots: Indiangrass (1) and Switch Grass (2) for three different trapping periods.

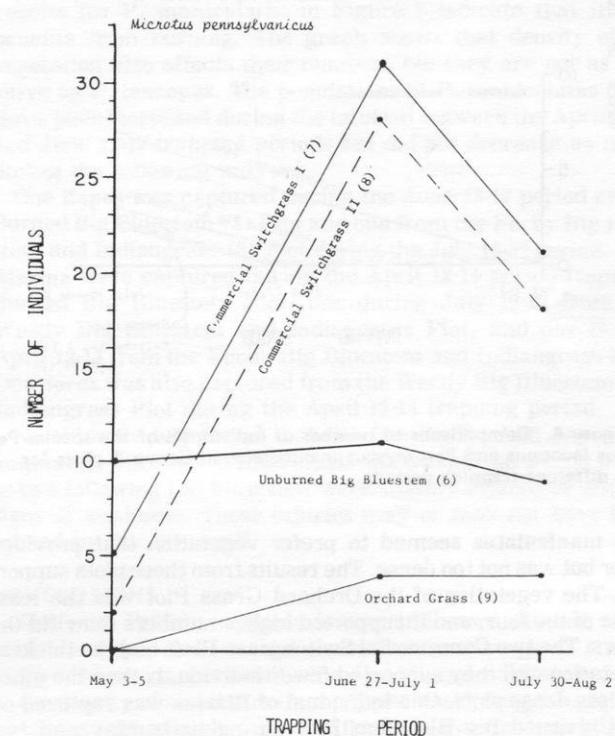


Figure 3. Comparisons of number of individuals of *Microtus pennsylvanicus* in Group 2 plots: Unburned Big Bluestem (6), Commercial Switchgrass I (7), Commercial Switchgrass II (8), and Orchard Grass (9) for three different trapping periods.

but the ground was almost devoid of litter. This is reflected in the results from the early May trapping period in which the Unburned Big Bluestem Plot maintained a higher population during the spring. The populations of the two Commercial Switchgrass Plots proved favorable for a short time as the population increased greatly during May and June, but it had begun to decline almost as fast by late July. The vegetation of Commercial Switchgrass I was slightly taller and denser than Commercial Switchgrass II because the former was planted three weeks earlier and hand-weeded during its first summer of growth. This would explain the slight difference in otherwise identical population curves.

The Orchard Grass Plot did not seem to provide a suitable habitat for *M. pennsylvanicus* when compared with the prairie plots. No captures at all were recorded for the first trapping period and it maintained only a fraction of the population that the prairie plots supported.

Figure 4 shows the number of individuals of *P. leucopus* and *P. maniculatus* present on the plots. The presence of *P. leucopus* was minimal on all but the Orchard Grass Plot. There were no individuals present on the plot during the early May first trapping period, but five were present by late June. The number again dropped to zero by August 1. This may have been due to competition from increasing numbers of *P. maniculatus* and the sudden influx of *Zapus hudsonius* of which four individuals were captured during the last trapping period.

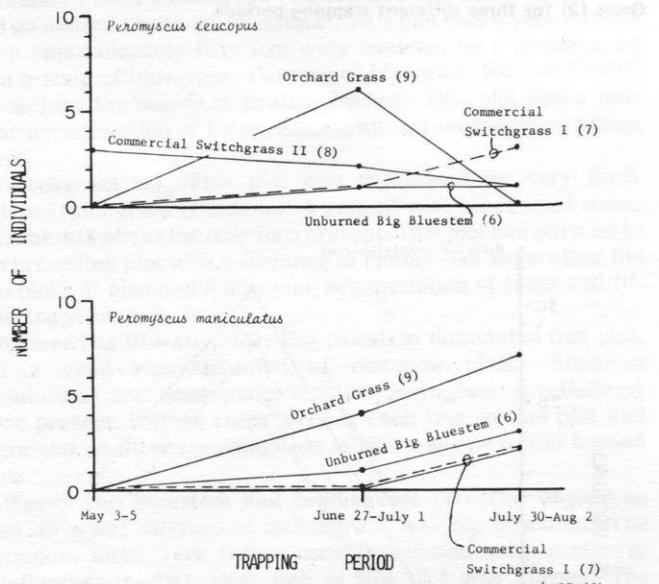


Figure 4. Comparisons of number of individuals of the species *Peromyscus leucopus* and *Peromyscus maniculatus* in Group 2 plots for three different trapping periods.

P. maniculatus seemed to prefer vegetation that provided cover but was not too dense. The results from these plots support this. The vegetation of the Orchard Grass Plot was the least dense of the four, and it supported higher numbers than did the others. The two Commercial Switchgrass Plots had the thickest vegetation and they supported fewer individuals than the other two less dense plots. One individual of *Blarina* was captured on the Unburned Big Bluestem Plot during early May and two individuals during late July-early August. One individual of *M. ochrogaster* was captured during late July-early August on this plot. One individual of *Blarina* from Commercial Switchgrass I and two from Commercial Switchgrass II were also captured during this last trapping period. One individual of *Mus* from each of the two plots was captured during late June. Commercial Switchgrass I also yielded one individual of *Sorex* in early May.

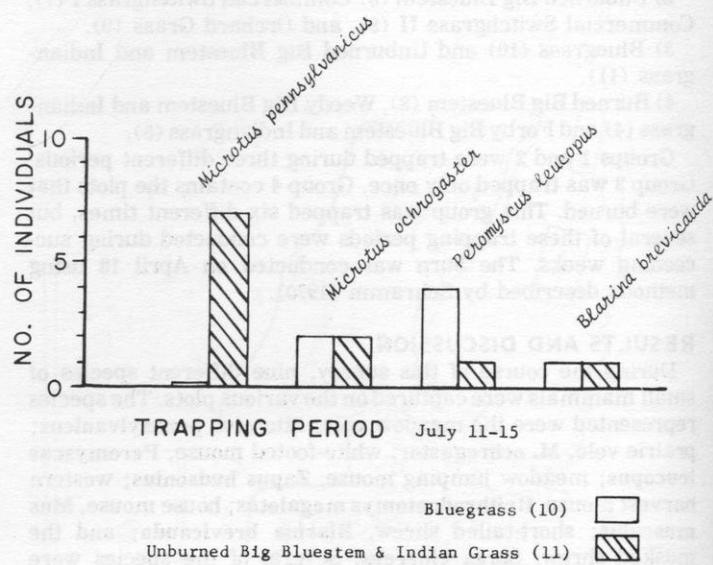


Figure 5. Comparisons of number of individuals for the four species of small mammals found in Group 3 plots: Blue Grass (10) and Unburned Big Bluestem and Indiangrass (11) for one trapping period.

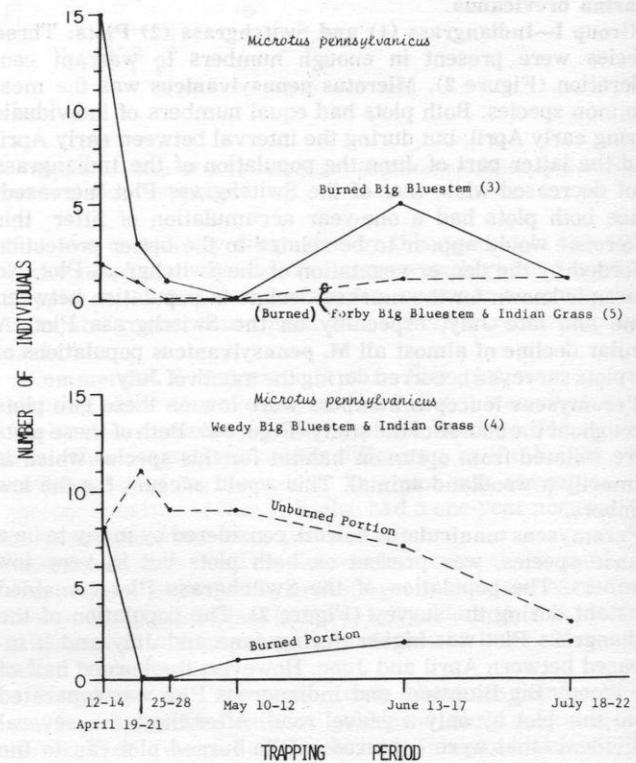


Figure 6. Comparisons of number of individuals of *Microtus pennsylvanicus* found on the burned plots, Burned Big Bluestem (3) and Forby Big Bluestem and Indiangrass (5) and a comparison of the same species for burned and unburned halves of the Weedy Big Bluestem and Indiangrass (4) Plot for six different trapping periods.

Four individuals of *Zapus* were captured from the Orchard Grass plot during the last period as were one *Blarina* from each of the periods early May and late June. There were no captures at all for the Orchard Grass plot during early May.

Group 3—Bluegrass (10), Unburned Big Bluestem and Indiangrass (11). These two plots were trapped for only one four-day period in mid-July (Figure 5).

Microtus pennsylvanicus showed a definite preference for the Unburned Big Bluestem and Indiangrass Plot (11) over the

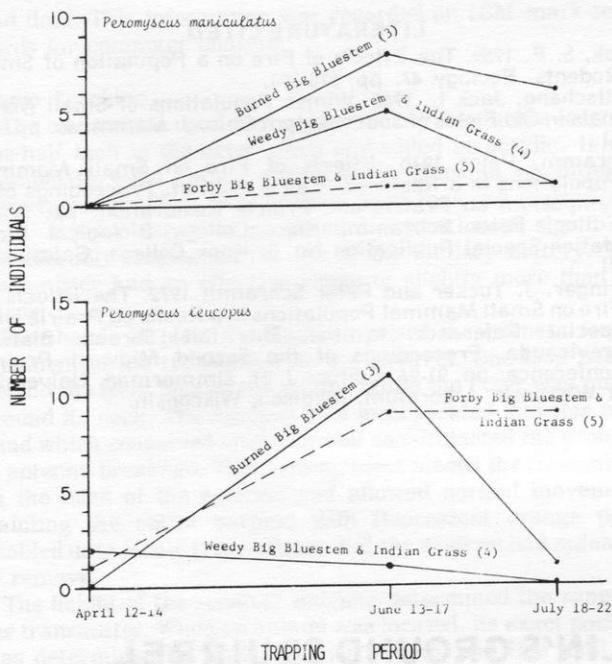


Figure 7. Comparisons of numbers of individuals of the species *Peromyscus leucopus* and *Peromyscus maniculatus* in the burned Group 4 plots: Burned Big Bluestem (3), Forby Big Bluestem and Indiangrass (5), and Weedy Big Bluestem and Indiangrass (4) (burned and unburned portions totaled) for three different trapping periods.

weedy Bluegrass Plot (10), where it was virtually absent. *P. leucopus* preferred this more open weedy plot over the prairie plot. *Blarina* was present on both plots in very low numbers.

An equal number of *M. ochrogaster* were captured on both plots. This species was found in low numbers on several of the plots, with most of them concentrated in those plots which were located on relatively high, dry ground. This corresponds with the evidence found by Gottschang (1965) who found that when *M. ochrogaster* and *M. pennsylvanicus* populations are found together the latter prefers the moister swales while *M. ochrogaster* prefers the dryer hilltops.

Group 4—Burned Big Bluestem (3), Weedy Big Bluestem and Indiangrass (4), Forby Big Bluestem and Indiangrass (5). On April 18 a burn was conducted on parts of the prairie at the field station. All of the Burned Big Bluestem (3) and Forby Big Bluestem and Indiangrass (5) Plots were burned. Half of the Weedy Big Bluestem and Indiangrass (4) Plot was burned and the other half of the plot left unburned for comparison. These three plots were trapped on six different occasions with the first three trappings occurring during the first three consecutive weeks (Figures 6 and 7).

In Figure 7, data for the Weedy Big Bluestem and Indiangrass (4) Plot include both the burned and unburned portions. When comparing the results from both figures 6 and 7 it should be noted that only half of one plot (4) was burned and that the Forby Big Bluestem and Indiangrass Plot had only ten traps per line. Also, the April 12-14 trapping period was conducted before the burn.

Within a few days after the burn there were no individuals of any species residing on any of the burned plots. A few isolated captures on these plots appeared to be individuals that were foraging out on the burn from nearby stands of vegetation. Figure 6 which shows the results for all six trapping periods supports the above point. Results for *M. pennsylvanicus* in the burned and unburned portions of the Weedy Big Bluestem and Indiangrass Plot (Figure 6) are especially interesting. Immediately following the burn (April 19-21) there were no individuals present in the burned portion and the unburned portion showed an increase of three individuals. The population of the unburned portion then stabilized at nine individuals for the next

two trapping periods, April 25-28 and May 10-12. By the June 13-17 trapping period the population was at its preburn level.

The populations of the burned areas increased slowly as the growing vegetation increased in density. The populations on the burned areas reached their peak during the June 13-17 trapping period but it was only a fraction of their pre-burn levels. Cook (1959) found that *M. californicus* needed suitable cover with at least a one-year accumulation of litter. The reason behind the decrease in numbers between the June 13-17 and July 18-22 trapping periods in the Burned Big Bluestem (3) and the unburned portion of the Weedy Big Bluestem and Indiangrass (4) Plots is not known (Figure 6). A similar decrease occurred at about this time in several of the plots (Fig. 2, Fig. 3). The number of *M. ochrogaster* increased following the burn in all but the Forby Big Bluestem and Indiangrass (5) Plot which was isolated from other suitable habitat by a plowed area. This may have been due to decreased competition from *M. pennsylvanicus*.

Figure 7 shows the results from all three plots for *P. leucopus* and *P. maniculatus*. In general, the numbers of both species increased following the burn. *P. leucopus* invaded, in large numbers, the two plots, Burned Big Bluestem (3) and Forby Big Bluestem and Indiangrass (5) which were close to the wooded areas. By the July 18-22 trapping period, when the vegetation had again become too dense, the population of the Burned Big Bluestem Plot had returned to its pre-burn level. The population of the Forby Big Bluestem and Indiangrass Plot didn't decrease at this time. The vegetation on this plot was not as dense and the isolation of this plot prevented other species from moving in. The plowed area surrounding this plot was overgrown with annual weeds. The weedy Big Bluestem and Indiangrass (4) Plot was isolated from any favorable *P. leucopus* habitat and it did not show an increase following the burn.

Springer and Schramm (1972) found that *P. leucopus* was about the only species which benefitted from burning, but the results for *P. maniculatus* in Figure 7 indicate that it also benefits from burning. The graph shows that density of the vegetation also affects their numbers but they are not as sensitive as *P. leucopus*. The populations of *P. maniculatus* of all three plots increased during the interval between the April 12-14 and June 13-17 trapping periods but did not decrease as much during the following interval.

One *Zapus* was captured during the June 13-17 period on the Burned Big Bluestem (3) Plot and one from the Forby Big Bluestem and Indiangrass (5) Plot during the July 18-22 period. Two *Blarina* were captured during the April 12-14 period from the Burned Big Bluestem Plot, one during July 18-22 from the Weedy Big Bluestem and Indiangrass Plot, and one during April 12-14 from the Forby Big Bluestem and Indiangrass Plot. One *Sorex* was also captured from the Weedy Big Bluestem and Indiangrass Plot during the April 12-14 trapping period.

No evidence was found that the fire itself killed any small mammals, but several individuals were captured within a day or two following the burn that were slightly injured or showed signs of weakness. These injuries may or may not have been caused by the fire itself.

CONCLUSIONS

1. Restored Prairie supports larger and more diverse small mammal populations than non-native, pasture grass stands.
2. Fire, or more specifically the fire-altered habitat, reduces the density of small mammal populations during the growing season immediately following the burn with the exception of *P. leucopus* and *P. maniculatus*.
3. Litter accumulation and density of vegetation play a major role in determining the numbers and species of small mammals present in a given grassland habitat.

A study conducted in an area with larger stands of prairie grasses would reveal more meaningful and clear-cut relationships between small mammal populations and

vegetational composition. Many of the plots in this study were small and presented problems in eliminating external influences from other nearby stands. The size of the plots and the mosaic of the restored prairie prevented any enlargements of the trapline size used.

ACKNOWLEDGMENTS.

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RADIO-TRACKING THE FRANKLIN'S GROUND SQUIRREL IN A RESTORED PRAIRIE

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Abstract. This paper reports on a study of the movements of the Franklin's ground squirrel as followed by radio-tracking and trap-mark-recapture methods in a restored tall-grass prairie on the Knox College Biological Field Station, Knox County, west-central Illinois.

A harness for attaching a radio transmitter to the squirrel was perfected and a technique for following the squirrel in the field was developed. Radio-tracking revealed a preference for restored prairie plots. In one case, tracking demonstrated heavy use of a wooded area by an adult male. Activity was found to be greatest during periods of bright sunlight and was particularly concentrated in the afternoon hours.

Radio-tracking indicated a home range of 2.25 acres for adult females and 1.5 acres for adult males during mid-summer, after parturition. These data, combined with trap-recapture results, showed a seasonal variation in the area used by a particular squirrel. This variation differed with the sex and reproductive condition of the individual.

This study of the activity and movements of the Franklin's ground squirrel (*Spermophilus franklinii*) was carried out on the Knox College Biological Field Station located in Knox County in west-central Illinois. The study area consisted of a portion of the field station approximately 30 acres in size which has been restored to native prairie grasses. Field work for the project was completed during a ten week period in the summer of 1972.

Little is known of the habits of the Franklin's ground squirrel primarily as a result of the fact that it is highly secretive in nature. Furthermore, its preference for the tall grass areas of the prairie makes direct observation virtually impossible. Thus indirect methods of study such as radio tracking and trap, mark and recapture were employed to determine the factors affecting activity and the size of the home range.

The Franklin's ground squirrel was introduced to the field station in 1969 as a part of the restoration project. This squirrel is considered to have been a native of the tall grass prairie and was thus re-established in order to recreate more accurately the original prairie community. Previous studies concentrated on the status of the colony and the success of the introduction (Van Petten and Schramm 1972). Presently, laboratory studies are being conducted on the reproductive development of the squirrels during hibernation.

MATERIALS AND METHODS

The dominant grasses of the study area included big bluestem

(*Andropogon gerardii*), little bluestem (*Andropogon scoparius*), switchgrass (*Panicum virgatum*), and indiangrass (*Sorghastrum nutans*). Dominant forbs were compass plant (*Silphium laciniatum*), prairie dock (*Silphium terebinthinaceum*), stiff goldenrod (*Solidago rigidula*), and pale purple coneflower (*Echinacea pallida*). Various weeds such as meadow parsnip (*Pastinaca sativa*), milkweed (*Asclepias syriaca*), sweet clover (*Melilotus sp.*), tall goldenrod (*Solidago altissima*) and foxtail (*Setaria sp.*) were present.

An area recently plowed bordered the east side of the prairie. Although primarily covered by weeds, it contained two small prairie plots. Woods surrounded part of the prairie; the remainder being bounded by unrestored grassland.

Trapping

In this portion of the study, an irregular grid was laid out which followed the contour of the prairie areas. Stations were placed at 105 ft. intervals with two traps per station. In all, 46 stations were placed on the grid.

Havahart squirrel traps were used in the study. These traps were modified by permanently closing one door and wiring the treadle so that action only on the farthest end would spring the trap. In addition, the treadles were spring loaded and adjustable to prevent the capture of such light animals as birds and smaller rodents.

Captured individuals were examined for toe clip, I.D. number, sex and reproductive condition, weight, location, time

and date. This information was recorded on IBM mark-sense cards for computer analysis.

Radio Tracking

The transmitter used was approximately two inches long and one-half inch in diameter when embedded in acrylic. It was possible to build radios which would transmit on different frequencies enabling us to monitor more than one squirrel at a time. A pulse capacitor produced a discontinuous signal and considerably lengthened the life of the Mallory battery. This transmitter had an effective range of slightly more than 100 yards.

Two bands of plastic tubing comprised the harness for attachment of the transmitter to the squirrel. One loop passed behind the front legs of the animal while the other was placed around its neck. The antenna was incorporated into this neck band which conserved space as well as eliminated the problem of antenna breakage. This arrangement placed the transmitter on the back of the squirrel and allowed normal movement. Painting the entire harness with fluorescent orange paint enabled us to locate transmitters that the squirrel had managed to remove.

The height of the receiver antenna determined the range of the transmitter. When an animal was located, its exact position was determined by walking a north-south grid line until the signal was determined to be strongest directly east or west. A similar procedure along an east-west grid line then pinpointed the squirrel and the coordinates of its position in the grid could be recorded along with the time of day.

Locating burrows necessitated tracking while the individual was underground. A signal was located as described above, and approached. When in the immediate vicinity of the strongest signal, the antenna would be disengaged from the receiver. This area was then examined with the receiver alone. A signal obtained with just the receiver indicated that the transmitter was less than five feet away. From this point, it was a simple matter of visually locating the burrow.

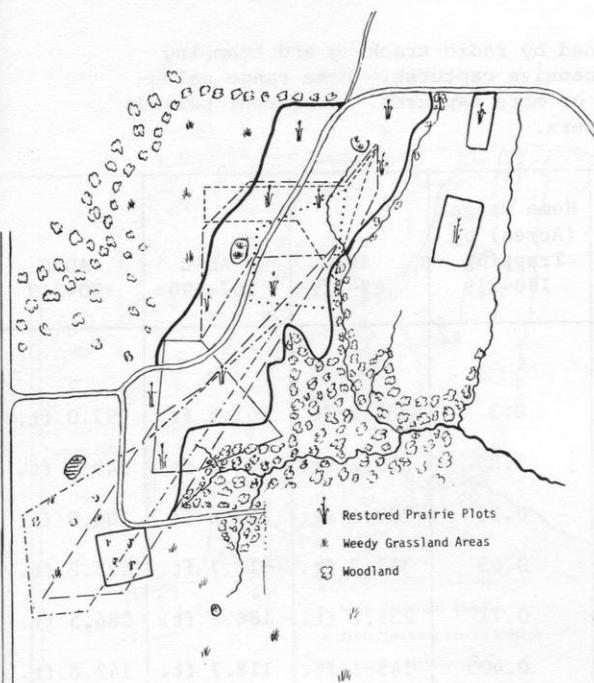


Figure 1. Areas over which six different females ranged during trapping study. Note the overlapping, colonial aspect of the areas used. Each squirrel had 12 or more captures.

RESULTS AND CONCLUSIONS

Trapping

In the trapping study, a total of 31 squirrels were captured. Of these, 13 were adults in a ratio of 2 males to 11 females. The 18 young captured and marked appeared so late in the study period that the data collected was insufficient for home range calculations.

Figure 1 represents the areas of heavy use as indicated by trapping for the 6 females with a significantly high number of captures (at least 12). The areas encompassed are presented in Table 1. Home ranges were calculated by the exclusive boundary strip method. The important inference from these data is that the home ranges of these squirrels greatly overlap. Several females are seen to use almost identical parts of the prairie, and evidently no squirrel is relegated to an inferior portion of the habitat.

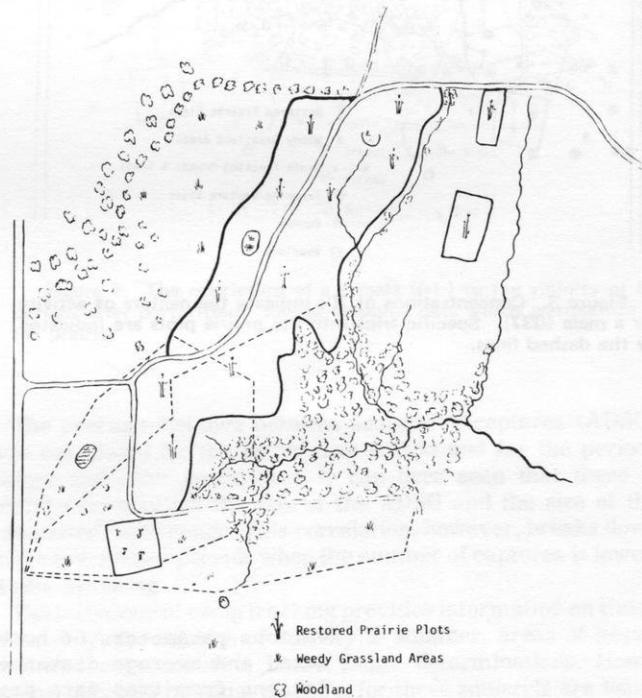


Figure 2. Dashed lines outline the areas in which the only two males present were followed by radio tracking and trapping. Evidently neither squirrel is relegated to an inferior habitat by the other.

This aspect of Franklin's behavior is borne out by Figure 2 which shows the areas over which the two adult males were trapped. Again, there is considerable overlap in home range. Home ranges calculated for the males are larger than for the females by a factor of 2 or 3.

Another result of this part of the study was that there was a difference in the area of activity between the morning and afternoon trappings. Most of the captures shown in the prairie plot were recorded in the afternoon while activity in the weedy grassland to the southwest was highest in the morning hours. The result is an important confirmation of the conclusions from radio tracking.

Table 1 presents several other calculations of parameters of home range based on the trapping data. The calculations of home range were broken down into the periods before and after the approximate date of parturition. For 037 (male) the home range, as calculated from trapping, remained nearly the same throughout the summer. For the other male, 74, however, the calculated range dropped by a factor of two. Subsequent radio tracking showed that he had moved off the grid, explaining this result. For four of the six females, the home range was smaller after parturition than before.

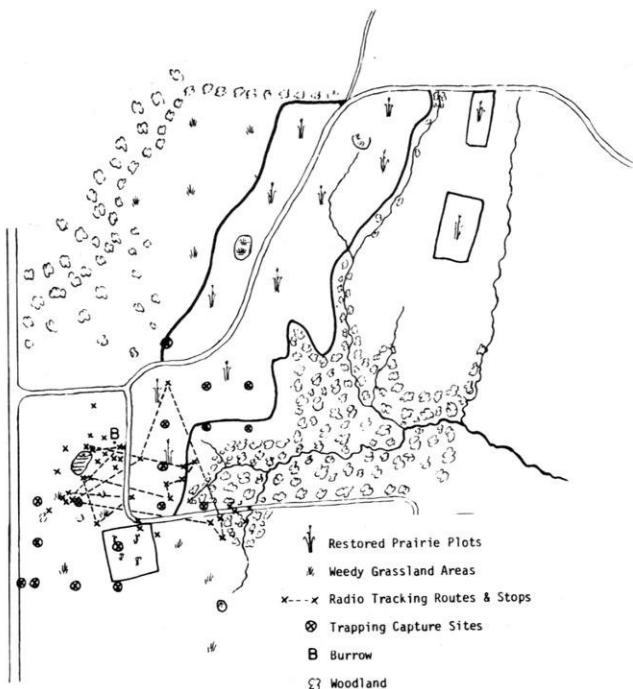


Figure 3. Concentrations of X's indicate the centers of activity for a male (037). Specific trips into the prairie plots are indicated by the dashed lines.

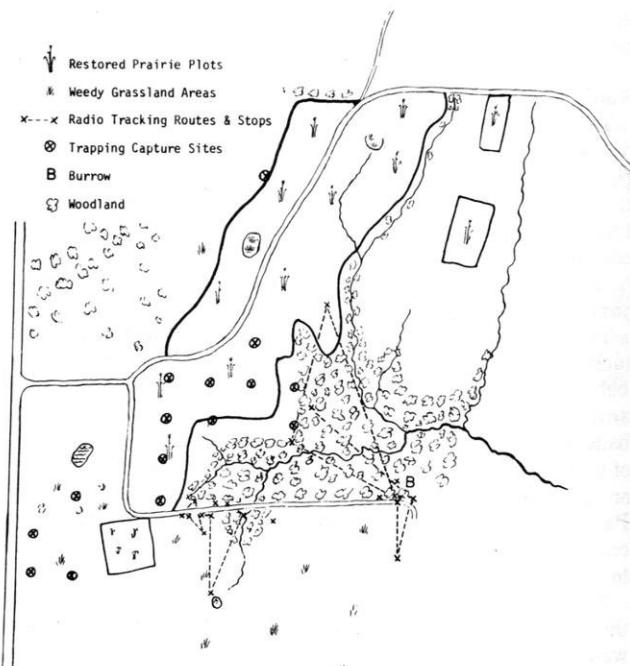


Figure 4. The seasonal variation in area of heavy use of a male (74) is indicated. The trapping study conducted early in the summer shows heavy prairie activity while the later tracking project demonstrates movement into the woods.

TABLE 1. Various parameters of home range obtained by radio tracking and trapping data, and average distance between successive captures. Home range calculations from trap data are based on 12 or more captures. Different periods of the summer are indicated by day numbers.

Squirrel No.	Sex	Home Range (Acres) by Radio Tracking	Home Range (Acres) by Trapping 167-219	Home Range (Acres) by Trapping 167-190	Home Range (Acres) by Trapping 190-219	ADSC 167-219	ADSC 167-190	ADSC 190-219
037	Male	1.46	9.3	7.4	8.3	384.8 ft.	361.8 ft.	397.0 ft.
74	Male	--	7.8	7.8	3.8	379.2 ft.	482.9 ft.	249.7 ft.
78	Female	2.27	2.4	0.481	0.33	128.4 ft.	163.6 ft.	104.9 ft.
71	Female	2.32	5.8	1.26	0.63	357.7 ft.	613.7 ft.	175.2 ft.
01-	Female	.732	4.3	0.835	0.71	239.2 ft.	186.2 ft.	286.5 ft.
01	Female	--	2.5	0.355	0.405	145.2 ft.	118.7 ft.	142.8 ft.
68	Female	--	4.7	0.935	0.582	248.6 ft.	179.2 ft.	440.6 ft.
052	Female	--	3.2	0.608	0.860	187.5 ft.	167.5 ft.	183.3 ft.

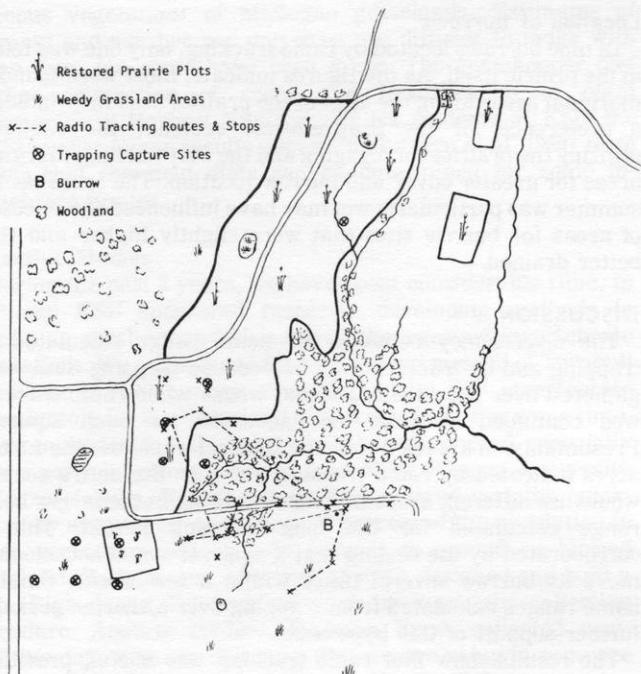


Figure 5. Movements and activity of a female (71). Note the specific trips into the prairie plots.

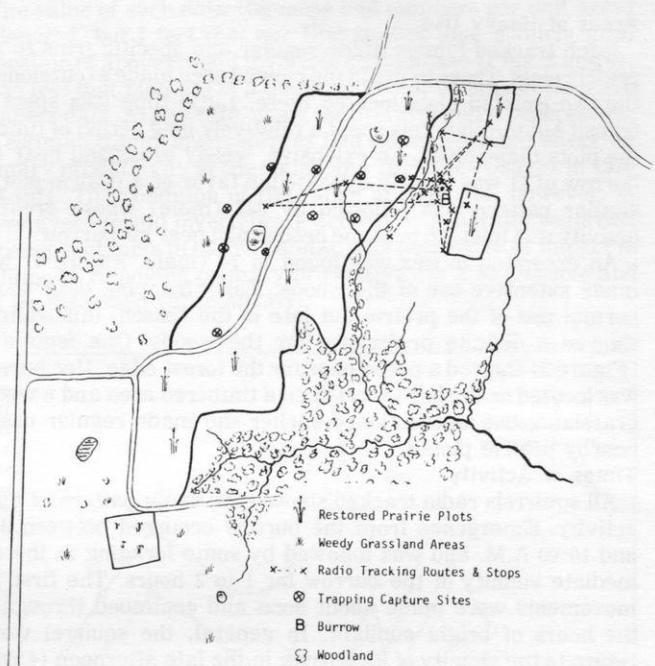


Figure 7. The restriction of a female (01-) to the vicinity of her burrow after parturition. Earlier trapping data shows normal use of the prairie.

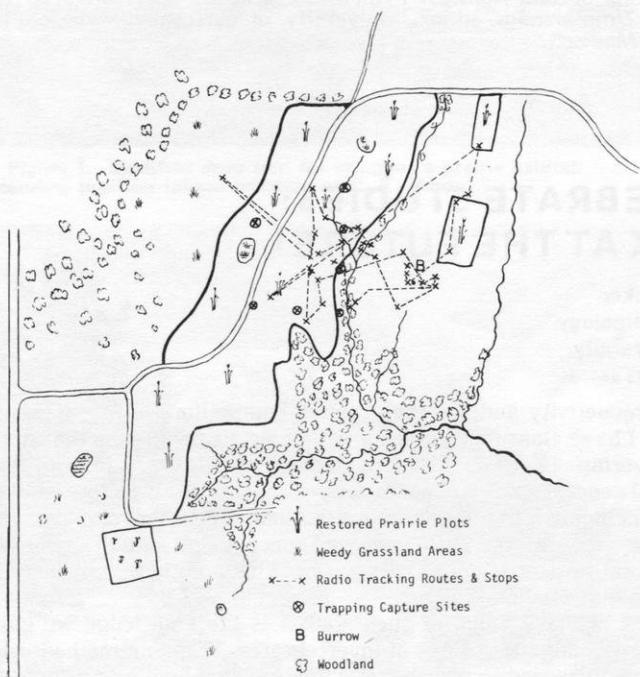


Figure 6. This female (78) is also seen to make definite movements from her burrow in a weedy area into particular prairie areas.

The average distance between successive captures (ADSC) was calculated for the entire trap period and for the periods before and after parturition. It can be seen that there is correlation between the size of the ADSC and the size of the calculated home range. This correlation, however, breaks down in the two shorter periods when the number of captures is lower.

Radio Tracking

The technique of radio tracking provides information on times of activity, the relation of activity to weather, areas of heavy use, and very accurate home range determinations. Home ranges obtained by radio tracking for these squirrels are listed in Table 1. The composites (Figures 3 thru 7) show the centers of activity for two males and three females. Dotted lines indicate the routes taken by the squirrels on days in which every movement was recorded.

Home Range

Radio tracking revealed home ranges of 2 to 3 acres for two of the three females tracked (Figures 5 and 6). There was daily variation in the area utilized which seemed to be weather dependent (see below). On a given day, under favorable conditions, 71 would range over an area of 1.5 to 1.75 acres.

At first glance, the data from 01- (Figure 7) would seem inconsistent with that presented above. This female was tracked over a total area of 0.7 acres. Each day she would use only 0.3 acres or less, remaining in the immediate vicinity of her burrow. This is explained by the fact that she was radio tracked during the week following parturition. Trapping data support this hypothesis since 01- was trapped over a different and larger area away from her burrow before parturition.

The male, 037, (Figure 2) was found to have a slightly smaller home range than these females. This may be explained by the fact that after breeding, when the radio tracking data was compiled, the males may have been preparing for hibernation. It is known that the males hibernate in late summer or early fall.

Areas of Heavy Use

Each tracked female made regular and specific trips to the prairie plots. Those living in the plowed area made excursions to the two isolated plots located there. Little time was spent in transit but the squirrels spent a relatively long period of time in the plots themselves. An extensive, weedy grassland near the burrow of 71 was largely bypassed in favor of a prairie plot. A similar pattern was followed by 037 (male) whose greatest activity was found to be in the prairie plot near his burrow.

An exception to this was found in 74 (male, Figure 4) who made extensive use of the woods. Early trapping data shows normal use of the prairie but late in the season, this squirrel showed a definite preference for the woods. One female 71 (Figure 5) showed a preference for the forest edge. Her burrow was located on the border between a timbered area and a weedy grassland, but as mentioned earlier she made regular use of nearby prairie plots.

Times of Activity

All squirrels radio tracked showed the same pattern of daily activity. Emergence from the burrow occurred between 9:00 and 10:00 A.M. and was followed by some foraging in the immediate vicinity of the burrow for 1 to 2 hours. The first big movements were made about noon and continued throughout the hours of bright sunlight. In general, the squirrel would return to the vicinity of its burrow in the late afternoon (4:00 to 5:00 P.M.) where there would be activity, sometimes in and out of the burrow, until 8:00 P.M. when the squirrel would go underground for the night.

Effect of Weather

In each case, the effect of weather on activity was great. Maximum activity was recorded on sunny, warm days when there was little or no wind. This was reflected also in the number of captures in the trapping study. Rain and/or overcast skies would restrict the squirrel to an area near its burrow.

These effects are best illustrated by the behavior of female 78. On a particularly bright, warm day she was tracked over 2.1 acres. The next day, which was overcast and threatening, saw her use an area of approximately 0.7 acres near her burrow. Particularly warm weather increased the activity of the squirrels. On such days activity began earlier, in some cases by nearly 2 hours. Activity lasted just as late but would reach its peak earlier.

Location of Burrows

Of nine burrows located by radio tracking, only one was found in the prairie itself. As the figures indicate, most were found in marginal areas along the edge of the prairie. This may indicate a preference for the prairie-forest ecotone; the squirrels utilizing the prairies for foraging and the surrounding, marginal areas for greater cover and burrow location. The fact that the summer was particularly wet may have influenced the selection of areas for burrow sites that were slightly higher and thus better drained.

DISCUSSION

The discrepancy between the home range calculated by trapping and by tracking may be because trapping data were gathered over a period of several weeks while radio tracking was continued at most for one week for each squirrel. Presumably, in a week's time the squirrel would use the 1.5 to 3 acres indicated by radio tracking but over the entire season, would use different areas this size, resulting in the larger home range calculated for the long trapping period. This is corroborated by the finding that a squirrel would occasionally move its burrow several times within a few weeks. Smaller home ranges calculated from trapping over a shorter period is further support of this hypothesis.

The results show that radio tracking was useful, providing more information than trapping alone. Since every movement of the squirrel can be known, home range calculations are more accurate. However, the use of both radio tracking and trap-recapture enabled us to explain some data which otherwise would have appeared incongruous. An example of this is the confirmation by trapping that 01- made use of the prairie, which radio tracking did not indicate.

ACKNOWLEDGMENT

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RANGELAND INVERTEBRATE STUDIES: A REVIEW AND A LOOK AT THE FUTURE¹

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This paper concerns some of the research programs on rangeland invertebrates at Kansas State University (KSU), in the Grassland Biome of the International Biological Program (IBP), and some other areas. Discussion includes invertebrates in general; information on actual impact is known for only a few groups such as grasshoppers which undoubtedly pose the greatest presently known invertebrate threat to rangeland

productivity and are the greatest competitors of livestock.

I have classified studies into four arbitrary groups that may overlap: (1) Faunal studies (including dietary, biological, and all general studies of a subjective nature), (2) Objective studies (including estimates or determinations of numbers and biomass for a unit area), (3) Bioenergetic (energy flow) studies, and (4) Total impact studies (energy flow plus additional impact).

Faunal Studies

A primary value of such studies is the knowledge we gain concerning the ecology of invertebrates. Trapping methods are usually varied so that the total fauna is sampled. An example of such a study was given earlier in this conference by participants from Knox College. Evans and Murdoch (1968) have also conducted such a study covering 18 years and including insects normally found in the "Field Layer Community" (on her-

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baceous vegetation) of Michigan grasslands. Estimates of biomass and number per unit area are difficult to make with these data, but some have been made. The grasshopper diet studies (dissection of crops and identification of plant fragments) of Herbert Knutson and his students at KSU the past 15 years (some results appear in Mulkern et al. 1969) have shown that the field diets can be determined for some invertebrate groups.

Objective Studies

During the past 3 years, we have spent considerable time, in IBP and KSU sponsored research, developing methods to determine numbers and biomass of aboveground invertebrate populations. We initially used the quick-trap method of Turnbull and Nicholls (1966) which was adapted by IBP invertebrate investigators for the Grassland Biome research. For some time, however, we felt that this method could be improved, especially after a personal communication from P. W. Riegert, University of Saskatchewan, Regina, whose data showed that the quick-trap may account for only about 35 percent of the population in dense vegetation and only 50 percent in grazed or burned grassland. C. E. Mason, a student at KSU, designed and built a trap (Figs. 1 and 2) which we think improves the collecting procedure. Another student, Rodman Reed, collected comparative data with our new trap that we are using to compare with data from the trapping design used by the IBP.

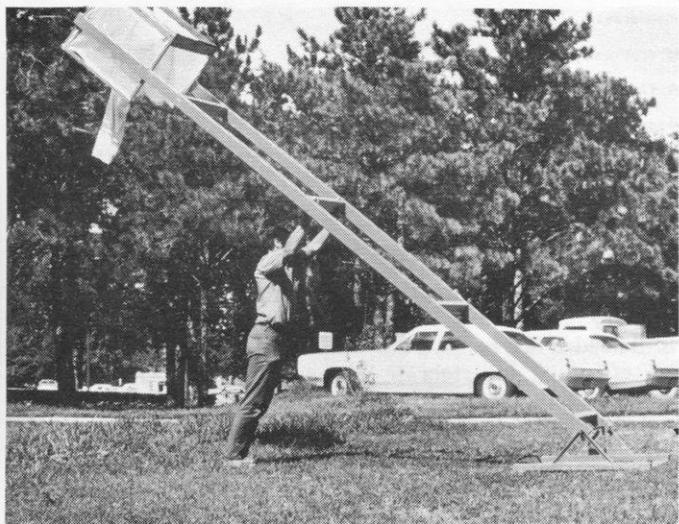


Figure 1. Modified drop trap for sampling a prairie habitat: Ascending position (photo courtesy of C. E. Mason).

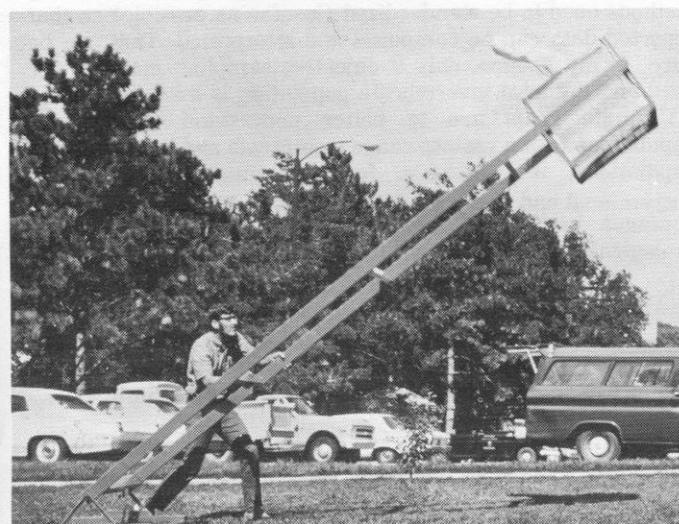


Figure 2. Modified drop trap for sampling a prairie habitat: Descending position (photo courtesy of C. E. Mason).

The value of such data (biomass and numbers per unit area) is debated, but I feel that our IBP studies give a fairly good indication of aboveground invertebrate biomass (Figs. 3 and 4). I also feel that biomass is a better indicator of impact than are numbers data. At any rate, using the literature on bioenergetics, we estimated that invertebrates had no appreciable effect on primary productivity at the Oklahoma IBP Site (Osage) in 1970 and 1971. The condition of the range at that site, however, is above average and invertebrate activity is generally regarded as being negligible in such a habitat. The possibility of impact in addition to removing primary productivity is also possible and will be discussed subsequently.

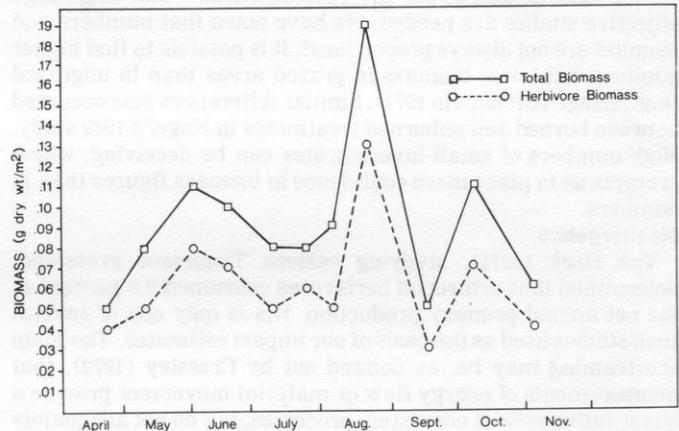


Figure 3. Total invertebrate and herbivore biomass for the grazed treatment, Osage Site, Oklahoma for 1971 (data from Reed and Blocker 1972).

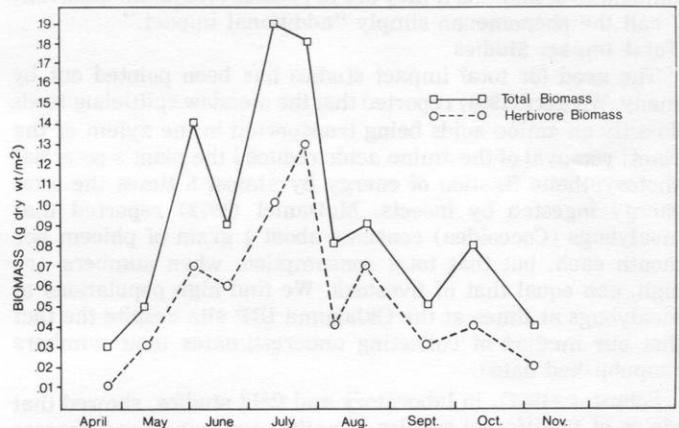


Figure 4. Total Invertebrate and herbivore biomass for the ungrazed treatment, Osage Site, Oklahoma for 1971 (data from Reed and Blocker 1972).

Wide differences in research conclusions sometimes result from varied trapping methods. For example, Evans and Murdoch (1968) used a variety of methods and reported results (% herbivores) in numbers. Reed and Blocker (1972), on the other hand, based their estimates of herbivores on biomass data (g/m²). The former based their results on upper strata insects (excluding apterygotes) while the latter considered all aboveground arthropods. Consequently, Reed and Blocker's estimates of herbivore percentages were much lower.

Bertwell (1972), using our KSU unit-area sampler, has studied aboveground Coleoptera for 2 years in tallgrass prairie. He reported that Chrysomelidae accounted for 10.5 percent of numbers and 20.7 percent of the total Coleoptera biomass in 1971 and 6 percent of the numbers and 11.7 percent of the biomass in 1972. Similar calculations for Curculionidae showed that its numbers and biomass were even greater than Chrysomelidae in

1972 (2.6 and 6.2 percent, respectively, in 1971 and 7.8 and 13.3 percent in 1972). When calculated as herbivore percentages, results were similar but, of course, higher.

The above figures differed strikingly from those of H. G. Nagel, Kearney State College (personal communication), whose results were based on sweep-net samples taken during 1969 in the same general area. Nagel reported a much higher percentage of Chrysomelidae and a much lower figure for Curculionidae; he found almost no Carabidae, but that group comprised a major part of the Bertwell study. I think that the differences in results are primarily due to trapping method; however, results vary from year to year and habitat to habitat.

Such data, as well as our IBP results, indicate that long range objective studies are needed. We have noted that numbers and biomass are not always proportional. It is possible to find higher numbers but lower biomass in grazed areas than in ungrazed (e.g., Osage IBP data in 1971). Similar differences also occurred between burned and unburned treatments in Nagel's 1969 study. High numbers of small invertebrates can be deceiving, which prompts us to place more confidence in biomass figures than in numbers.

Bioenergetics

Van Hook (1971), studying eastern Tennessee grassland, determined that arthropod herbivores consumed 9.6 percent of the net annual primary production. His is only one of several such studies used as the basis of our impact estimates. The main shortcoming may be, as pointed out by Crossley (1972), that measurements of energy flow or material movement provide a quantitative view of ecosystem processes, but do not adequately explain ecosystems. Thermostats on electric heaters, controlling the flow of electricity but consuming only a small part of that flow, provide an analogy to arthropods in terrestrial systems. Ecosystem models will need to incorporate controlling influences of animals if they are to predict ecosystem behavior. I call the phenomenon simply "additional impact."

Total Impact Studies

The need for total impact studies has been pointed out by many. Wiegert (1964) reported that the meadow spittlebug feeds directly on amino acids being transported in the xylem of the plant; removal of the amino acids reduced the plant's potential photosynthetic fixation of energy by almost 5 times the total energy ingested by insects. McDaniel (1972) reported that mealybugs (Coccoidea) consume about 1 gram of phloem per month each, but that total consumption, when numbers are high, can equal that of livestock. We find high populations of mealybugs at times at the Oklahoma IBP site despite the fact that our method of collecting underestimates their numbers (unpublished data).

Schuster (1967), in laboratory and field studies, showed that yields of 35 different species of native and introduced grasses were significantly reduced by rhodesgrass scale (*Antonia graminis*) approximately 30 percent in primary production on South Texas ranges (Table 1). They successfully controlled the scale biologically. His is one of few studies on rangeland pests, other than grasshoppers, to establish total impact. Bioenergetics data and information on the numbers and biomass of scale per unit area that caused a 30 percent decrease in primary productivity would have greatly enhanced the study. Bertwell (1972) observed that Curculionidae and Chrysomelidae may help regulate numbers of some undesirable forb species.

Process Studies

Various IBP grassland process studies were proposed for 1972 to study the impact of several other insect groups, but results are not yet available. The results, when available, can be correlated with the objective data gathered during the past several seasons. That, I think, is the greatest value of present IBP grassland invertebrate data.

Soil Investigations

I have omitted soil invertebrates, but belowground fauna may strongly influence productivity. Data are scarce for grasslands,

TABLE 1. Reductions in yield and plant mortality percentages resulting from rhodesgrass scale infestation on grasses in greenhouse test.¹

Grass	Yield loss (percent)	Plants killed (percent)
Hybrid sourgrass	32.4	42.5
Wright threeawn	8.4	0.0
Red grama	25.4	74.4
Buffel sandbur	18.8	55.0
Coast sandbur	37.8	42.5
Fringed windmillgrass	86.9	
Rhodesgrass	18.0	49.3
Nash windmillgrass	12.7	0.0
Arizona cottontop (<i>glabrous</i> sp.)	88.3	85.0
Texas cottontop	36.4	83.3
Mourning lovegrass	17.4	0.0
Tumble lovegrass	48.7	65.6
Sand lovegrass	24.3	0.0
Green sprangletop	29.0	55.0
Knotroot bristlegrass	63.4	85.0
HBK bristlegrass	0.0	0.0
Johnsongrass	38.0	0.0
Sand dropseed	29.1	0.0
Four flowered trichloris	32.4	0.0
Texasgrass	25.9	0.0

¹Data from Schuster, 1967 (20 of 35 species included).

and IBP data to now are inconclusive.

Summary

Still needed is a method that will enable us to determine the total effect of invertebrate herbivores (considered as an ecological unit, perhaps) of rangeland. Such information, coupled with that gained from other types of studies discussed here, would give us the ability to determine whether or not invertebrates are worthy competitors of cattle and wildlife.

We will be disadvantaged so long as we dismiss the impact of invertebrates (other than grasshoppers or other noticeable pests) on rangeland. We need to know enough about their ecology and biology to better assess their roles. Collecting methods need to be standardized (insofar as possible) so that reported data can be compared and interpreted. That can be done, in my opinion, only if objective sampling methods are used and the total invertebrate population is assessed.

Ultimate goals are to better understand invertebrate populations within various range treatments and to manipulate populations, if necessary, for maximum production for recreational and commercial purposes on our ever decreasing acreages of rangeland, while maintaining them in an ecologically sound condition.

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