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Jon K. Piper

The Land Institute, 2440 East Water Well Road, Salina, Kansas

Mark C. Gernes

The Land Institute, 2440 East Water Well Road, Salina, Kansas

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VEGETATION DYNAMICS OF THREE TALLGRASS PRAIRIE SITES

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

Abstract. As part of research to develop a sustainable agriculture that incorporates many aspects of the North American Prairie, 1) the seasonal phytomass levels supportable by native prairie and 2) how plant taxa shift in temporal importance within the community were examined. This report summarizes the first two years of a study documenting community patterns on three tallgrass prairie sites in Saline County, Kansas that differ in soil type and annual productivity. Average August phytomass at the three sites ranged from 284 to 682 g/m² in 1986 and from 377 to 1077 g/m² in 1987. Diversity declined with standing crop biomass and from spring to summer at all sites. Although big bluestem (*Andropogon gerardii* Vitman) dominated all sites, legumes represented as much as 26% of total phytomass on the poorest site. Some composite species were ubiquitous, but never constituted more than 5% of vegetation. Spring forbs and cool-season grasses were of greatest importance in April and May. The results, in concert with other ongoing research, have implications for the design of perennial seed crop mixtures suited for the Great Plains.

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

INTRODUCTION

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

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

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

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

METHODS

Productivity and Species Composition

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

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

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

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

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

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

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

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

Phenology

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

RESULTS

Productivity and Species Composition

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

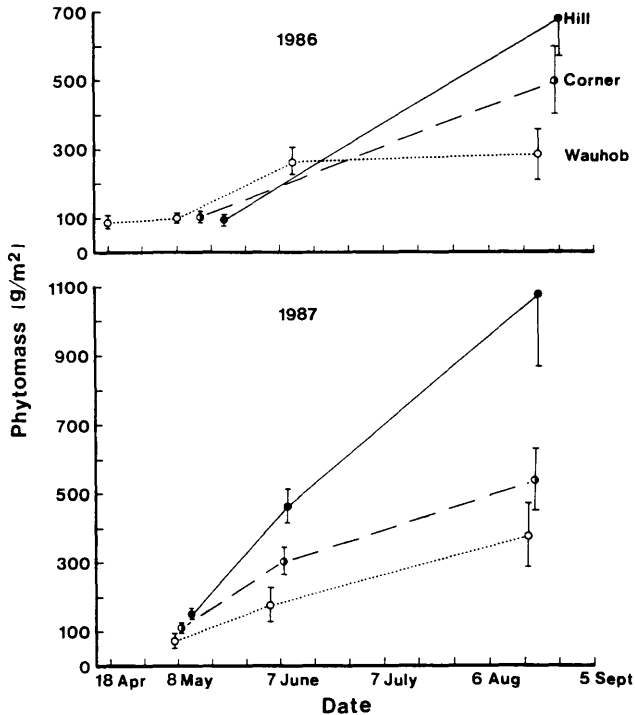


FIG. 1. Mean annual aboveground production (g/m^2) for three prairie sites in 1986 and 1987. Vertical bars denote standard errors.

Table 1. Seasonal aboveground phytomass (mean grams/ $m^2 \pm$ S.E.) within 12 quadrats ($0.25 m^2$) at three sites in 1986.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Phenology

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

DISCUSSION

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

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

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

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

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

standing phytomass was lowest, then declined toward peak production (August).

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

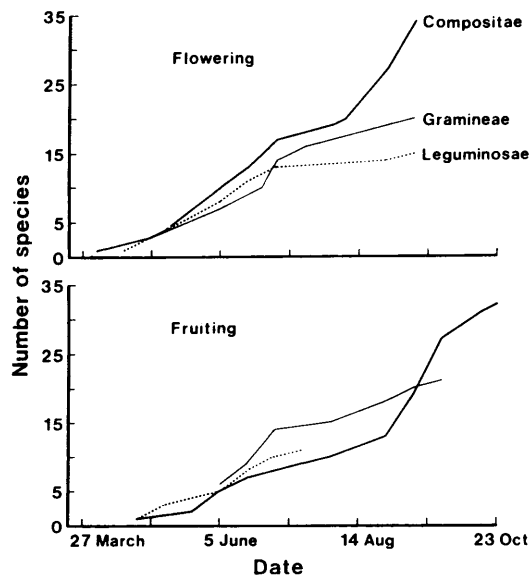


FIG. 2. Cumulative number of composite, grass, and legume species flowering and fruiting in Land Institute native prairie during 1987.

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

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

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

Relevance for Sustainable Agriculture

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

Native prairie on marginal soils, without synthetic inputs, sup-

ported phytomass equal to or exceeding that produced by most major grain crops (Piper 1986), although harvest index is higher in annual grains. This productivity derives from the ability of warm-season perennial grasses to adapt to their environment, the tight nutrient budget with which prairie plants function (Knapp and Seastedt 1986), and the differential distribution of species' demands for resources over the growing season (Risser 1985). In many situations, C_3 and C_4 grasses co-occur with deeply-rooted forbs. Within these communities both seasonal and spatial partitionings of nutrients are feasible. Kendall (1987) has investigated whether these types of partitionings are possible in agronomic mixes involving perennial crop candidates.

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

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