

Composition of prairie plant communities on productive versus unproductive sites in wet and dry years

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Abstract: A natural productivity gradient was used to test questions about plant species composition, diversity, and sensitivity to environmental change of prairie vegetation within the tallgrass region. From 1986 to 1992 I monitored seasonal net aboveground production and species composition at four sites with soils that differed in texture and percent organic matter, pH, and concentrations of NH_4 , total N, K, Ca, Mg, and SO_4 . Four years of the survey featured above normal precipitation and 3 were drought years. August standing crop averaged 566 ± 307 , 419 ± 143 , 268 ± 158 , and $232 \pm 148 \text{ g} \cdot \text{m}^{-2}$ at the four sites. Production generally increased with soil fertility (i.e., percent organic matter, total N, and K) and precipitation. The two more productive sites featured higher percentages of grass biomass, but legumes were rare. The site with the lowest soil N supported the consistently highest legume biomass and lowest grass biomass among sites. The least productive site displayed the highest percentage of composites. Species evenness, but not richness, was inversely related to August biomass for all sites. There were significant differences in production across years, as well as in percentages of grass, legume, and composite biomass. Total plot richness ranged from 24 to 40 species sampled per year at site 2 to 51–53 species at site 4, and tended to decline in the dry year 1989. Poor soils, although less productive overall, appear to prevent dominance by tall grasses and thereby maintain relatively more diverse spring and summer floras. Increased light availability near the soil surface probably enables the persistence of low-growing plants. Evenness, but not richness, varied among sites. The patterns of plant community composition have implications for restoration ecology as well as the design of prairielike perennial grain mixtures.

Key words: diversity, evenness, plant community, prairie, soil type, variability.

Résumé : Les auteurs ont utilisé un gradient de productivité naturelle afin d'évaluer les questions pertinentes sur la composition, la diversité et la sensibilité aux changements environnementaux des espèces venant en prairies dans la région des herbes hautes. De 1986 à 1992, l'auteur a suivi la production saisonnière épigée et la composition en espèces, sur quatre sites dont les sols diffèrent par la texture et le pourcentage de matière organique, le pH et les teneurs en NH_4 , en azote total, en K, Ca, Mg et SO_4 . Au cours des sept années d'observation, quatre ont montré des précipitations supérieures à la normale et dans trois cas la sécheresse a prévalu. En août, la biomasse sur pied est en moyenne de 566 ± 307 , 419 ± 143 , 268 ± 158 et $232 \pm 148 \text{ g} \cdot \text{m}^{-2}$ pour les quatre sites. La production augmente généralement avec la fertilité du sol p.ex., pourcentage de matière organique, N total et K) et la précipitation. Les deux sites les plus productifs sont caractérisés par des pourcentages plus élevés de biomasse herbacée, mais les légumineuses sont rares. Le site montrant la teneur la plus faible en azote dans le sol possède toujours une plus forte biomasse de légumineuses et une plus faible biomasse d'herbacées, pour l'ensemble des sites. Le site le moins productif porte le plus forte pourcentage de composées. L'uniformité des espèces est inversement reliée avec la biomasse d'août sur tous les sites, ce qui n'est pas le cas avec leur richesse. On observe des différences significatives dans la production au cours des années, ainsi que de la biomasse relative des herbacées, des légumineuses et des composées. La richesse totale des parcelles va de 24 à 40 espèces échantillonnées par année au site 2 à 51–53 espèces au site 4, et a tendu à décliner au cours de l'année sèche de 1989. Les sols pauvres, bien qu'ils soient généralement moins productifs, semblent empêcher la dominance par les herbacées hautes et maintiennent conséquemment des flores printanières et estivales relativement plus diversifiées. Une augmentation de la lumière disponible près de la surface du sol permet probablement aux espèces basses de persister. L'uniformité, mais non la richesse, varie entre les sites. Les patrons de composition

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de la communauté végétale ont des implications pour la restauration écologique ainsi que pour la définition de mélanges de semences de grains pérennes ressemblant à ceux de la prairie.

Mots clés : diversité, uniformité, communauté, végétale, prairie, type de sol, variabilité.
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Introduction

Remnant plant communities of the North American Great Plains exist as prime examples of inherently sustainable biotic communities in which complex webs of interdependent plants, animals, and microbes garner, retain, and efficiently recycle critical nutrients, thus providing excellent models of structural patterns that can achieve tight nutrient cycling, and solar-driven energy flow, that are crucial to sustainability. In addition to being highly productive, North American prairies consist of diverse species assemblages, whose composition varies across soil types. Prairie communities tend to resist species loss and invasion by exotics and are resilient during short-term climatic variation (Weaver 1968). Because prairie communities have both spatial and temporal aspects, this descriptive study of prairie plant communities had three general considerations.

First, how does the composition of prairie plant communities differ between relatively productive and relatively unproductive sites? Numerous descriptive and experimental studies show that several aspects of the growing environment, especially soil quality, can influence plant species composition (Williams 1978; Tilman 1987, 1990; Gibson and Hulbert 1987; Inouye and Tilman 1988; Aerts et al. 1990; Wedin and Tilman 1990; Tilman and Olff 1991). For example, greater proportions of C₄ grass species should occur in habitats characterized by lower levels of shade and drier soils than C₃ grasses, which should favor cooler, wetter, and deeper soils (Barnes and Harrison 1982; Christie and Detling 1982; Monson et al. 1986). In addition, C₃ and C₄ grasses should be arrayed according to differences in rate of soil N depletion, with many C₄ species likely to tolerate lower concentrations of available soil N than C₃ species (Björkman et al. 1976; Brown 1978). As a final pattern, there should be a preponderance of N-fixing species on low-N versus high-N soils as N-fixing species would have an advantage where soil N is limiting (Scarisbrick and Ivins 1970). Here, I focused on four major functional or taxonomic groups that together represent the majority of vegetation on the prairie: C₄ grasses, C₃ graminoids (grasses and sedges), N-fixing species (legumes and *Ceanothus herbaceus* (Bond 1976)), and composites.

Second, because prairie communities tend to be diverse as well as stable, I examined how such community attributes as species richness (which I use interchangeably with diversity) and evenness differ between relatively productive versus relatively unproductive sites. Productive sites may feature higher dominance by one or few species, through disproportionate suppression or mortality of smaller or shade-intolerant species, leading potentially to lower diversity and evenness than less-productive sites (Wilson and Tilman 1991, 1993). Experimental studies that amended herbaceous plant communities with N fertilizer showed an increase in productivity, an increase in the dominance of a few species, and a sometimes dramatic reduction in richness (Reed 1977; Bakelaar and Odum 1978; Tilman 1987).

Third, because prairie plant communities consist almost entirely of perennials, it is important to examine the characteristics of plant communities over several growing seasons in order to sample year to year variability. In particular, both tall- and short-grass prairies are characterized by precipitation extremes (Weaver 1968; Lauenroth and Sala 1993), with pronounced effects on growth and relative abundance of species in different years. To best generalize about prairie communities, it is necessary to examine year to year changes in aboveground biomass, species composition and representation by major taxonomic or functional groups, species richness and evenness, and relative change among sites. Species composition could change if precipitation differences influence colonization, extinction, or relative growth of different species. Year to year changes in species composition or relative abundance could in turn influence evenness or diversity if species are lost or gained, or become more or less evenly represented. Lastly, because interactions between soil quality and weather can affect different prairie plant communities in different ways, productive and less productive sites may respond differentially, in terms of either biomass or species composition, to annual differences in precipitation.

To examine these questions, I used a study system that enabled direct comparison of plant communities occupying very different soil types but in close proximity to one another and therefore experiencing the same seasonal and year to year weather changes. The 7-year study period encompassed years during which annual and growing season precipitation were well above or below the 30-year norm.

Methods

Description of study sites

From 1986 to 1992, I surveyed vegetation at four prairie sites occupying relatively unproductive to productive soils located within a radius of 0.4 km in Saline County, Kansas, U.S.A. (section 5 T15S R2W Hutchinson Quadrangle, 38°44'N, 97°34'W), within the western edge of the tallgrass prairie region (transition between Bluestem Prairie and Bluestem – Grama Prairie sensu Küchler 1974). The vegetation here is dominated by several C₄ grasses: *Andropogon gerardii*, *Andropogon scoparius*, *Bouteloua curtipendula*, *Panicum virgatum*, and *Sorghastrum nutans*.¹

Sites 1 and 2 represented relatively productive, typical tallgrass prairie communities. Sites 3 and 4 displayed shorter and sparser standing crops and therefore serve as examples of less productive communities. Site 1, a 6–7% slope with southwest aspect, occupied a Longford silt loam (fine, montmorillonitic, mesic Udic Argiustolls). Site 2, a 5–7% west-facing slope, also occupied a Longford silt loam. Depth to bedrock at these sites is > 152 cm, with few fine pebbles in the B horizon. Site 3 was on a west-facing 27–37% slope

¹ Botanical nomenclature follows Great Plains Flora Association (1986). A list of all species sampled may be obtained from the author.

that had experienced topsoil erosion. Site 3 features a Clime soil (fine, mixed, mesic Udorthentic Haplustolls), with depth to shale ranging from 51 to 102 cm. Flat limestone fragments cover 0–15% of the surface. Site 4 was on a 13–16% south-facing slope, with Lancaster-Hedville Complex soils (fine-loaming to loamy, mixed, mesic Udic Argiustolls and Lithic Haplustolls). Depth to sandstone varies from 10 to 102 cm, with <5% hard sandstone fragments in the B horizon (Palmer et al. 1992). All four sites lie between 390 and 400 m elevation. The sites experienced seasonal cattle grazing and periodic spring burning prior to 1986. The study was not designed to separate the effects of burning from precipitation. To reduce litter accumulation during the study, then, I burned the sites in March of 1987, 1990, and 1992, which coincided with years of above normal precipitation.

To characterize physical and chemical properties of soils at the four sites, I collected soil cores in June, August, and December. Field sampling consisted of collecting four representative cores from each plot to a depth of 100 cm. Plant litter was removed from the soil surface before each core was collected. Each core was separated into the following depth increments: 0–30, 30–60, and 60–100 cm. Soil samples were then composited by depth, returned to the laboratory, and air dried at 30°C to constant mass. The samples were ground, then analyzed for pH (potentiometrically in a 1:1 soil–water slurry), Bray P (P-1 method), 1 M KCl-extractable NO₃ and NH₄, and exchangeable K, Ca, and Mg (1 M ammonium acetate extractant). Total N and organic C were measured colorimetrically. Sulfate S was determined by the turbidimetric measurement of barium sulfate. Details of procedures are in Technicon Industrial Systems (1977) and North Dakota Experiment Station (1988). Analyses were done at the Soils Testing Laboratory at Kansas State University, Manhattan, Kans.

In general, sites 1 and 2 were higher in organic matter, total N, and K throughout the soil profile, and NH₄ at intermediate depths (Table 1). In contrast, sites 3 and 4 had generally higher pH, with site 3 showing consistently higher Ca to 30 cm and site 4 generally displaying the highest Ca, Mg, and SO₄ at the lowest depths. The generally more clayey soils of sites 3 and 4 suggest both lower percolation rates and availability of water for plant growth.

Precipitation data were obtained from the Salina reporting station approximately 7 km WNW of the field sites. Annual precipitation was above the 1950–1980 average (73.5 cm) in 1986 (80.2 cm), 1987 (83.5 cm), 1990 (87.4 cm), and 1992 (92.7 cm), and below the average in 1988 (46.1 cm), 1989 (58.5 cm), and 1991 (60.6 cm) (National Oceanic and Atmospheric Administration 1986–1992 records).

Sampling procedure

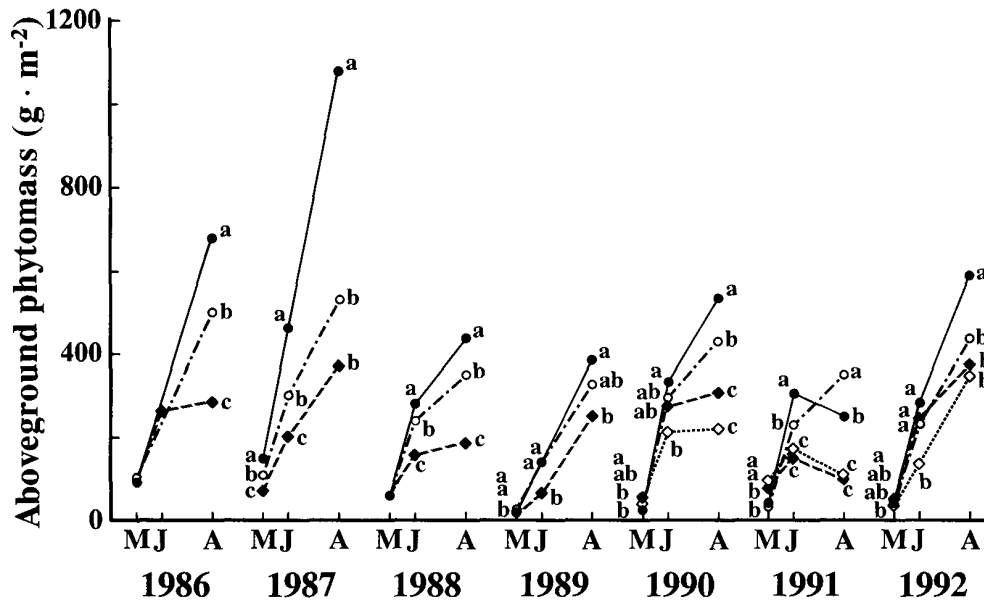
I established four 7 × 16 m permanent sampling areas, one area per site, encompassing representative vegetation at sites 1–3 in early April 1986 and at site 4 in April 1990. Within each plot I sampled aboveground live phytomass systematically within twelve 50 × 50 cm quadrats in May, June, and August from 1986 to 1992. The May sampling dates coincided with the time that such ephemeral forbs as *Lomatium foeniculaceum*, *Androstephium caeruleum*, and *Microseris cuspidata* flowered and set seed, but most C₄ grasses were just emerging. The June sampling dates corresponded to flowering and peak aboveground mass of such C₃ grasses as

Table 1. Characteristics of soils at four prairie sites.

Depth and site	Texture (sand – silt – clay)	pH	% organic matter	NH ₄	NO ₃	Total N	P	K	Ca	Mg	SO ₄
0–30 cm											
Site 1	26:52:22	6.18 ± 0.21c	3.80 ± 0.22a	6.95 ± 4.02	0.52 ± 0.21	1620 ± 50a	5.32 ± 3.63	384 ± 16a	2060 ± 80c	480 ± 30b	4 ± 4
Site 2	29:48:23	6.15 ± 0.31c	3.58 ± 0.29a	7.45 ± 3.41	0.52 ± 0.51	1400 ± 280ab	5.78 ± 4.30	339 ± 19b	2440 ± 130b	450 ± 50b	4 ± 4
Site 3	28:38:34	7.52 ± 0.13a	1.60 ± 0.29c	3.40 ± 0.98	0.65 ± 0.58	780 ± 80c	4.08 ± 3.22	197 ± 29c	3730 ± 200a	520 ± 40b	4 ± 3
Site 4	40:35:25	6.70 ± 0.60b	2.28 ± 0.10b	3.82 ± 1.13	0.30 ± 0.24	1170 ± 300b	1.98 ± 0.49	178 ± 9c	1690 ± 290d	810 ± 100a	9 ± 5
30–60 cm											
Site 1	18:42:40	6.32 ± 0.24b	1.68 ± 0.17a	4.60 ± 1.34a	0.25 ± 0.29	840 ± 50a	2.12 ± 2.02	284 ± 40a	2890 ± 180	810 ± 30b	5 ± 4b
Site 2	28:38:34	6.38 ± 0.29b	1.32 ± 0.22b	4.52 ± 1.44a	0.18 ± 0.24	670 ± 190ab	1.50 ± 0.71	226 ± 30b	2780 ± 120	570 ± 60c	2 ± 4b
Site 3	18:32:50	7.70 ± 0.22a	0.60 ± 0.14c	1.52 ± 0.39b	0.10 ± 0.20	330 ± 30c	2.88 ± 2.10	139 ± 9c	2950 ± 560	690 ± 150bc	1 ± 2b
Site 4	24:37:39	7.40 ± 0.26a	0.78 ± 0.10c	2.05 ± 0.52b	0.25 ± 0.17	520 ± 170bc	0.38 ± 0.25	144 ± 5c	3610 ± 820	1340 ± 30a	245 ± 112a
60–100 cm											
Site 1	26:36:38	6.72 ± 0.30b	1.00 ± 0.16	3.50 ± 0.88	0.25 ± 0.33	590 ± 90a	1.25 ± 0.65b	212 ± 32a	2780 ± 200b	800 ± 60b	7 ± 7b
Site 2	40:30:30	6.52 ± 0.40b	0.92 ± 0.10	4.38 ± 2.19	0.20 ± 0.28	440 ± 100b	1.25 ± 0.29b	175 ± 23ab	2370 ± 260b	460 ± 50c	14 ± 16b
Site 3	18:36:46	7.83 ± 0.15a	0.73 ± 0.51	3.57 ± 2.47	0.13 ± 0.23	320 ± 40b	2.33 ± 0.29a	142 ± 19b	2700 ± 550b	710 ± 40b	1 ± 2b
Site 4	17:35:48	7.42 ± 0.21a	0.55 ± 0.06	3.72 ± 1.32	0.15 ± 0.17	330 ± 110b	1.12 ± 0.63b	161 ± 15b	7390 ± 2740a	1710 ± 150a	704 ± 305a

Note: Concentrations of nutrients are in micrograms per gram. Values are means ± SD, n = 4. Within a depth, means followed by the same letter do not differ at p < 0.05 (ANOVA, Duncan's multiple range test).

Fig. 1. Mean aboveground biomass at three sampling periods for three or four prairie sites, 1986–1992. Within a sampling period, means with the same letter do not differ at $p < 0.05$ (ANOVA, Duncan's multiple range test). $n = 12$ samples per mean. ●, site 1; ○, site 2; ◆, site 3; ◇, site 4.



Poa pratensis, *Dicanthelium oligosanthes*, and *koeleria pyramidata*. The August sampling coincided with the flowering period of the dominant C_4 grasses and represented near peak live phytomass on the prairie. I clipped to ground level the vegetation representing the current year's growth within each sample frame, separated the plants by taxon, then dried the samples at 60°C to constant mass and weighed them to the nearest 0.01 g. In 1986, I divided the vegetation into grasses, legumes (Fabaceae and Mimosaceae), and composites, and combined the rest (i.e., Liliaceae, Lamiaceae, Apiaceae, etc.). Beginning in 1987, I separated the samples by species in the field prior to drying. No 0.25-m² area was ever clipped twice.

Data analysis

For each sampling date, I compared aboveground and percent aboveground phytomass among sites by Model I ANOVA and assessed differences among groups using Duncan's multiple range test ($\alpha = 0.05$). I used Pearson's correlation to examine associations between variables.

From the 1987 through 1992 data, I calculated species richness and evenness. Richness (S) is the number of plant species sampled per quadrat or site. Evenness, a measure of equitableness among species, is $H'/\ln S$, where H' is the information index (Peet 1974)

$$[1] H' = -\sum p_i (\ln p_i)$$

using relative biomass (p_i) of each species in the sample.

To examine differences in relative change in peak (August) standing crop among sites from 1987 to 1988, and from 1988 to 1989, I tested for significant site by year interactions by model I ANOVA, with site and year as fixed variables. Any such interactions indicated that sites responded relatively differently to annual changes in precipitation and other environmental variables. To measure relative change year to

Table 2. Total species richness for four prairie sites, 1987–1992.

Year	Site 1	Site 2	Site 3	Site 4
1987	34	32	38	—
1988	37	40	45	—
1989	28	24	35	—
1990	43	39	35	53
1991	36	31	39	52
1992	37	38	42	51

year, I calculated coefficients of variation (CV) for biomass and diversity across years for different sites.

Results

Community composition across sites

In nearly all instances, total aboveground live biomass increased from the May to August samplings (Fig. 1). An exception occurred in the dry year of 1991 when biomass at three of the sites declined from June to August. Biomass was generally higher at sites 1 and 2 than at sites 3 and 4, with the site differences most distinct in August.

I collected from 24 to 53 identifiable plant species within quadrats on the four sites from 1987 to 1992 (Table 2). The predominant seasonal pattern among plant groups was an increasing percentage of biomass represented by grasses from May to August at all sites (Fig. 2). Grasses represented the majority of aboveground mass at all sites. Sites 1 and 2 were fairly similar in species composition, comprising primarily grasses, whereas sites 3 and 4 featured a higher richness of forb species. Nitrogen-fixing species were well represented at site 3, uncommon at site 4 (range 0.4–2.3% of biomass), and very rare (<1% of biomass) at sites 1 and

Fig. 2. Mean percent grasses, legumes, and composites at three sampling periods for three or four prairie sites, 1986–1992. Within a sampling period, means with the same letter do not differ at $p < 0.05$ (ANOVA, Duncan's multiple range test). $n = 12$ samples per mean. Symbols as in Fig. 1.

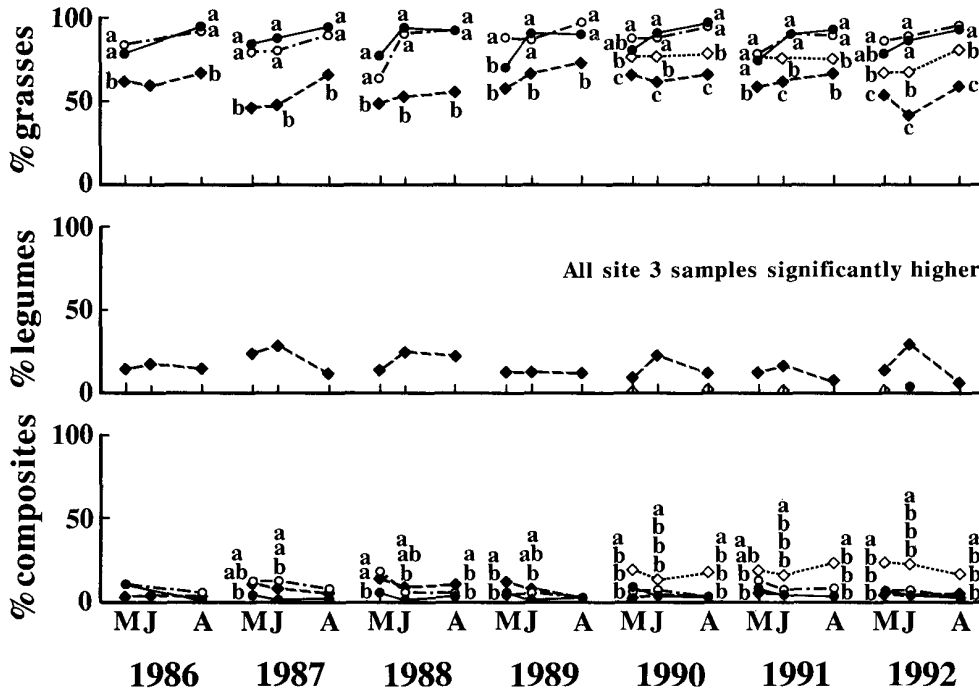


Table 3. Means for several variables at four prairie sites.

Site	August biomass ($g \cdot m^{-2}$)		% C ₃		% composites	% N-fixing spp.	Richness	Evenness
	% grasses	graminoids	% C ₄	grasses				
1	566	87.0	17.4	75.0	4.8	0.2	9.1	0.494
2	419	87.6	10.6	79.8	8.0	0.0	10.1	0.543
3	268	59.3	0.0	58.7	7.3	17.1	8.4	0.647
4	232	75.4	1.7	74.0	19.7	1.2	11.9	0.637

Note: Means are across years and except for August biomass, across sampling periods.

2 (Table 3). The proportion of total biomass represented by composites was consistently low at sites 1 through 3, but generally higher in May than in August (Fig. 2). Site 4 was unusual in featuring a relatively high proportion of composites, as high as 24.0% of biomass in May 1992.

Richness and evenness across sites

There were few consistent seasonal changes in the two diversity measures (Fig. 3). Richness either peaked in June, or declined from the May to August samplings, reflecting a shift from spring species, which were largely dormant by mid-summer, to species that thrived from midsummer on. Hence, the midseason peak in richness reflects the overlap between early season species (i.e., ephemeral forbs and C₃ graminoids) and late summer species (i.e., C₄ grasses and some composites). Evenness in most cases tended to remain constant across the season, or to decline from May to August.

Sites differed in terms of the diversity indexes. Communities at sites 1 and 2 were generally less even than at sites 3 and 4 (Fig. 3). Both sites 2 and 4 tended toward richer sam-

ples. For all years combined, biomass at each site was most often inversely related to evenness (Table 4), indicating that greater biomass was associated with greater dominance, especially in August. The results also suggest relationships between overall biomass and richness.

There was a notable scale effect on species richness. Total plot richness was highest at site 4 (Table 2). At the level of the 0.25-m² quadrats, however, richness was high at both sites 2 and 4 (Fig. 3). In other words, more plant species overall were present at the less productive site, but each species was encountered less frequently in samples than were species at the more productive sites, which were more uniformly distributed across the site and thus more frequently encountered.

Year to year differences

The wet years, 1986, 1987, 1990, and 1992, were associated with greater phytomass production, with a peak of 1078 $g \cdot m^{-2}$ at site 1 in 1987 (Fig. 1). Conversely, the dry years of 1988, 1989, and 1991 supported relatively low

Fig. 3. Mean species richness and evenness at three sampling periods for three or four prairie sites, 1987–1992. Within a sampling period, means with the same letter do not differ at $p < 0.05$ (ANOVA, Duncan's multiple range test). $n = 12$ samples per mean. Symbols as in Fig. 1.

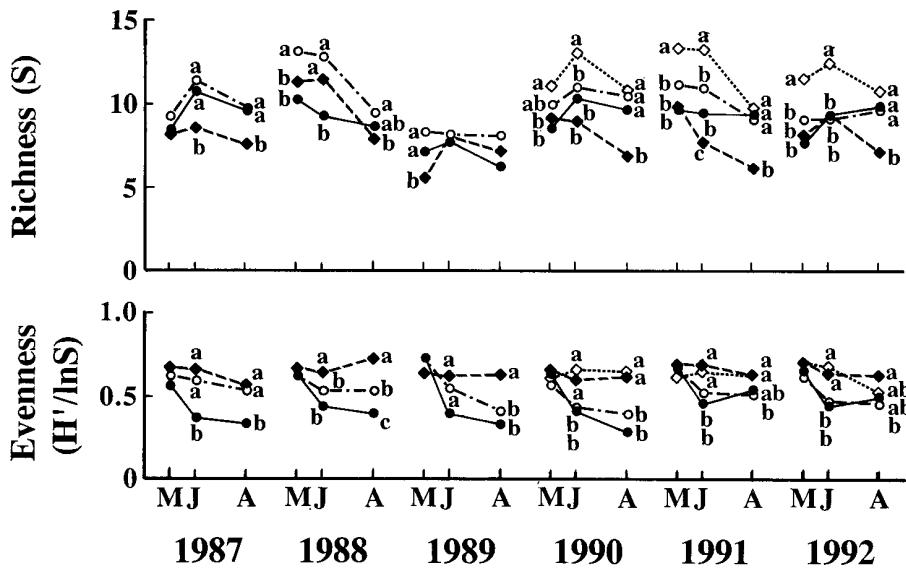


Table 4. Relationship between biomass, evenness, and richness across 6 years for four prairie sites.

Sample period and site	Biomass vs. evenness	Biomass vs. richness
May		
Site 1	-0.34**	ns
Site 2	ns	ns
Site 3	ns	0.45***
Site 4	0.40*	0.42*
June		
Site 1	ns	0.36**
Site 2	-0.25*	0.32**
Site 3	-0.36**	ns
Site 4	ns	ns
August		
Site 1	-0.44***	ns
Site 2	-0.39***	0.35**
Site 3	-0.29*	0.27*
Site 4	-0.51**	ns

Note: Values are Pearson's correlation coefficients; $n = 72$ for sites 1–3; $n = 34$ for site 4.
 *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

biomass production. Precipitation data essentially formed two clusters over the 7 years (Fig. 4), tempering the interpretation of significant associations between precipitation and biomass. Nevertheless, previous 12-months precipitation appeared to correlate better with peak standing crop than did growing season precipitation, and explained from 51% of August biomass on site 1 to 97% of August biomass on site 4 (previous 12-months precipitation vs. biomass: site 1, $r^2 = 0.51$; site 2, $r^2 = 0.75$; site 3, $r^2 = 0.68$; site 4, $r^2 = 0.97$; growing season precipitation vs. biomass: site 1, $r^2 = 0.25$; site 2, $r^2 = 0.42$; site 3, $r^2 = 0.65$; site 4, $r^2 =$

0.96). The combination of above average precipitation and spring burning, which favors the growth of tallgrass prairie plants, in 1987 likely led to site 1 showing its highest productivity that year. However, 1990 and 1992 were also years in which above average precipitation was coupled with spring burning, yet these years were less productive than 1987. This somewhat lower production in 1990 and 1992 relative to 1987 may reflect a lag in recovery of biomass following a previous dry year.

In some cases, there were distinct year to year differences in representation by the major functional or taxonomic groups (Fig. 2). Despite a few differences, there were no consistent patterns in percentage grass among years for any site. At sites 1 and 2, percentage of C_3 graminoids was highest in 1988 and 1989 for the May sampling, and highest in 1987 and 1988 for the June and August samplings. At sites 2 and 3, percentage composites in May peaked in the dry years, 1988 and 1989, indicating that composites assume relatively more importance in spring in dry years. Percentage of N-fixing species, predominant at site 3 only, was as high as 30.8% of biomass in 1987, but there were no significant year to year differences at this site. In most cases, proportions of the four groups did not differ across years, indicating that biomass of the groups varied with total above-ground biomass.

The diversity indexes also varied across years in some cases. Richness was generally lowest in the drought year of 1989, owing to either loss or enforced dormancy early in the growing season (Fig. 3). At site 1, richness in June and August was lowest in 1989. At site 2, richness in May and June was also lowest in 1989. At site 3, May richness was lowest in 1989 and June richness was high in 1988. In contrast, evenness at sites 1 and 2 was high in the dry years of 1989 and 1991, and low in the wet year of 1987.

There were significant site by year interactions for biomass in all situations, for percent composites in May, and for

Fig. 4. Mean August aboveground biomass versus two precipitation indexes for four prairie sites over 7 years. $n = 12$ samples per mean. Symbols as in Fig. 1.

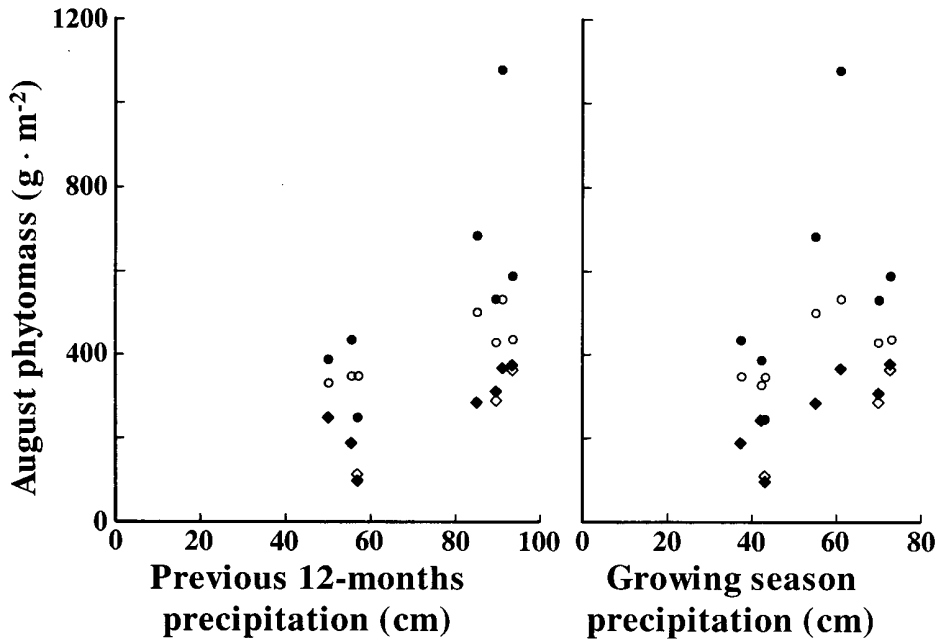


Table 5. Coefficients of variation across years for four prairie sites, 1986–1992.

Month and site	Biomass	Richness	Evenness
May			
Site 1	74.4	13.5	8.8
Site 2	51.4	17.3	7.9
Site 3	43.4	22.2	3.0
Site 4	55.4	10.1	6.7
June			
Site 1	34.2	11.1	8.0
Site 2	24.5	15.6	11.3
Site 3	37.7	14.9	4.2
Site 4	21.2	3.3	2.0
August			
Site 1	48.7	14.8	24.7
Site 2	19.2	8.8	12.7
Site 3	36.4	8.8	7.9
Site 4	57.2	5.2	6.1

Note: CVs for site 4 are for 1990–1992 only.

August evenness. Year to year variability in biomass or richness was not associated with site productivity (Table 5), although CVs for evenness were generally lower for sites 3 and 4 than for sites 1 and 2. For all sites and sampling periods, biomass was more variable than richness and evenness. Coefficients of variation for August evenness were inversely related to site productivity.

Discussion

Community composition across sites

The species composition of grasslands can be strongly influenced by soil characteristics (Williams 1978; Gibson and Hulbert 1987; Wedin and Tilman 1990). My results reflected

patterns reported elsewhere. The more productive sites were characterized primarily by tall C_4 grasses, about 20% C_3 graminoids, but legumes were virtually absent. The site with relatively low soil N featured shorter C_4 grasses, typically 20–30% N-fixing species, but no C_3 graminoids. Thus, it appeared that C_3 grasses were more dependent on high available soil N than C_4 grasses. Typically, a greater proportion of C_3 grasses are found in grassland habitats with deeper soil, greater soil water availability, less sunlight, and higher available N (Barnes and Harrison 1982; Tilman and Olf 1991). Studies using experimental N gradients have borne this out, with such C_4 grasses as *Andropogon scoparius* and *Andropogon gerardii* outcompeting C_3 grasses on low N soils (Inouye and Tilman 1988; Tilman 1990), and added N favoring the growth of two perennial C_3 grasses, *Poa pratensis* and *Agropyron repens*, relative to *Andropogon scoparius* (Wilson and Tilman 1991).

Nitrogen-fixing species should be favored on relatively N-poor soils where N is the primary factor limiting growth (Foote and Jackobs 1966; Tilman 1987). Under conditions of low N availability, N-fixing species should have a growth rate advantage over other plants, whereas at high N competition would instead be for light. Moreover, additions of N fertilizer can increase percentage grass biomass and reduce the proportion of legumes in experimental pastures (Scarlsbrick and Ivins 1970). Again, my results reinforced this general observation, with such N-fixing species as *Amorpha canescens*, *Astragalus crassicaarpus*, *Baptisia australis*, *Ceanothus herbaceus*, *Dalea candida*, *Dalea purpurea*, *Psoralea argophylla*, and *Schrankia nuttallii* together representing an average 17% of the aboveground biomass at the site with lowest available soil N concentration.

It was unclear why composites were so abundant at site 4, where soil water may have been more limiting than soil N. The high SO_4 below 30 cm may indicate a salt-rich soil that may have been associated with the proliferation of halophytic

or xerophytic species. It is notable that some particularly drought-hardy composites (e.g., *Aster ericoides*, *Liatris punctata*, and *Solidago rigida*) were common at this site.

Richness and evenness across sites

Inverse relationships between productivity and species diversity are documented for many two-dimensional ecosystems, including grasslands (Al-Mufti et al. 1977; Grime 1979), old-fields (Mellinger and McNaughton 1975), and heath scrublands (Specht and Rayson 1957). Experimental increases in productivity, through added N or water, for example, can significantly increase plant biomass production in old-fields, pastures, and native prairies while significantly decreasing species diversity as shade-intolerant species are apparently displaced by taller competitors (Kirchner 1977; Reed 1977; Bakelaar and Odum 1978; Tilman 1987). Hence, low evenness and diversity are largely an effect of productivity, as higher productivity is often associated with increased dominance. Moreover, competition from one or a few dominant species, which can thereby limit the presence and abundance of other species in a community, can have a greater effect at high soil resource levels (Tilman 1987; Kirchner 1977; Goldberg and Miller 1990; Gurevitch et al. 1990). This phenomenon should lead to stable species coexistence under less productive conditions but increased dominance leading to competitive exclusion in more favorable environments (Bazzaz and Harper 1976; Mahmoud and Grime 1976; Goldberg and Miller 1990). In grasslands, increased soil productivity should favor the taller, more vigorous components that preempt light and space, increasing the intensity of above-ground competition and leading to suppression or local extinction of shorter species (Wilson and Tilman 1991, 1993).

Therefore, total biomass of the dominant species in a plot may be a good predictor of competition and therefore inversely related to evenness and diversity. Such a prediction was borne out in the present study. Where soils were deeper, mesic, and more fertile, the community structure of the sites appeared to be dominated by tallgrasses, primarily *Andropogon gerardii*, relative to shorter species. Conversely, the less-favorable soils of sites 3 and 4 supported less growth of tall species, allowing the stable coexistence of many low-growing species, and higher evenness and diversity. Inverse relationships between percent biomass of such tall grasses as *Andropogon gerardii* and evenness and diversity were also observed for prairie sites in eastern Oklahoma (Collins 1987).

Year to year changes

At least three important factors, soil quality, annual precipitation, and spring burning, affect plant production on the North American tallgrass prairie. Where soil was relatively deep and fertile, at site 1, August aboveground growth averaged $566 \text{ g} \cdot \text{m}^{-2}$ for the 7 years, and exceeded $1000 \text{ g} \cdot \text{m}^{-2}$ in 1987. Spring burning typically enhances growth of emerging shoots by removing litter from previous years and thereby increasing soil temperature and light at the soil surface (Knapp and Seastedt 1986). Spring burning in 1987, 1990, and 1992 could not be separated from the effect of higher precipitation in these years, however. This enhancement of growth was somewhat more pronounced at

the more productive sites than at the less productive sites, and precipitation correlated better with peak standing crop at the poor sites. This may have been due to the relative effects of litter at each site. In a mesic year in which spring burning has occurred, plant growth exceeds that which would be explained by precipitation alone. Conversely, in a dry, non-burn year, the insulating effect of litter could help conserve soil water, allowing more growth than would be predicted at low precipitation levels. Extensive bare ground at sites 3 and 4 suggests that plant growth at these sites was probably limited more by such factors as soil quality, slope, and aspect than by thickness of leaf litter. Effective precipitation is lessened at these sites because of slopes that promote runoff, lack of a closed canopy to intercept raindrops, and lack of soil organic matter to absorb and retain water. This suggests that burning effects should be less pronounced at these sites, as it is on shortgrass prairie relative to tallgrass prairie (Knapp and Seastedt 1986), making plant growth at these sites more directly tied to soil water.

Fluctuation in precipitation is the principal cause of plant growth variability in grassland communities (Coupland 1958). Aboveground biomass can fluctuate widely from year to year, and is typically predicted by annual and growing season precipitation (Shiflet and Dietz 1974; Lauenroth and Sala 1993). The 3rd and 4th years, 1988 and 1989, were 2 consecutive years of below average precipitation, 37 and 20% below the 30-year norm, respectively. Low precipitation again in 1991 (18% below the norm) contributed to the ongoing soil water deficit. Because of this drought, both overall production and the production of many individual species declined. At site 1, in particular, there was a more than fourfold difference in August biomass between the 1991 low and the 1987 high. Annual precipitation for the 7-year study period had a CV of 24.1%, whereas biomass CVs were higher than this in 10 of 12 cases (Table 5).

Moreover, there can be a lag period of several years in recovery of biomass following dry years (Weaver 1968; Lauenroth and Sala 1993). Extended drought can cause plant or tiller mortality, thus decreasing capability of current vegetation to respond to high resource availability. In my study, 1992 biomass did not equal predrought biomass at sites 1 or 2, despite resumption of favorable precipitation.

In addition to biomass variation, species composition and relative abundance can change between wet and dry periods. An extreme instance occurred during the drought of the 1930s, when western wheatgrass (*Agropyron smithii*) supplanted tall grasses on much of the eastern Kansas prairie while many short grasses moved eastward. When normal precipitation resumed in the 1940s, the prairies reverted more or less to their predrought species compositions (Weaver 1968).

There exists three possible mechanisms to explain year to year changes in community composition on prairie. Species may colonize an area if, for example, increased soil water in a wet year favors seedling growth. Alternatively, species may go extinct locally because of drought or exclusion by tall species in wet years (Belsky 1992). Lastly, species may remain present at a site but differ in relative growth because of differential responses to annual precipitation. Thus, increased productivity in a given year could influence diversity and evenness by affecting colonization, local

extinction, or relative abundance. Extreme conditions, such as extended drought, can limit richness on grasslands by causing local extinction of annuals and rare perennial species (Tilman and El Haddi 1992).

I observed all three mechanisms, although colonization and extinction were relatively minor factors compared with annual changes in relative growth among species. The rare instances of colonization included mainly woody species from nearby wooded areas and fence lines (e.g., *Ulmus pumila* and *Toxicodendron radicans*) and weeds (e.g., *Bromus tectorum* and *Taraxacum officinale*) that tended to appear following wetter years. These species were reduced or eliminated by spring burning. Increased evenness in dry years arose largely via reduced growth of tall grasses, whereas richness was apparently reduced when some low-growing spring forbs (e.g., *Androstaphium caeruleum*) went dormant unusually early in the season, but did not die.

I expected the productive and less-productive sites to respond to favorable years in different ways, depending upon the extent to which factors other than precipitation influence growth on different soil types. For example, if production is governed primarily by nutrient supply on poor soils, then plant response to increased soil water in wet years will be limited, leading to lower year to year variability at these sites than at sites with deeper, more fertile soils. In the present study, however, precipitation was a somewhat better predictor of production on less productive sites than on more productive sites. This indicates that plant communities on more productive soils are somewhat "buffered" against year to year variability, whereas plants on poorer soils are poised to respond to flushes of available nutrients when soil water increases. Otherwise there were no consistent relationships between productivity and variability on my four sites (Table 5). A greater number of sites than I used may be needed to observe such relationships.

Differences in relative year to year change in species diversity among sites may also occur. For instance, species-rich communities may be more likely to lose species than depauperate communities, which may be more likely to gain species. Also, there may be an association between productivity and relative change in species diversity. Tilman and El Haddi (1992) documented a disproportionate loss of species, as a consequence of drought, from plots on high-N soils. In my study, in contrast, there were no consistent differences among sites in relative year to year change in species richness.

Plant biodiversity may therefore contribute directly to the resilience (sensu Pimm 1984) of grassland communities. Several recent studies showed that species-rich grasslands are more resistant to relative biomass change, following drought or grazing pressure, than species-poor communities (McNaughton 1985; Frank and McNaughton 1991; Tilman and Downing 1994). In 5 of 7 years of my study, site 3 had higher total richness than sites 1 and 2 (Table 2). Although my sample size was insufficient to test statistically a relationship between diversity and resilience, it is nonetheless interesting to note that 1990 (postdrought) August biomass was 82.1% of 1987 (predrought) biomass and 1992 biomass was 101.6% of 1987 biomass at the relatively more diverse site 3, whereas these percentages were 59.8 and 63.9% for the less diverse sites 1 and 2 combined. Unfortunately, I lack predrought data for the most diverse site (site 4) and so could

not include them in this analysis. Because the sites also occupied different soil types and supported different communities, it is not possible to separate the effect of diversity per se from the physiological characteristics of the constituent species.

Implications

How vegetation patterns differ across soil types, and vary across years, in prairie communities has direct relevance for restoration ecology as well as the composition of perennial grain polycultures designed for different soil types (Soule and Piper 1992). For instance, prairie mimics for relatively productive soils should feature a high proportion of C₄ grasses, smaller representations of C₃ grasses and composites, and less emphasis on N-fixing species. In contrast, a low-N soil might be expected to support a preponderance of C₄ grasses, sizable components each of N-fixing legumes and composites, but few if any C₃ grass species. Annual precipitation differences are likely to influence growth and species composition on different soils in different, possibly unpredictable ways. Restorations comprising relatively high species diversity may be more resistant to disturbance or year to year change and achieve stability sooner than communities with low diversity.

The diverse community structure and different types of resource use by plant species contribute to the persistence and resilience of the prairie ecosystem. An understanding of the factors that affect and stabilize community structure, and how prairie communities respond to climatic fluctuations, will be essential for restoring stable and diverse plant communities as well as designing sustainable perennial agricultural systems for the Great Plains modeled on the structural and functional aspects of the prairie ecosystem.

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