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Prairie plant guilds: a multivariate analysis of prairie species based on ecological and morphological traits

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Abstract

An ecomorphological analysis of the tallgrass prairie of central North America divided representative species of the native grassland flora into eight guilds or groups of species with similar life-form, phenology, and ecology. The guilds, segregated by multivariate analysis, are: (1) warm-season graminoids with Kranz anatomy and the Hatch-Slack photosynthetic pathway ('C4' grasses); (2) cool-season graminoids without Kranz anatomy, but with the common Calvin or C3 photosynthetic pathway (C3 grasses and sedges); (3) annuals and biennial forbs; (4) ephemeral spring forbs; (5) spring forbs; (6) summer/fall forbs; (7) legumes; and (8) woody shrubs. The study was based on 158 plant species indigenous to three upland prairie sites in northeastern Kansas. Each species was scored for 32 traits which fall into five broad categories: plant habit, leaf characteristics, stem structures, root structures, and reproductive traits, including phenology. A multivariate, detrended correspondence analysis sorted the 158 species into the eight principal groups or guilds. These groups were further supported by a cluster analysis and discriminant function analysis of the same data set. The discriminant function analysis determined that 94.3% of the species were correctly classified in their respective guilds, and that the guilds were statistically different. Results indicate that guild analysis offers a basis for detailed classification of grassland vegetation that is more ecologically focused than species composition, as the myriad of species (about 1,000 prairie species on the central plains of North America) vary in presence, cover, and importance with their individualistic distribution.

Abbreviations: C3 = C3 photosynthesis; C4 = C4 photosynthesis; LSD = least significant difference

Nomenclature: Great Plains Flora Association. 1991. Flora of the Great Plains. University Press of Kansas, Lawrence.

Introduction

The determination of guilds can be useful in developing an ecological understanding of communities (Simberloff & Dayan 1991). The term guild has been defined by Root (1967) as a group of species that exploit the same class of environmental resources in a similar way. He used this definition for different bird taxa that share the same or similar functional niche (e.g. guilds of leaf-gleaners or bark-gleaners).

Historically, the term guild was first used to describe groups of plants with similar lifestyles, and specifically four distinct guilds were named: lianes, epiphytes, saprophytes, and parasites (Schimper 1898). Guild is the literal translation of the German word 'Genossenschaft' originally adopted by Schimper who used it in a sense similar to a medieval union of skilled craftsmen plying the same trade. Plant guilds have not been tied to resources as obviously as animal guilds, perhaps because of the difficulty in reconciling plant diversity with notions that resource partitioning structures plant communities (Simberloff & Dayan 1991). The guild concept clearly foreshadowed the later idea of functional niche (Elton 1927). The term synusia is sometimes used as a synonym for guild, but generally implies a single layer (unistratal) plant community.

The guild concept is frequently discussed in the literature in terms of theory (Root 1967; Hawkins & MacMahon 1989; Simberloff & Dayan 1991) and as applied to management (Severinghaus 1981; Verner 1984; Szaro 1986; Reader 1988). For plant communities, guild has been used to describe a group of invasive, wind-dispersed prairie plants that colonize earth mounds made by badgers in Iowa (Silvertown 1987; Platt 1975). Guild has also been used in a successional sense by Hubbell & Foster (1986) to accommodate various subgroups of ecologically similar species in tropical rain forest in Panama (e.g. gap-phase specialists and shade tolerant trees and shrubs). Although all of these studies apply the guild concept to plants, there is a wide array of definitions. Recognizing that mechanisms of resource partitioning in plant communities have not been clearly linked to plant diversity, our study defines plant guilds as being groups of species with similar morphological, physiological, and ecological traits. The traits used in this study, however, were chosen because they are important to resource partitioning. Taxonomically, a single guild may include widely unrelated species, genera, families or higher taxa that have evolved similar ecological attributes as a result of convergent evolution (Wells 1976).

In a recent review article on guilds, Simberloff & Dayan (1991) stated that for the guild concept to be used 'fruitfully,' two conditions must be met: (1) a clear statement is needed as to the criteria and considerations that have led to a particular guild assignment; and (2) if sympatric related biota are included in the study, the exclusion of one from the same guild as the other, should be explained. These two conditions were considered in our study of prairie plant guilds. In Simberloff & Dayan's discussion of plant guilds, they stated that Fowler & Antonovics (1981) doubted that a grassland plant community is divisible into well-defined guilds, although they recognized that Fowler & Antonovics found two temporal guilds-cool-season (C3) grasses, and warm-season (C4) grasses. This suggestion of ill-defined grassland guilds by Fowler & Antonovics is not particularly surprising. The grassland system they studied was in Durham County, North Carolina, where in the area studied 'there is no natural grassland' (Fowler & Antonovics 1981), a large percentage (over 40%) of the species were non-native, and the area studied was mowed once a month during the growing season (probably favoring the grasses), which gave the area an appearance that ranged from a lawn to a rough pasture.

Ordination as a guild determination tool

Ordination of plant species on the basis of ecological and morphological similarity provides an objective quantitative means of classifying species into guilds. Ecological and morphological trait analyses have previously been used to interpret the groups and ordination of species in tallgrass prairies particularly for determination of life history characteristics affecting indicator, modal, and weedy species categories of prairie forbs (Havencamp & Whitney 1983), to arrange species along a gradient from wet to dry prairies (Knight 1965), and to characterize local environmental variables affecting plant species distribution in and around buffalo wallows (Polley & Collins 1984). We have sought to identify traits capable of sorting the myriad of tallgrass prairie species into a series of ecomorphological guilds by means of multivariate analysis. A broad spectrum of ecological and morphological traits was used to cast as wide a net as possible. Although patterned on similar lines, the study differs from that of Wells (1976) in having no specific orientation toward succession and in using two different methods of multivariate analysis:detrended correspondence analysis and cluster analysis.

The multivariate analysis was performed on a data matrix based on 32 ecological and morphological traits characterizing 158 species that comprise most local prairies in northeast Kansas and tallgrass prairie in general. The ecomorphological analysis included five broad categories: plant habit, leaf characteristics, stem structures, root structures, and reproductive traits, including phenology. The primary goal of this research is to determine if meaningful guilds of prairie species can be established through unbiased criteria – a multivariate analysis of ecological and morphological traits. Secondly, we would like to demonstrate that guilds may offer a better way to understand and interpret the diversity of tallgrass prairie plant life forms.

Study area

The study area consists of three native tallgrass prairies in northeast Kansas. All sites are upland prairie classified in the bluestem prairie area of Kansas (Kuchler

1974). Sites were selected for their richness of native species and relative lack of disturbance since European settlement. The three sites were also selected for their different management treatments, including burning, haying, and moderate grazing, to maximize the range of native prairie species likely to be found.

The first prairie site is the four-hectare Rockefeller Native Prairie of the University of Kansas, located 12 kilometers north of Lawrence, Kansas (Sec. 33, T11 S, R20E). The site contains Pawnee & Grundy silty clay loams (fine montmorillonitic, mesic Aquic Argiudolls). Since 1956, this site was managed by annual and biennial burning (Fitch & Hall 1978).

The second site is the two-hectare Palmer Prairie, a native prairie hay meadow, located about 16 kilometers SE of the first site (about 6 kilometers NNW of Eudora, KS., Sec. 29, T12S, R21 E). The soils of this site are Shelby loam and a Vinland-Sibleyville complex (primarily loam, mixed mesic shallow, typic Hapludolls). This site is managed through annual mowing and haying and has not been grazed in the recent past (personal communication with the owner, 1990).

The third site is part of a 65-hectare native grass pasture, located on the S & S Ranch, five kilometers north of the first site (Sec. 20, T11S, R20E). The soils in the sampled upland area are Martin-Oska silty clay loam and Martin silty clay loam (primarily a loam, mixed mesic shallow, typic Hapludolls). The area is seasonally grazed annually with moderate stocking rates (greater than 7.5 hectares/cow-calf unit) and has a past history of occasional overgrazing (personal communication with manager, 1990).

Materials and methods

Sampling and character analysis

During the 1989 and 1990 growing seasons, the three study sites were inventoried every seven to ten days to determine species composition and to collect data for the ecological and morphological traits. A total of 203 species was found at the three study sites. The species list was reduced to 158 by eliminating those species that were non-native, those from the adjacent wooded areas that do not reproduce on the prairie sites (under current management as prairies) and those for which insufficient data were collected. The 158 native prairie plants analyzed in this study are listed in Appendix 1. Species names and nativity are from the Flora of the Great Plains (Great Plains Flora Association 1991).

The species eliminated from the study, whose primary habitat is the adjacent wooded area, include mostly tree species (e.g., red elm, *Ulmus rubra* and ash, *Fraxinus americana*) and understory species (e.g., may apple, *Podophyllum peltatum*). These species all had poor reproductive success, low cover values, and never developed a dominant aspect on these sites because these sites are managed to be prairies through mowing, burning, and grazing. Furthermore, four rare species (e.g., the western prairie fringed orchid, *Platanthera oraeclara*), were not used because seeds or leaves could not be obtained.

Data for 32 traits (variables) that are presumed to be important to plant ecology, morphology, and resource use were collected and grouped into the five categories (Table 1). In an effort to make all variables discrete, for four traits (plant height, leaf size, time of flowering, and seed weight) the data were divided into three equal-sized classes (for small or early, medium, and large or late). The large and small classes are coded as distinct traits because each of these classes are distinct from the medium class and may confer special adaptive advantages to plant species that have this class trait. Fieldwork and samples measured in the lab also provided data for the following variables: graminoid/bulb, erect/decumbent, long/short growth period, cool/warm season, cauline/rosette leaves, leaf phyllotaxy, leaf length-to-width ratios, simple/compound leaves, presence/absence of basal leaf sheaths, cuticle luster, herbaceous/woody stems, clonal ability, and bunch/sod root structures. Botanical literature for the region (Bare 1979; Steyermark 1981; Great Plains Flora Association 1991) provided information on the following variables: annual/perennial, presence of bulbs, ability to fix atmospheric nitrogen, time of flowering, flowering duration, mode of pollination, and gravity or wind/zoophilous seed dispersal. The prairie plant ecology literature (Weaver 1919, 1954, 1968; Phillips Petroleum Company 1959; Downton 1975) provided information on photosynthetic pathway, fibrous/fascicled root system, deep/shallow rooting, and foliage palatability to herbivores.

In addition to data on ecological and morphological traits, 50 randomized quadrats (each 1.0 m^2) were sampled in late June 1989 from each of the three study areas. This data was collected to determine the cover values of the guilds. Sampling was conducted during this time of year in order to include both early spring species along with warm-season vegetation. Voucher specimens were deposited in the R. L. McGregor

Table 1. Ecological and morphological traits of prairie plants and scoring values.

Traits	Scoring values	
1. Habit		
Erect/Decumbent	0=Erect	1=Decumbent or Prostrate
Height, tall	0=Medium	1=Tall ($\geq$1 m)
Height, short	0=Medium	1=Short ($\leq$0.5 m)
Graminoid/Forb	0=Graminoid	1=Forb
Clones, large	0=Not clonal	1=Forms large clone (>2 m)
Bunch or sod	0=Bunch	1=Sod or mat
Duration	0=Perennial	1=Annual or Biennial
Growth period	0=Long season	1=Short (<2 months)
2. Leaves		
Season of active growth	0=Cool season	1=Warm season
Cauline/Rosette	0=Cauline	1=Basal rosette
Phyllotaxy	0=Spiral	1=Opposite or whorled
Leaf length/Width ratio	0=Narrow, small	1=Broad, large (<12:1)
Leaf size, small	0=Medium	1=Small ($\leq$2 cm^2)
Leaf size, large	0=Medium	1=Large ($\geq$15 cm)
Leaf division	0=Entire	1=Divided
Leaf compounding	0=Simple	1=Compound
Leaf sheathing	0=Basal sheath	1=No sheath
Photosynthetic pathway	0=C3	1=C4
Cuticle luster	0=Bright green	1=Hairy or Glaucous
3. Stem		
Woodiness	0=Herbaceous	1=Woody
4. Root structures		
Bulb	0=No bulb	1=Bulb or Corm
Rooting habit	0=Fibrous	1=Fascicle or Tap
Rooting depth	0=Deep	1=Shallow (<1 m)
Nitrogen fixation	0=None	1=N-fixation root nodules
5. Reproduction		
Flowering, early	0=Other	1=Early (Ave. before June 2)
Flowering, late	0=Other	1=Late (Ave. after July 31)
Flowering duration	0=Brief	1=Long (>2 months)
Mode of pollination	0=Wind	1=Zoophilous
Mode of seed dispersal	0=Wind, Gravity	1=Zoophilous
Seed weight, light	0=Medium	1=Light ($\leq$0.03 mg)
Seed weight, heavy	0=Medium	1=Heavy ($\geq$0.5 mg)
Palatability	0=Palatable	1=Unpalatable to herbivores

Herbarium at the University of Kansas (KANU). Percent species coverage in each quadrat was determined by estimating the sum of greatest spread of foliage for each species using Daubenmire's principles of sampling (Daubenmire 1959).

Data analysis

The ordination of species was conducted by using detrended correspondence analysis in the computer program CANOCO (Ter Braak 1987). Detrended correspondence analyses are useful for ordination of environmental data because they produce results that can more easily be interpreted than other multivariate techniques (Hill & Gauch 1980; Peet *et al.* 1988). The program CANOCO detrends the data mathematically by using polynomials, providing users a repeatable analytic detrending technique.

The interpretation of the first two ordination axes of the detrended correspondence analysis was assisted by correlating (using the Pearson product moment) the location of each species in the detrended correspondence analysis plot with the 32 ecological and morphological traits (using the raw data matrix). The result is that the ecological and morphological traits can be correlated to the X and Y axis. This technique has been used previously for correlating multivariate plot points with ecological characteristics (Polley & Collins 1984).

A cluster analysis of the data set was conducted using Ward's method in the SPSS/PC+ software package (SPSS 1988). This agglomerative hierarchical technique was used to determine if the ordination of prairie plant species by a detrended correspondence analysis would be corroborated by a second classification technique using the same data set.

To determine if the eight guilds were statistically different, rather than just being products of sampling variability, the data set was also subjected to discriminant function analysis using Mahalanobis distance as the selection criteria (SPSS 1988). A chi-square test for the observed Wilks' lambda of the canonical discriminant functions was used as a statistical test.

Paired T-tests were used to determine differences in cover of plant species between the three prairies and between the guilds. Raw data for species coverage from individual prairies was analyzed using paired T-tests in the SPSS/PC + software package (SPSS 1988) and the Bonferroni T-statistic (Sachs 1984). The paired T-tests for the cover values of all species between paired prairies were made using the absolute value of the difference in cover between species for each paired prairie compared to zero (where zero is the difference if the cover values of species on prairies is equal).

In order to determine if there were differences between the cover by guilds, paired T-tests were used to compare cover values of species within guilds between prairies for the sampled plots. In addition, to test differences between guilds for the three variables in the study with continuous data (plant height, seed weight, and leaf size), the raw data of species in guilds were compared using one-way analysis of variance (ANOVA) and the least significant difference (LSD) technique for multiple comparison of means of guilds using SPSS PC+ (SPSS 1988).

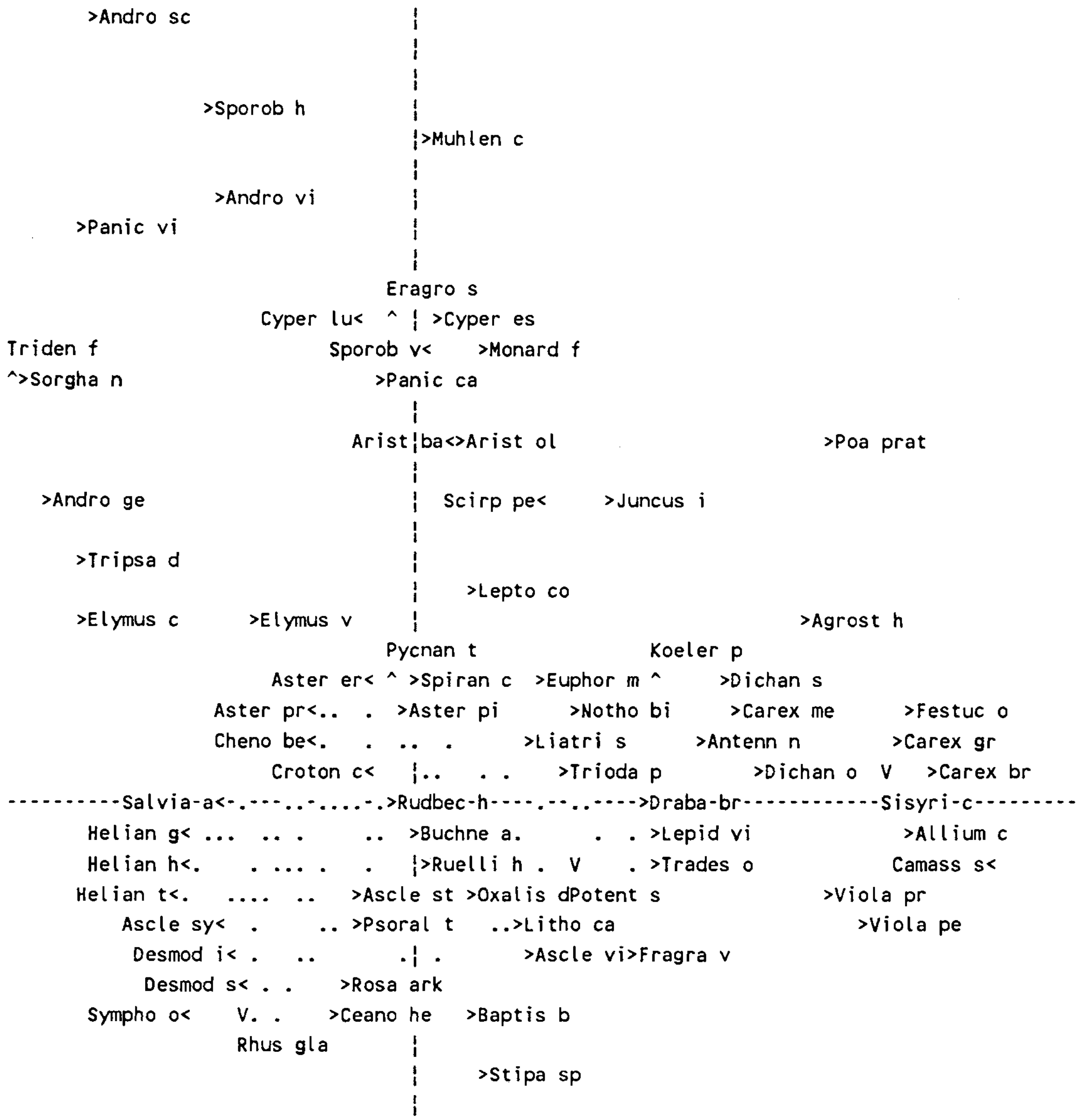
Results

The first axis of the detrended correspondence analysis explains 36% of the variation and the first four axes of the analysis explain 95% (Fig. 1). Individual species were assigned to guilds (Appendix 1) based on their location in this plot, and their life forms (the latter correspond, in part, to their gross taxonomic relationships). The C4 grass guild, C3 grass guild, and ephemeral spring perennials were most easily seen in the plots and were separated out, followed by the remaining logical groups. The individual species are coded by letter (Fig. 2) in the detrended correspondence analysis plot, designating one of the eight guilds. The eight groups or guilds of species resulting from the variables are listed in Table 2, along with representative species.

Cluster analysis of the data set resulted in similar groups, adding corroborative evidence to the existence of these groups (Fig. 3). The C3 photosynthetic pathway grass and sedge guild and the C4 grass guild were the two most clearly defined groups in both analyses.

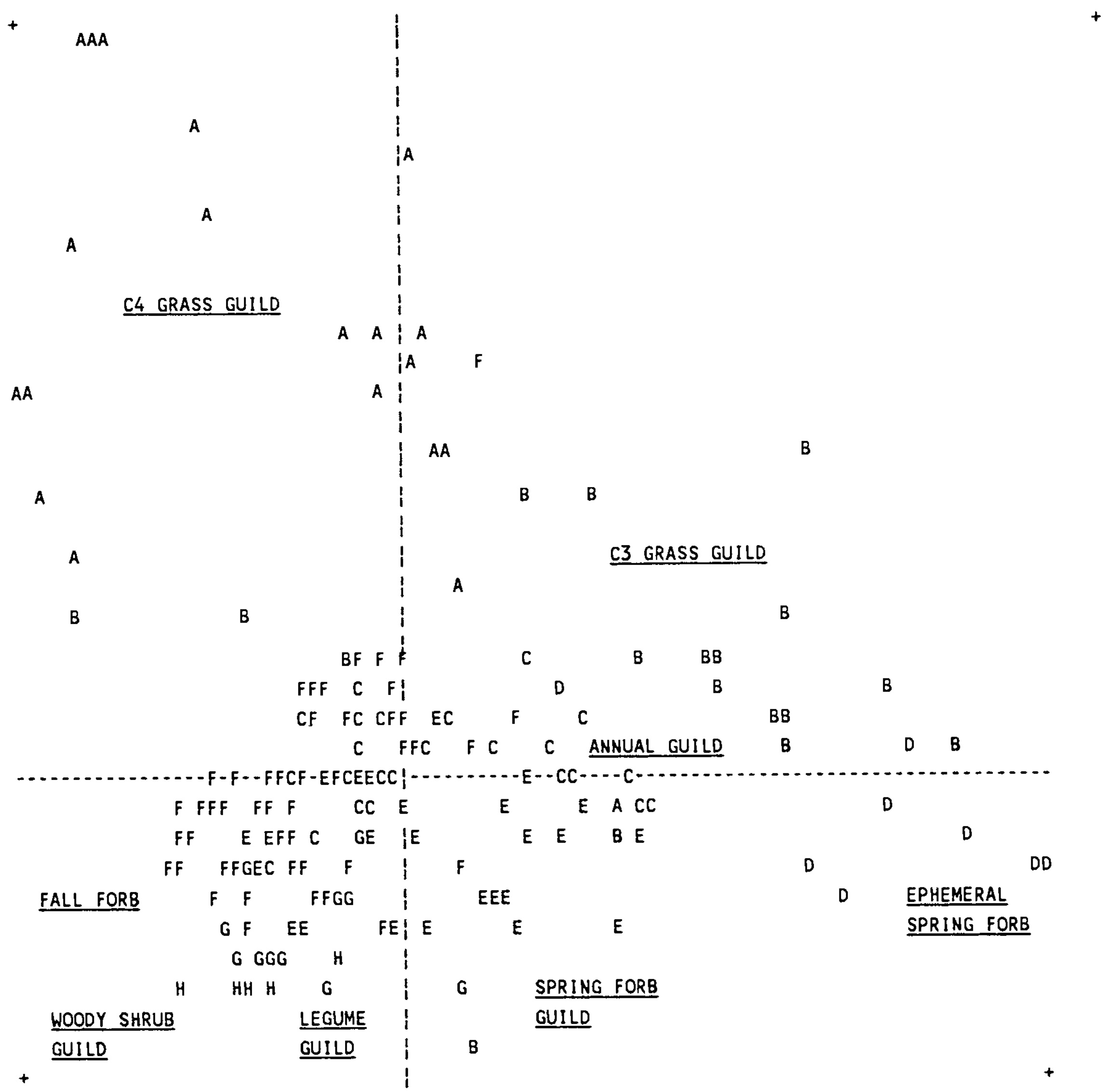
Discriminant function analysis provided statistical evidence that the eight guilds are not just randomly chosen clouds of points, but represent the data set as 94.3% (150 out of 158) of the prairie species are correctly classified in one of the eight guilds (Fig. 4). Using the Chi-square test for the observed Wilks' lambda of each of the seven canonical discriminant functions, it was determined that the means of the discriminant functions are statistically different in all eight guilds.

Correlations (of the 158 species positions in the detrended correspondence analysis with the 32 ecological and morphological traits) determined which traits most highly influence the position of these prairie species and subsequently the groups or guilds of species. For the X axis, the following ecological and morphological traits had the most significant positive correlations ($p<0.001$): decumbent or prostrate stem, short height, short growth period, leaves in basal rosettes, small leaf size, bulbs, shallow rooting depth, and early flowering (Table 3). The most significant negative correlations for the X axis were: forb life form, tall height, active growth during the warm season, large leaf size, C4 photosynthetic pathway, large clones, late flowering, long flowering duration, and heavy seed weight (Table 3). For the Y axis, the traits with the most significant positive correlations were: C4 photosynthetic pathway, early flowering, and light



	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	.36	.30	.16	.13

Fig. 1. First two axes of a detrended correspondence analysis of species positions from 32 morphological and ecological traits of 158 prairie species, and eigenvalues for the first four axes. Species names abbreviated (see Appendix 1 for abbreviations) and printed where space allows. Species located at arrows, which point to species names. Some arrows represent more than one species. Species too close to print are marked with a '.'



	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	.36	.30	.16	.13

Fig. 2. Guild groupings of species on first two axes of detrended correspondence analysis of species positions from 32 morphological and ecological traits of 158 prairie species, and eigenvalues for the first four axes. Letters mark individual species in the following guilds: A=C4 grasses; B=C3 grasses; C=annuals; D=ephemeral spring forbs; E=spring forbs; F=summer and fall forbs; G=legumes; H=woody shrubs.

seed weight (Table 3). The traits most negatively correlated with the Y axis were: forb life form, large leaf length/width ratios, compound leaves, sheathed leaves, woodiness, tap or fascicle roots, nitrogen fixation root nodules, early flowering, zoophilous mode of pollination, heavy seed weight, and unpalatability to herbivores (Table 3).

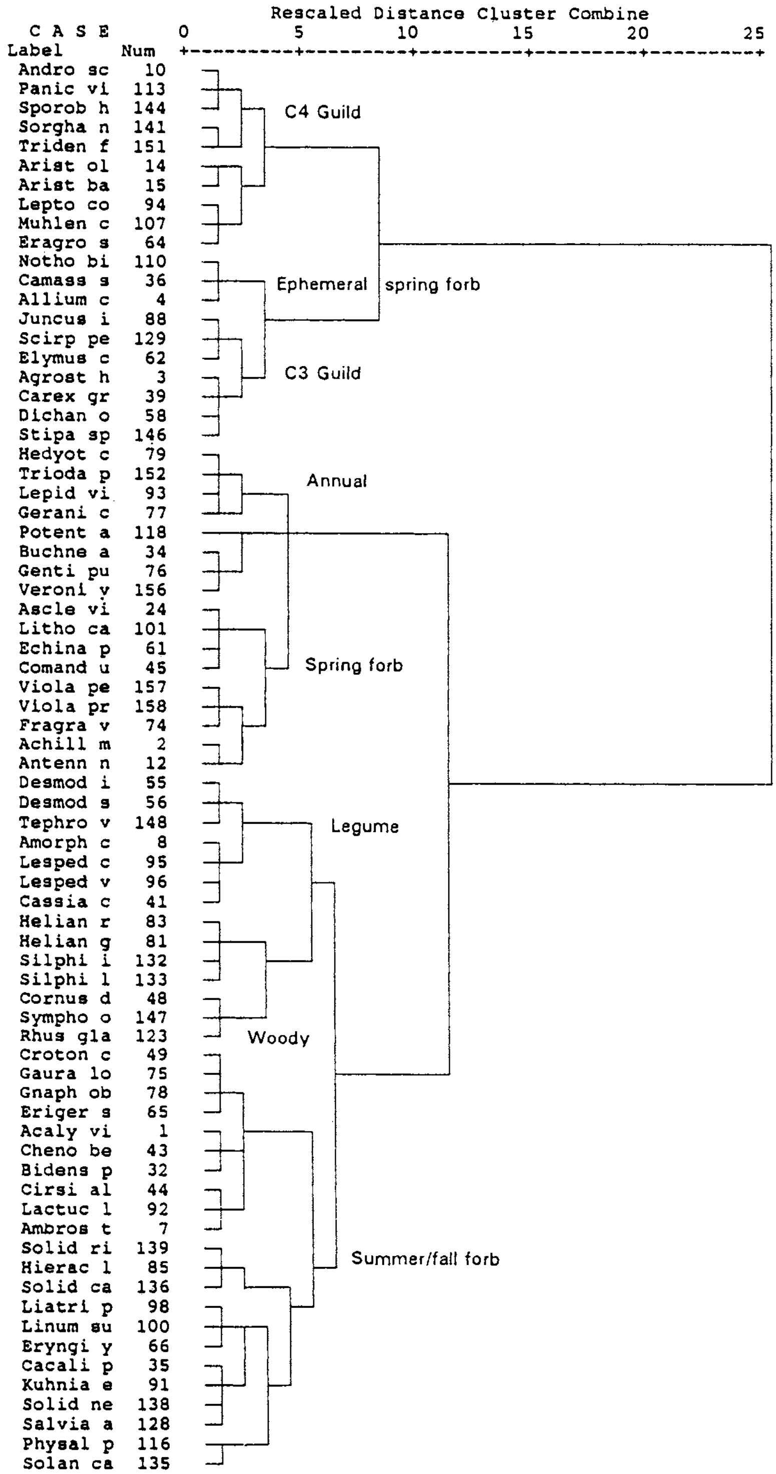
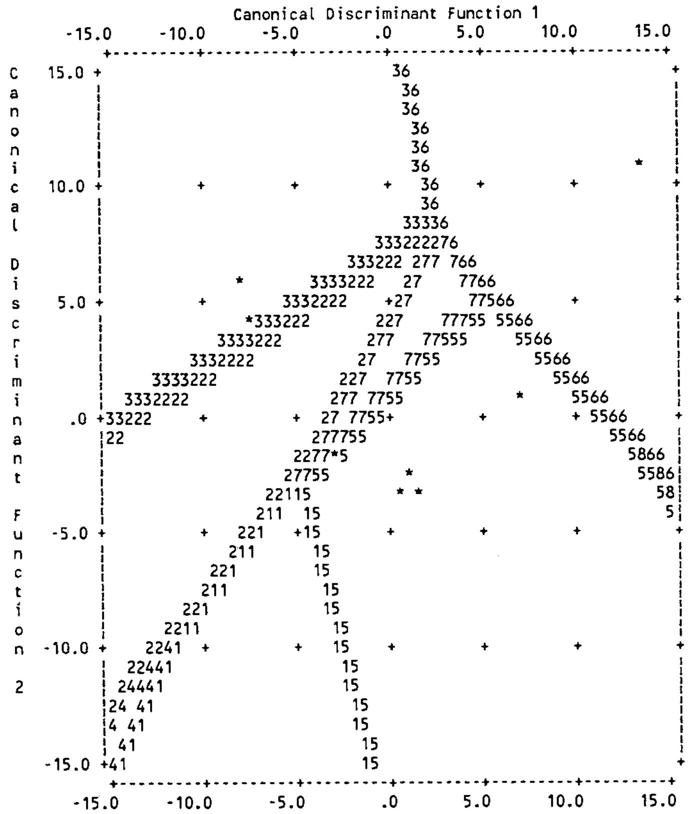


Fig. 3. Hierarchical cluster analysis dendogram using Ward method, showing representative tallgrass prairie species (abbreviations in Appendix 1) and guilds.



Fcn	Eigenvalue	Pct of Variance	Cum Pct	Canonical Corr	After Fcn	Wilks' Lambda	Chi- square	df	Sig
					0	.000001	1865.020	224	.0000
1*	33.6836	47.38	47.38	.9855	1	.000042	1379.181	186	.0000
2*	21.3829	30.08	77.46	.9774	2	.000950	953.344	150	.0000
3*	4.9017	6.89	84.35	.9113	3	.005608	710.137	116	.0000
4*	3.7570	5.28	89.64	.8887	4	.026679	496.469	84	.0000
5*	3.1232	4.39	94.03	.8703	5	.110005	302.391	54	.0000
6*	2.9317	4.12	98.15	.8635	6	.432504	114.828	26	.0000
7*	1.3121	1.85	100.00	.7533					

* Marks the 7 canonical discriminant functions remaining in the analysis.

Classification results:

No. of Predicted Group Membership

Actual group	Cases	1	2	3	4	5	6	7	8
Annual	23	23	0	0	0	0	0	0	0
C3	18	0	17	1	0	0	0	0	0
C4	20	0	2	18	0	0	0	0	0
Spring Emphemeral	8	0	1	0	7	0	0	0	0
Summer/Fall Forb	47	2	0	0	0	45	0	0	0
Legumes	12	0	0	0	0	0	12	0	0
Spring forb	24	0	0	0	0	3	0	21	0
Woody shrub	6	0	0	0	0	0	0	0	6

Percent of 'grouped' cases correctly classified: 94.30%

Fig. 4. Territorial map of discriminant analysis for 158 prairie species in eight guilds, labeled as 1=Annual; 2=C3 grass; 4=ephemeral spring forb; 5=summer/fall forb; 6=legume; 7=spring forb; 8=woody shrub; and *=group centroids. Statistics on canonical discriminant function and classification given below.

Table 2. Tallgrass prairie plant guilds. Guild name and species.

Guild	Representative species	
	Species	Common name
A) C_4 Photosynthetic pathway grasses and sedges	*Andropogon* spp.	Bluestems
B) C_3 Photosynthetic pathway grasses and sedges	*Dichanthelium* spp.	Panic grasses
	Carex spp.	Sedges
C) Annuals and biennials	*Ambrosia artemisiifolia*	Common ragweed
	Acalypha virginica	Three-seeded mercury
D) Ephemeral spring forbs	*Viola* spp.	Violets
E) Spring forbs	*Echinacea pallida*	Purple coneflower
	Lithospermum spp.	Puccoons
F) Summer/fall forbs	*Silphium laciniatum*	Compass plant
	Eryngium yuccifolium	Button snakeroot
	Helianthus spp.	Sunflowers
	Aster spp.	Asters
G) Legumes	*Amorpha canescens*	Leadplant
	Dalea spp.	Prairie clovers
	Baptisia spp.	Wild indigos
H) Woody shrubs	*Rhus glabra*	Smooth sumac
	Cornus drummondii	Rough-leaved dogwood

Total plant cover values per plot were greater than 100% and approach 200% for both the Rockefeller Native Prairie and the Palmer prairie (total values for the 50 quadrats were 92.165 and 92.130 respectively, where 50.000 equals 100%). These plant cover values show the significant overlap of species, resulting in cover values greater than 100%. Species coverage data compiled from 50 quadrats from each of the three study sites are presented in Table 4 for the dominant species. As other tallgrass prairie studies have shown for numerous sites throughout the tallgrass prairie bioregion (Weaver & Fitzpatrick 1934; Eyster-Smith 1984; Gibson & Hulbert 1987; Glenn & Collins 1990) plots were dominated by warm season, tall grasses with big bluestem, *Andropogon gerardii*, and little bluestem, *A. scoparius*, having the greatest coverage. In addition, five of the six species with greatest coverage were grasses. The cover values for sampled prairie species differed statistically among all three prairies (Table 5). However, when these species were grouped by guild, paired T-tests of cover between prairies did not differ statistically for any guild (Table 5), implying that species within these guilds can functionally replace each other.

Guilds of Tallgrass Prairie Species

Eight prairie plant guilds were delimited by using multivariate techniques. These guilds occurred on all three prairie sites, even though individual species presence and abundance varied. These eight groups have unique ecological roles in the tallgrass prairie as discussed below. In their respective guilds, the location of species on the first two axes of the detrended correspondence analysis was correlated with 32 ecological and morphological traits. Traits whose correlations were statistically significant for one of the two axes are presented below as characteristic features of each guild.

1. C4 Photosynthetic pathway (warm-season) grasses

This C4 photosynthetic pathway grass guild is composed of 21 species (13% of 158 prairie species studied; Appendix 1) that dominate the landscape of the tallgrass prairie ecosystem. These warm-season graminoids have Kranz anatomy and the Hatch-Slack photosynthetic pathway. Coverage data for the three prairie sites show dominance of the C4 grasses; they comprise between 48.9 and 66.3% of the canopy cover on these sites. This occurred with sampling in late June,

Table 3. Variables and correlation coefficients for species positions on the first two axes of a detrended correspondence analysis of 158 prairie species.

Positive traits	X1	Y1
Flowering, early	+0.6967**	-0.2814**
Rooting depth, shallow	+0.6374**	+0.1476
Growth period, short	+0.5713**	-0.1173
Height, short	+0.5610**	-0.0027
Basal rosette	+0.4580**	-0.0925
Bulbs	+0.4442**	-0.0947
Decumbent or prostrate stem	+0.3888**	-0.1396
Leaf size, small	+0.3354**	+0.1049
Sod or mat roots	+0.1648	+0.2355*
Seed weight, light	+0.1445	+0.3285**
Duration, annual or biennial	+0.1057	-0.0210
Leaves divided	+0.0167	-0.1373
Zoophilous pollination	-0.0418	-0.6730**
Leaves hairy or glaucous	-0.0422	-0.1539
Zoophilous seed dispersal	-0.0795	-0.1913*
Leaves compound	-0.1095	-0.3041**
Nitrogen fixation root nodules	-0.1476	-0.2696**
Woodiness	-0.1586	-0.2519**
Leaf length/width ratio, large	-0.1713	-0.5808**
Not palatable to herbivores	-0.1792	-0.2479**
Phyllotaxy, opposite/whorled	-0.2075*	-0.2151*
Rooting habit, tap or fascicle	-0.2359*	-0.4728**
Forb life form	-0.2646**	-0.6599**
Photosynthetic pathway, C4	-0.2684**	+0.8234**
Seed weight, heavy	-0.2699**	-0.3981
Flowering duration, long	-0.2784**	+0.0583
Clones, large	-0.2802**	-0.1412
Leaf size, large	-0.3768**	-0.1545
Height, tall	-0.4773**	-0.1357
Growth during warm season	-0.6651**	+0.1741

One-tailed significance: * - 0.01, ** - 0.001.

well before their rapid growth during the warm season. Other studies of the region also show C4 grass dominance (Weaver & Fitzpatrick 1934; Curtis 1959; Ray 959; Dix & Smeins 1967; Weaver 1968; Eyster-Smith 1984; Diamond & Smeins 1985; Freeman & Hulbert 1985; Freeman & Gibson 1987; Marzolf 1988). The species in this guild essentially form the matrix of vegetation within which all the following guilds of species occur. In addition to the ecological and morphological traits studied, C4 grass cover (or biomass) responds positively to the management (or disturbance) treatments of fire and moderate to light grazing (Hulbert 1969; Peet *et al.* 1976; Collins & Wallace 1990).

2. C3 Photosynthetic pathway (cool-season) grasses and sedges

The C3 photosynthetic pathway grass and sedge guild is composed of 17 species (11 % of total) that are common to tallgrass prairies (Appendix 1). The term 'cool-season' is often applied to these graminoids because they make substantial growth during the cooler spring and fall seasons, although most have green foliage during the summer (Weaver 1954). They have the Calvin or C3 photosynthetic pathway.

Table 4. Cover values for the 50 prairie species with the greatest average values summed for the % cover for each of the 50 m^2 plots on the Rockefeller, Palmer, and S&S Ranch prairies, and Averages. P=present on the prairie, but not on quadrats. Also given are the number of species on each prairie and on the quadrats on each prairie. The * column is for abundance codes of each species, where A=abundant; S=sub-dominant; F=frequent; and I=infrequent. These codes result from dividing the cover values into appropriate classes.

Species	Rockefeller	Palmer	S & S	Average	*
Andropogon gerardii	29.020	18.450	14.795	20.7550	A
Andropogon scoparius	20.320	32.510	8.190	20.3400	A
Ambrosia artemisiifolia	0.380	0.010	20.380	6.9233	A
Stipa spartea	0.010	9.700	0.000	3.2367	A
Sorghastrum nutans	5.030	1.410	0.990	2.4767	A
Sporobolus heterolepis	5.680	1.650	0.010	2.4467	A
Silphium laciniatum	5.920	P	0.000	1.9737	A
Rhus glabra	5.350	P	0.000	1.7837	A
Amorpha canescens	2.730	P	1.200	1.3103	A
Tephrosia virginiana	0.000	3.740	0.000	1.2467	A
Poa pratensis	0.090	0.745	2.465	1.1000	A
Echinacea pallida	P	3.280	0.000	1.0937	A
Rudbeckia hirta	P	2.665	P	0.8890	A
Panicum virgatum	0.160	0.625	1.685	0.8233	A
Coreopsis palmata	P	2.020	0.000	0.6737	A
Helianthus rigidus	1.600	0.390	0.000	0.6633	A
Eryngium yuccifolium	1.880	P	0.000	0.6270	A
Aster ericoides	P	1.755	0.000	0.5853	S
Linum sulcatum	0.005	1.690	0.000	0.5650	S
Solidago rigida	1.685	P	0.000	0.5620	S
Antennaria neglecta	P	1.665	0.000	0.5553	S
Tridens flavus	0.005	1.180	0.430	0.5383	S
Comandra umbellata	1.580	P	0.000	0.5270	S
Lespedeza violacea	1.530	P	P	0.5107	S
Ceanothus herbaceus	1.170	0.210	0.000	0.4600	S
Aster praealtus	1.280	0.025	0.000	0.4350	S
Tripsacum dactyloides	1.020	0.210	P	0.4103	S
Solidago missouriensis	0.490	0.730	0.000	0.4067	S
Euphorbia corollata	0.850	0.315	0.000	0.3883	F
Erigeron strigosus	0.025	1.095	0.010	0.3767	F
Rosa arkansana	0.070	0.680	P	0.2503	F
Dichanthelium oligosanthes	0.115	0.455	0.165	0.2450	F
Potentilla arguta	0.000	0.705	0.000	0.2350	F
Solidago canadensis	0.680	0.000	P	0.2270	F

3. Annuals and biennial forbs

The annual and biennial forb guild is composed of 23 opportunistic species (14.5% of total) that generally colonize disturbed sites. Annual and biennials comprise a small percentage of the total species coverage in ungrazed prairies managed with burning or mowing. Annual and biennials covered only 0.8% of the total area on the Rockefeller Native Prairie, which is managed by biennial burning. Annuals and biennials covered 3.5% of the sampled area of the Palmer Prairie, which is managed by yearly haying. In contrast, annual and biennials covered 39.0% of sampled area on the S & S ranch, which is managed by grazing and has a past history of periodic overgrazing. The trend

Table 4. Continued.

Species	Rockefeller	Palmer	S & S	Average	*
Koeleria pyramidata	P	0.670	0.000	0.2237	F
Carex brevior	0.115	0.090	0.455	0.2200	F
Juncus interior	P	0.000	0.655	0.2187	F
Baptisia bracteata	0.350	0.295	0.000	0.2150	F
Salvia azurea	0.205	0.320	P	0.1753	F
Gentiana puberulenta	0.060	0.330	0.000	0.1300	F
Vernonia baldwinii	P	P	0.375	0.1257	F
Oxalis dillenii	0.100	0.220	0.030	0.1167	I
Aster sericeus	0.000	0.345	0.000	0.1150	I
Apocynum cannabinum	0.305	0.005	0.025	0.1117	I
Helianthus grosseserratus	0.300	0.000	0.000	0.1000	I
** Total for 158 species	92.165	92.130	52.435	78.9100	
# of Species on Prairie	152	165	98	138	
# of Species on Quadrats	67	66	27	53	

of increasing annual cover with increasing animal disturbance has been shown to be widespread throughout the Prairie Bioregion (Drew 1947; Launchbaugh 1955; Collins 1987; Gibson 989).

4. Ephemeral spring forbs
The ephemeral spring forb guild is composed of eight species (5% of total) that initiate growth in the fall or very early in the spring and have ephemeral foliage. These species have the earliest average flowering time, the shortest stature (forming the lowest synusium of vegetation), and lose their photosynthetic abilities during the summer when taller warm-season grasses overtop them.

5. Spring forbs
The spring forb guild of 22 species (13.9% of total) is similar to the ephemeral spring forb guild, but differs in being composed of species that emerge and flower later in the spring, are taller, and remain green throughout the growing season. The species in this guild make up much of the showy spring wildflower bloom that characterizes prairies.

6. Summer/fall forbs
The summer/fall forb guild of 48 species (30.3% of total) comprises the largest group of forbs. These generally tall and coarse species grow in association with the warm-season grasses, and they flower and set seed in the summer and fall. Species in this guild can have seeds that are either light and wind-dispersal (*Aster* and *Solidago*) or heavy and animal or gravity-dispersed (*Helianthus* and *Silphium*).

7. Legumes
The legume guild of 11 species (7.0% of total) comprises forbs that have compound leaves with an odd number of leaflets and have the ability to fix atmospheric nitrogen (Bare 1979).

8. Woody shrubs
The woody shrub guild of 6 species (3.8% of total) is composed of woody species that have some of their over-wintering buds above the ground's surface. These species persist in managed prairie remnants because they resist the effects of fire and mowing. Pastures in the study area are often invaded by trees, but they do not persist when clipping (whether by grazing or machinery) is accompanied by fire.

Species with unusual guild positions

Six species were classified in two guilds. Four are annual grasses, one was an annual legume, and one is a woody legume. In addition, there were five species whose locations in the detrended correspondence analysis plots were anomalous for the guild in which they were placed. These guild anomalies are discussed in Appendix 2.

Differences in plant height, seed weight, and leaf size by guild

A one-way ANOVA of the log(10) transformed raw data for each of the three continuous variables showed that there are significant differences between the prairie plant guilds for plant height, seed weight, and leaf size (Table 6, 7, and 8).

Plant height

The mean plant height of guilds ranged from a low of 2.94 dm for the ephemeral spring forb guild to 16.00 dm for the woody shrub guild (Table 6). When paired comparisons of plant heights of guilds were made using the LSD procedure for log(10) transformed data, the ephemeral spring forb guild was significantly shorter than the other seven prairie plant guilds. The woody shrub guild was significantly taller than all other guilds except the relatively tall legume and summer/fall forb guilds. The legume guild was significantly taller than the ephemeral spring forb, woody, spring forb, and summer/fall forb guilds. The summer/fall forb guild was also significantly taller than the ephemeral spring forb, woody shrub, spring forb, annual, and C3 photosynthetic pathway grass and sedge guilds.

Seed weight

The mean seed weight of guilds ranged from a low of 0.137 mgs for the ephemeral spring forb guild to 7.760 mgs for the woody shrub guild (Table 7). When paired comparisons of seed weights of guilds were made using the LSD procedure for log(10) transformed data, the summer/fall forb and woody shrub guilds had significantly heavier seed weights than all other guilds.

Leaf size

The mean leaf size of prairie plant guilds ranged from a low of 6.76 sq cm for the C3 photosynthetic pathway grass and sedge guild to 97.28 sq cm for the woody shrub guild (Table 8). When paired comparisons of guilds were made using the LSD procedure for log(10) transformed data, the woody shrub guild had significantly larger leaves than all other guilds, except the summer/fall forb and spring forb guilds. In addition, the spring forb guild had significantly larger leaves than the annual and C3 grass guilds, and both the legume and summer/fall forb guilds were significantly larger than the annual and biennial forb guild.

Discussion

There have been several attempts to classify prairie species into groups. Weaver (1954) classified tallgrass prairie species into four main groups:grasses of lowlands, grasses of uplands, forbs of lowlands, and forbs of uplands. Curtis (1959) viewed Wisconsin prairies as a continuum and divided them into five moisture-related groups of species:wet prairie species, wet-mesic, mesic, dry-mesic, and dry species. More recently, prairie species have been looked at as core and satellite species (Collins & Glenn 1991; Glenn & Collins 1990; Gotelli & Simberloff 1987).

Division of the numerous tallgrass species into interpretable groups can facilitate our understanding of prairie plant community ecology. This study focused on upland tallgrass prairies in northeast Kansas with considerable plant species diversity. Ecomorphological analysis of the 158 native species on these prairies sorted them into eight guilds:

1. warm-season C4 photosynthetic pathway grasses;
2. cool-season C3 photosynthetic pathway grasses and sedges;
3. annual and biennial forbs;
4. ephemeral spring forbs;
5. spring forbs;
6. summer/fall forbs;
7. legumes; and
8. woody shrubs.

Since the majority of these species are widely distributed in the tallgrass prairie bioregion in central North America, these guilds may have meaning beyond northeast Kansas.

The guilds were defined by a quantitative method, detrended correspondence analysis, and supported through cluster analysis and objectively tested through discriminant function analysis. These techniques meet Simberloff and Dayan's first condition that a clear methodology for guild assignment and verification. Their second condition, concerning sympatric related biota, is met through the descriptive review of each guild, which justifies the cases where sympatric related biota are placed in different guilds.

Multivariate techniques can be useful in providing information on the relationships between prairie plants and their environment that were not available through traditional floristic analysis techniques. Significant differences were found among guilds in plant height, with the shortest guild (ephemeral spring perennial forbs) and the tallest (woody shrubs) the most contrasting in paired comparisons to other guilds. These differences

Table 5. One-tailed T-tests. Comparisons of differences between prairies of species coverage for all species and for each guild. For each comparison, the following are given: the number of species compared, the mean (difference) and standard error, and the significance.

Prairie Comparison	# of species Compared	(Difference) Mean & Standard Error	Significance
FOR ALL SPECIES			
Palmer-Rockefeller	158	0.5807± 0.212	*
Rockefeller-S&S	158	0.5975±0.137	**
Palmer-S&S	158	0.5836±0.184	**
FOR THE C4 GRASS GUILD			
Palmer-Rockefeller	19	1.6676±0.834	N.S.
Rockefeller-S&S	19	2.0326±0.972	N.S.
Palmer-S&S	19	1.6482±1.276	N.S.
FOR THE C3 GRASS GUILD			
Palmer-Rockefeller	19	0.6747±0.506	N.S.
Rockefeller-S&S	19	0.2103±0.127	N.S.
Palmer-S&S	19	0.7550±0.507	N.S.
FOR THE ANNUAL GUILD			
Palmer-Rockefeller	23	0.1661±0.084	N.S.
Rockefeller-S&S	23	0.8828±0.869	N.S.
Palmer-S&S	23	1.0263±0.883	N.S.
FOR THE EPHEMERAL SPRING FORB GUILD			
Palmer-Rockefeller	8	0.0263±0.016	N.S.
Rockefeller-S&S	8	0.0194±0.010	N.S.
Palmer-S&S	8	0.0231±0.016	N.S.
FOR THE SPRING FORB GUILD			
Palmer-Rockefeller	22	0.3961±0.179	N.S.
Rockefeller-S&S	22	0.1298±0.079	N.S.
Palmer-S&S	22	0.3064±0.170	N.S.
FOR THE SUMMER/FALL FORB GUILD			
Palmer-Rockefeller	48	0.4104±0.145	N.S.
Rockefeller-S&S	48	0.3270±0.136	N.S.
Palmer-S&S	48	0.1539±0.067	N.S.
FOR THE LEGUME GUILD			
Palmer-Rockefeller	11	0.7723±0.396	N.S.
Rockefeller-S&S	11	0.3250±0.182	N.S.
Palmer-S&S	11	0.5036±0.341	N.S.
FOR THE WOODY GUILD			
Palmer-Rockefeller	8	1.2042±0.842	N.S.
Rockefeller-S&S	8	1.1492±0.859	N.S.
Palmer-S&S	8	0.1500±0.111	N.S.

N.S. = Not Significant; * = significant at the 0.05 level; ** = significant at the 0.001 level.

are not surprising as these groups of species have different phenologies and occupy the two extremes of synusial position in prairie vegetation. The ephemeral spring forb guild species (e.g. yellow-eyed grass, *Hypoxis hirsuta*, and prairie violets, *Viola* spp.) are of the lowest-layer synusia, conspicuous in spring-time bloom, when the tallgrass mulch has been flattened by winter snow, or previously removed by haying or burning. The species in this guild ripen seeds under the cover of emerging, taller synusia, particularly the warm-

Table 6. One-way Analysis of Variance of log(10) of prairie plant height by guild. LSD Procedure showing multiple comparison of means.

Source	D.F.	Sum of Squares	Mean Sauares	F Ratio	F Prob.
Between groups	7	3.2261	.4609	6.7848	.0000
Within groups	150	10.1891	.0679		
Total	157	13.4151			

LSD Procedure; (*) Denotes pairs of groups significantly different at the 0.05 level.

Mean	Group	Groups Guild name (abbreviation)	4	7	1	2	3	6	5	8
.4041	4	Ephemeral Spring Forb (ESP)								
.6157	7	Legume (LEG)	*							
.6677	1	Annual (ANN)	*							
.7107	2	C3 Grass (C3)	*							
.7600	3	C4 Grass (C4)	*							
.8417	6	Summer/Fall forb (FAL)	*	*						
.8898	5	Spring forb (SPR)	*	*	*	*				
1.0766	8	Woody shrub (Woo)	*	*	*	*	*			

Statistics and graph for untransformed data

Group	Count	Mean	Standard Deviation	Standard Error	95% Conf Int for Mean
ANN	23	6.2000	4.7684	.9943	4.1380 to 8.2620
C3	18	5.5417	2.3534	.5547	4.3713 to 6.7120
C4	20	6.6825	3.5924	.8033	5.0012 to 8.3638
ESP	8	2.9375	1.6765	.5927	1.5359 to 4.3391
SPR	47	8.6064	4.2553	.6207	7.3570 to 9.8558
FAL	12	7.9167	4.3161	1.2460	5.1743 to 10.6590
LEG	24	4.9500	2.9045	.5929	3.7236 to 6.1764
WOO	6	16.0000	13.1301	5.3603	2.2210 to 29.7790
Total	158	7.0494	4.9572	.3944	6.2704 to 7.8283

season C4 grasses. At the other extreme in plant height, the woody shrub guild species (e.g. rough-leafed dogwood, *Cornus drummondii*; blackberry, *Rubus ostryifolius*; and smooth sumac, *Rhus glabra*) comprise an upper synusial layer that can dominate both grasses and forbs by casting shade that light-starves sun-loving species underneath them. If these woody shrub species are not controlled by fire, mowing, or grazing, they will play an important part in the successional process from tallgrass prairie to forest (Hulbert 1969; Peet *et al.* 1976; Collins & Wallace 1990).

Significant differences in seed weight were also found between guilds. The legume and woody shrub guilds had distinctly heavier seeds compared to all other guilds. Legumes (e.g. the prairie clovers, *Dalea* spp.; and the tickclovers, *Desmodium* spp.) and woody shrubs (rough-leaved dogwood and smooth sumac) have heavy seeds which are generally dispersed by animals or gravity. These heavy-seeded legumes contrast with the two grass guilds, which have light-weight, wind-dispersed seeds. The ephemeral spring forb and annual/biennial forb guilds have light seeds; both groups are composed primarily of species that generally complete their life cycles quickly and disperse large quantities of light-weight seeds. The guilds with the heaviest seeds (woody shrubs, summer/fall forbs, legumes, and spring forb guilds) are from species

Table 7. One-way Analysis of Variance of log(10) of prairie plant seed weight by guild. LSD Procedure showing multiple comparison of means.

Source	D.F.	Sum of Squares	Mean Squares	F Ratio	F Prob.
Between Groups	7	20.1665	2.8809	3.6405	.0012
Within Groups	150	118.7045	.7914		
Total	157	138.8710			

LSD Procedure; (*) Denotes pairs of groups significantly different at the 0.05 level.

Mean	Group	Groups Guild name (abbreviation)	3	1	2	4	5	7	6	8
−1.3038	3	C4 Grass (C4)								
−1.2938	1	Annual (ANN)								
−1.1212	2	C3 Grass (C3)								
−1.0795	4	Ephemeral Spring Forb (ESP)								
−0.9510	5	Spring Forb (SPR)								
−0.9213	7	Legume (LEG)								
−0.2187	6	Summer/Fall Forb (FAL)	*	*	*	*	*	*		
0.1971	8	Woody Shrub (WOO)	*	*	*	*	*	*		

Statistics and graph for untransformed data

Group	Count	Mean	Standard Deviation	Standard Error	95% Conf Int for Mean
ANN	23	.2943	0.5464	0.1139	0.0580 to 0.5306
C3	18	0.6086	1.8525	0.4366	−0.3126 to 1.5298
C4	20	0.2725	0.8892	0.1988	−0.1437 to 0.6886
ESP	8	0.1369	0.1583	0.0560	0.0046 to 0.2693
SPR	47	1.8316	6.1573	0.8981	0.0237 to 3.6394
FAL	12	0.9209	0.8189	0.2364	0.4006 to 1.4412
LEG	24	0.5313	1.1071	0.2260	0.0638 to 0.9988
WOO	6	7.7596	16.5180	6.7434	−9.5747 to 25.0939
Total	158	1.1438	4.7641	0.3790	0.3951 to 1.8924

that are photosynthetically active throughout the growing season and are animal dispersed.

Significant differences in leaf size were also found between the woody shrub guild (having the largest leaves) and the majority of other guilds. Species of the woody shrub guild are effective at capturing large amounts of light and casting dense shade. The C3 grass and sedge guild species (e.g. sedges, *Carex* spp.; and panic grasses, *Dichanthelium* spp.) have the smallest leaves, significantly smaller in size than the woody shrub and summer/fall forb guilds. These cool-season species have numerous small, narrow leaves that are relatively low to the ground and often in a near-vertical position.

The three prairies studied have significant differences in their species coverage (Table 4, 5). This difference is not surprising as individual species coverage varies noticeably among these three prairies even though they are geographically close and are all on upland sites. In addition, the three sites sampled had different management practices (burning, mowing, and grazing, respectively) and slightly different soil types. However, when the species are grouped by guild, the cover values do not differ statistically, indicating overall consistency of guild composition (i.e., complementary replacement of one species by another within a guild in these prairies).

Prairie plant guilds may help us better understand and interpret the distribution and plant associations of

Table 8. One-way Analysis of Variance of log(10) of prairie plant leaf size by guild. LSD Procedure showing multiple comparison of means.

Source	D.F.	Sum of Squares	Mean Squares	F Ratio	F Prob.
Between Groups	7	7.9672	1.1382	3.2122	.0034
Within Groups	150	53.1492	0.3543		
Total	157	61.1164			

LSD Procedure; (*) Denotes pairs of groups significantly different at the 0.05 level.

Mean	Group	Groups Guild Name (abbreviation)	1	2	3	4	6	7	5	8
0.39328	1	Annual (ANN)								
0.60452	2	C3 Grass (C3)								
0.70748	3	C4 Grass (C4)								
0.72205	4	Ephemeral Spring Forb (ESP)								
0.83857	6	Summer/Fall Forb (FAL)	*							
0.86303	7	Legume (LEG)	*							
0.93800	5	Spring Forb (SPR)	*	*						
1.42041	8	Woody Shrub (WOO)	*	*	*	*	*			

Statistics and graph for untransformed data

Group	Count	Mean	Standard Deviation	Standard Error	95% Conf Int for Mean
ANN	23	7.8726	14.9115	3.1093	1.4244 to 14.3208
C3	18	6.7594	7.7290	1.8217	2.9159 to 10.6030
C4	20	9.0595	9.4004	2.1020	4.6600 to 13.4590
ESP	8	7.1400	5.8864	2.0812	2.2189 to 12.0611
SPR	47	23.8860	49.0192	7.1502	9.4934 to 38.2785
FAL	12	9.9025	6.8298	1.9716	5.5630 to 14.2420
LEG	24	19.2492	34.0221	6.9447	4.8829 to 33.6154
WOO	6	97.2800	177.2964	72.3810	88.7784 to 283.3384
Total	158	17.8999	47.2158	3.7563	10.4805 to 25.3193

species in a tallgrass prairie community. Traditional Clementsian plant community associations have not been very useful to plant ecologists who study prairies because of the complexity of the mix of species in these communities. For this reason, the prairie plant associations established by Clements' student Weaver, e.g., the big bluestem consociation and the switchgrass-wild rye association (Weaver & Fitzpatrick 1934) have rarely been referred to in the recent literature, and other plant species-specific groups have not been established.

It has long been recognized that there are groups of similar species found on tallgrass prairies, most notable are the native warm-season (C4) grasses, cool-season (C3) grasses, and legumes (Weaver 1954, 1968). This study is the first to use multivariate analysis supported by statistical tests to delimit these three guilds and an additional five guilds that characterize tallgrass prairies. The establishment of prairie plant guilds offers a basis for classification of tallgrass prairies that is more ecologically focused than species composition. Analysis of prairie from a guild perspective can allow for a better understanding and interpretation of the diversity of life forms and life history of tallgrass prairie species. Prairie plant guilds may also provide a useful framework for field ecologists to more easily classify or grade the quality of tallgrass prairie remnants.

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Appendix 1. List of 158 prairie plants, name codes for figures, and guilds (second guilds are listed for species that could be placed in more than one guild). Names from Flora of the Great Plains (Great Plains Flora Association, 1991).

Scientific name	Name code	Guild (2nd Guild)
Acalypha virginica	Acaly vi	Annual
Achillea millefolium	Achill m	Spring ephemeral
Agrostis hyemalis	Agrost h	C3 grass
Allium canadense	Allium c	Spring ephemeral
Ambrosia artemisiifolia	Ambros a	Annual
Ambrosia psilostachya	Ambros p	Summer/fall forb
Ambrosia trifida	Ambros t	Annual
Amorpha canescens	Amorph c	Legume (Woody shrub)
Andropogon gerardii	Andro ge	C4 grass
Andropogon scoparius	Andro sc	C4 grass
Andropogon virginicus	Andro vi	C4 grass
Antennaria neglecta	Antenn n	Spring forb
Apocynum cannabinum	Apocy ca	Summer/fall forb
Aristida oligantha	Arist ol	C4 grass (Annual)
Aristida basiramea	Arist ba	C4 grass (Annual)
Artemisia ludoviciana	Artemi l	Summer/fall forb
Asclepias meadii	Ascle me	Spring forb
Asclepias stenophylla	Ascle st	Summer/fall forb
Asclepias sullivantii	Ascle su	Summer/fall forb
Asclepias syriaca	Ascle sy	Summer/fall forb
Asclepias tuberosa	Ascle tu	Spring forb
Asclepias verticillata	Ascle ve	Summer/fall forb
Asclepias viridflora	Ascle vf	Spring forb
Asclepias viridis	Ascle vi	Spring forb
Aster ericoides	Aster er	Summer/fall forb
Aster oolentangiensis	Aster oo	Summer/fall forb
Aster pilosus	Aster pi	Summer/fall forb
Aster praealtus	Aster pr	Summer/fall forb
Aster sericeus	Aster se	Summer/fall forb
Baptisia bracteata	Baptis b	Legume
Baptisia lactea	Baptis l	Legume
Bidens polylepis	Bidens p	Annual
Bouteloua curtipendula	Boute cu	C4 grass
Buchnera americana	Buchne a	Spring forb
Cacalia plantaginea	Cacali p	Summer/fall forb
Camassia scilloides	Camass s	Spring ephemeral
Camelina microcarpa	Camel mi	Annual
Carex brevior	Carex br	C3 grass
Carex gravida	Carex gr	C3 grass
Carex meadii	Carex me	C3 grass
Cassia chamaecrista	Cassia c	Legume (Annual)
Ceanothus herbaceus	Ceano he	Woody shrub
Chenopodium berlandieri	Cheno be	Annual
Cirsium altissimum	Cirsi al	Summer/fall forb
Comandra umbellata	Comand u	Spring forb
Conyza canadensis	Conyza c	Annual
Coreopsis palmata	Coreop p	Spring forb
Cornus drummondii	Cornus d	Woody shrub
Croton capitatus	Croton c	Annual
Cyperus strigosus	Cyper st	C4 grass
Cyperus lupulinus	Cyper lu	C4 grass
Dalea candida	Dalea ca	Legume
Dalea purpurea	Dalea pu	Legume
Delphinium virescens	Delph vi	Spring forb
Desmodium illinoense	Desmod i	Legume
Desmodium sessilifolium	Desmod s	Legume
Dichanthelium acuminatum	Dichan a	C3 grass
Dichanthelium oligosanthes	Dichan o	C3 grass
Dichanthelium sphaerocarpon	Dichan s	C3 grass
Draba brachycarpa	Draba br	Annual
Echinacea pallida	Echina p	Spring forb
Elymus canadensis	Elymus c	C3 grass
Elymus virginicus	Elymus v	C3 grass
Eragrostis spectabilis	Eragro s	C4 grass
Erigeron strigosus	Eriger s	Annual
Eryngium yuccifolium	Eryngi y	Summer/fall forb

Appendix 1. Continued.

Scientific name	Name code	Guild (2nd Guild)
Eupatorium altissimum	Eupato a	Summer/fall forb
Euphorbia corollata	Euphor c	Spring forb
Euphorbia dentata	Euphor d	Annual
Euphorbia maculata	Euphor m	Annual (C4 grass)
Euthamia gymnospermoides	Eutham g	Summer/fall forb
Festuca octoflora	Festuc o	C3 grass (Annual)
Fimbristylis puberula	Fimbri p	C3 grass
Fragaria virginiana	Fragar v	Spring forb
Gaura longiflora	Gaura lo	Annual
Gentiana puberulenta	Genti pu	Summer/fall forb
Geranium carolinianum	Gerani c	Annual
Gnaphalium obtusifolium	Gnaph ob	Annual
Hedyotis crassifolia	Hedyot c	Annual
Helianthus annuus	Helian a	Annual
Helianthus grosseserratus	Helian g	Summer/fall forb
Helianthus hirsutus	Helian h	Summer/fall forb
Helianthus rigidus	Helian r	Summer/fall forb
Helianthus tuberosus	Helian t	Summer/fall forb
Hieracium longipilum	Hierac l	Summer/fall forb
Hordeum pusillum	Horde pu	C3 grass (Annual)
Hypoxis hirsuta	Hypox hi	Spring ephemeral
Juncus interior	Juncus i	C3 grass
Koeleria pyramidata	Koeler p	C3 grass
Krigia caespitosa	Krigia c	Annual
Kuhnia eupatoriodes	Kuhnia e	Summer/fall forb
Lactuca ludoviciana	Lactuc l	Spring forb
Lepidium virginicum	Lepid vi	Annual
Leptoloma cognatum	Lepto co	C4 grass
Lespedeza capitata	Lesped c	Legume
Lespedeza violacea	Lesped v	Legume
Liatris aspera	Liatri a	Summer/fall forb
Liatris pycnostachya	Liatri p	Summer/fall forb
Liatris squarrosa	Liatri s	Summer/fall forb
Linum sulcatum	Linum su	Annual
Lithospermum canescens	Litho ca	Spring forb
Lithospermum incisum	Litho in	Spring forb
Lobelia spicata	Lobel sp	Spring forb
Mirabilis albida	Mirabi a	Spring forb
Mirabilis nyctaginea	Mirabi n	Spring forb
Monarda fistulosa	Monard f	Summer/fall forb
Muhlenbergia cuspidata	Muhlen c	C4 grass
Muhlenbergia racemosa	Muhlen r	C4 grass
Myosotis verna	Myosot v	Annual
Nothoscordum bivalve	Notho bi	Spring ephemeral
Oxalis dillenii	Oxalis d	Spring forb
Panicum capillare	Panic ca	C4 grass
Panicum virgatum	Panic vi	C4 grass
Phlox pilosa	Phlox pi	Spring forb
Physalis longifolia	Physal l	Summer/fall forb
Physalis pumila	Physal p	Summer/fall forb
Poa pratensis	Poa prat	C3 grass
Potentilla arguta	Potent a	Spring forb
Potentilla simplex	Potent s	Spring forb
Psoralea tenuiflora	Psoral t	Legume
Pycnanthemum tenuifolium	Pycnan t	Summer/fall forb
Ratibida pinnata	Ratib pi	Summer/fall forb
Rhus glabra	Rhus gla	Woody shrub
Rosa arkansana	Rosa ark	Woody shrub
Rubus ostryifolius	Rubus os	Woody shrub
Rudbeckia hirta	Rudbec h	Summer/fall forb
Ruellia humilis	Ruelli h	Spring forb
Salvia azurea	Salvia a	Summer/fall forb
Scirpus pendulus	Scirp pe	C3 grass
Scleria triglomerata	Scleri t	C3 grass
Silene antirrhina	Silene a	Annual
Silphium integrifolium	Silphi i	Summer/fall forb
Silphium laciniatum	Silphi l	Summer/fall forb
Sisyrinchium campestre	Sisyri c	Spring ephemeral

Appendix 1. Continued.

Scientific name	Name code	Guild (2nd Guild)
Solanum carolinense	Solan ca	Summer/fall forb
Solidago canadensis	Solid ca	Summer/fall forb
Solidago missourensis	Solid mi	Summer/fall forb
Solidago nemoralis	Solid ne	Summer/fall forb
Solidago rigida	Solid ri	Summer/fall forb
Solidago speciosa	Solid sp	Summer/fall forb
Sorghastrum nutans	Sorgha n	C4 grass
Spiranthes cernua	Spiran c	Summer/fall forb
Sporobolus asper	Sporob a	C4 grass
Sporobolus heterolepis	Sporob h	C4 grass
Sporobolus vaginiflorus	Sporob v	C4 grass
Stipa spartea	Stipa sp	C3 grass
Symphoricarpos orbiculatus	Sympho o	Woody shrub
Tephrosia virginiana	Tephro v	Legume
Teucrium canadense	Teucri c	Summer/fall forb
Tradescantia ohiensis	Trades o	Spring forb
Tridens flavus	Triden f	C3 grass
Triodanis perfoliata	Trioda p	Annual
Tripsacum dactyloides	Tripsa d	C4 grass
Verbena stricta	Verben s	Summer/fall forb
Vernonia baldwinii	Vernon b	Summer/fall forb
Veronicastrum virginicum	Veroni v	Summer/fall forb
Viola pedatifida	Viola pe	Spring ephemeral
Viola pratincola	Viola pr	Spring ephemeral

Appendix 2. Species that were Difficult to Classify into a Guild

There were several species that were difficult to classify into one guild. Five species did not show an affinity for any particular guild on the detrended correspondence analysis plots. Six species have life form characteristics that allowed them to be placed into two different guilds. The species that could be classified into more than one guild included the five annual species, four of which are grasses: *Aristida basiramea*, *A. oligantha*, *Festuca octoflora*, and *Hordeum pusillum*. The threeawns, *Aristida* species, were included in the C4 grass guild and *F. octoflora* was included in the C3 grass guild due to their locations in the detrended correspondence analysis ordinations. Showy partridge pea, *Cassia chamaecrista*, is both a legume and an annual, and leadplant, *Amorpha canescens*, is both a legume and a shrub. Both of these species were classified with the legume guild due to their locations in the ordinations. With the exception of *F. octoflora*, all of these species were also grouped into their respective guilds by cluster analysis.

There were five species that could not be easily classified into any particular guild. They included the grasses:little barley, *H. ousillum; porcupine grass, Stipa spartea*; and marsh muhly, *Muhlenbergia racemosa*; and two prairie forbs: beebalm, *Monarda fistulosa*; and false garlic, *Nothoscordium bivalve*. Porcupine grass, which was placed in the C3 grass and sedge guild, had the largest leaf length/width ratio of any species and the heaviest seeds of any grass. The heavy seeds seem to have been an important factor for its anomalous position as the Y axis trends from heavy seeds at the bottom to light seeds at the top (see Fig. 3). The heavy seed weight factor and the annual nature of the species were factors in placing it into the C3 grass guild. The causes of *M. racemosa* having an anomalous position could not be determined and we placed it in the C3 grass guild. *M. fistulosa* had a position that was probably influenced by its relatively tall height and light seeds which placed it nearer to the top of the Y axis (see Fig 3) than the other summer/fall forbs. *N. bivalve* had large length/width ratios and was the latest ephemeral spring forb to flower, thus giving it a position further away than the majority of other species in the guild. With the exception of *H. pusillum*, all of these species were also grouped into their respective guilds by cluster analysis.