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Distribution and Abundance of Prairie Plant Species in the Loess Hills

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The species composition of grassland and ecotonal communities throughout the Loess Hills was studied between 1990 and 1993. Information pertaining to the latitudinal distribution of species in the Loess Hills, the abundance of species among community types (i.e., habitats), species persistence under woody encroachment, species associations, and resource partitioning among species is provided for the majority of grassland species occurring in the Loess Hills. The most abundant species on extant prairie in the Loess Hills include *Bouteloua curtipendula* (side-oats grama), *Schizachyrium scoparium* (little bluestem), *Andropogon gerardii* (big bluestem), *Cornus drummondii* (rough-leaved dogwood), *Aster ericoides* (heath aster), *Carex heliophila* (sun-loving sedge), *Sisyrinchium campestre* (blue-eyed grass), *Dichanthelium oligosanthes* (Scribner's panic grass), *Amorpha canescens* (lead plant), and *Asclepias verticillata* (whorled milkweed).

INDEX DESCRIPTORS: Loess Hills, mid-grass prairie, tallgrass prairie, ecotone, woody encroachment, habitat association, resource partitioning.

The Loess Hills landform is well known as one of Iowa's most distinctive physiographic regions (Bettis et al. 1986, Prior 1991). The loess deposition that occurred toward the end of the Pleistocene 30,000 to 18,000 years ago and its subsequent erosion into a labyrinth of interconnected ridges and spur ridges built a relatively rugged landscape where native habitats have endured better than in most of Iowa. The Loess Hills contains the majority of Iowa's remaining prairie (Farrar et al. 1985, Roosa et al. 1986). Although ecological interest in the prairie vegetation, and in disjunct species from the Great Plains in particular, has spanned nearly a century, most plant community research to date has focused on qualitative floristics (Bush 1895, Pammel 1895, Shimek 1909, Morrill 1953, Novacek et al. 1985), rather than quantitative ecology.

From 1990 to 1993, integrated studies in community, population, and physiological ecology were conducted to provide quantitative information on the ecology of grasslands in the Loess Hills. In the population studies, the abundance of prairie and ecotonal species was measured in various communities and habitats at many locations in the Loess Hills. This autecological approach generated a great deal of information pertaining to individual species biology and ecology, in particular: 1) the distribution and abundance of species among different habitats and along the latitudinal range of the Loess Hills, 2) the persistence of prairie species under woody encroachment, 3) species associations among prairie and ecotonal species, and 4) patterns of resource partitioning among species.

The principal objective of this paper is to serve as a reference for this body of ecological information. A floristic checklist for the Loess Hills published by Novacek et al. (1985) provided qualitative data on species occupying prairie, woodland, woodland edge, wetland, and ruderal habitats and totaled 703 species. In this paper, the prairie communities and adjacent edge were intensively studied along the entire latitudinal range of Iowa's Loess Hills. The two principal results are a floristic checklist that presents quantitative information on the distribution and abundance of 146 prairie species, and a species ordination that includes 101 of the most common of these species.

METHODS

Study Sites

Study sites were selected to represent the influence of topographical variability on extant Loess Hill prairie (Fig. 1). A study site was physically represented by two or more transects that originated on a ridgeline and extended downward across adjacent slopes or along spur ridges following environmental gradients associated with topography. All of the 26 study sites occurred on one or more of four possible soil types, including: the Hamburg series (a Coarse-silty, mixed, calcareous, mesic Typic Udorthent), the Ida soil (a Fine-silty, mixed, calcareous, mesic, Typic Udorthent), the Monona soil (a Fine-silty, mixed, mesic, Typic Hapludoll), and the Napier soil (a Fine-silty, mixed, mesic, Cumulic Hapludoll) (Clark and Nixon 1975). Additional information pertaining to the study sites and their soils is presented in Rosburg (1994).

Over the latitudinal range of the Loess Hills, from south to north, precipitation, mean temperature, and length of the growing season all decrease. In Fremont County in the southern portion of the Loess Hills, the average annual precipitation is 81 cm, the mean July temperature is 24.7°C, the mean January temperature is −4.2°C, and the average frost-free growing season is 165 days (Clark and Nixon 1975). In Plymouth County in the northern portion of the Loess Hills, the average annual precipitation is 69 cm, the mean July temperature is 23.6°C, the mean January temperature is −7.5°C, and the average growing season is 149 days (Worster and Harvey 1976).

Measurement of Species Abundance

The abundance of species was measured in community samples that were located at *either* 5, 10, or 15 m intervals along the transects that comprised study sites. The transects were variable in length

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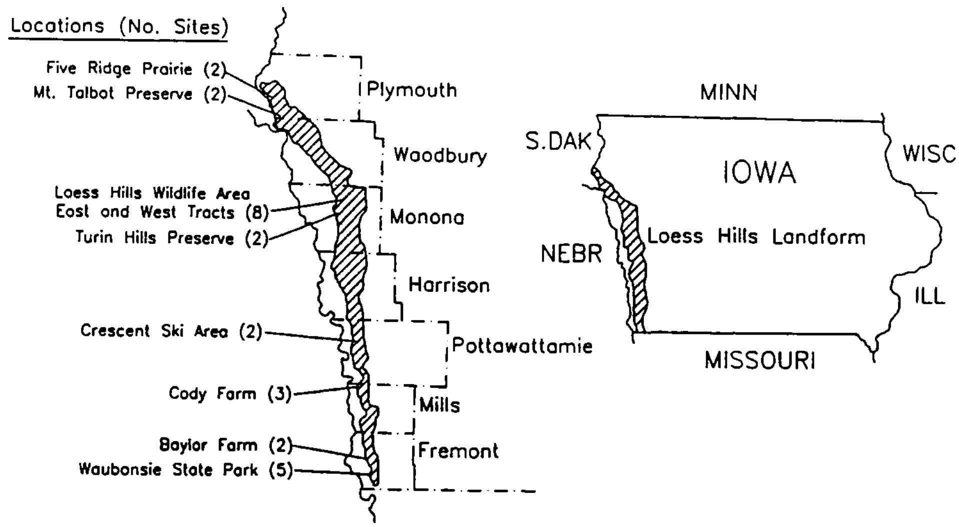

Fig. 1. Location of study sites in the Loess Hills.

Table 1. Indices used to record species abundance in each of the 40 subsamples (25 × 25 cm quadrats) per community sample.

PLANT LIFE FORM	ABUNDANCE INDEX 1 (LOW)	2 (MEDIUM)	3 (HIGH)
Forbs (stem or root crown density per subsample)	1 to 3	4 to 8	9 or more
Woody (stem density per subsample)	1 to 2	3 to 5	6 or more
Graminoids (basal area of tillers per subsample)	up to 10%	11 to 45%	46 to 100%

because they ended in either the ecotonal habitats adjacent to prairie or when an anthropogenic habitat was encountered.

Each community sample consisted of a 4 m × 7 m plot with a nested 2 m × 5 m subplot, and forty 25 cm × 25 cm quadrats nested within the 2 m × 5 m subplot. The identity and DMH (diameter at 1 m height) of all woody stems exceeding 2 m in height and within rhe 4 m × 7 m plot were recorded. All woody stems between 1 and 2 m in height (i.e., shrub size) that were within the 2 m × 5 m subplot were identified and counted, and a DMH of 1 cm was assigned to each stem. Woody stems less than 1 m in height were measured in the same way as herbaceous species. The abundance of herbaceous species was based on the numbers of stems, root crowns, or tillers in forty 25 cm × 25 cm quadrats distributed throughout the 2 m × 5 m subplot with a stratified random design (Rosburg 1994). Plant species rooted in each quadrat were assigned an abundance index, either a 1, 2, or 3, that represented either a low, medium or high abundance, respectively, and which was determined by objectively counting stems or root crowns or subjectively estimating the basal area of tillers of graminoids (Table 1). The abundance index essentially integrates both frequency and density components of species abundance in a way that could also be described as a weighted frequency.

The abundance of species in a community sample was the sum of the indices in the various subsamples. For woody species, it was the sum of the abundance indices in all 40 quadrats for the woody stems less than 1 m, plus the total DMH (recorded in cm, and considered an index of basal area) of all the stems greater than 1 m in height. For herbaceous species, it was the sum of their abundance indices in all 40 quadrats. The index of abundance in a community sample for herbaceous species could potentially range between 0 and 120, while woody species ranged from 0 to approximately 150. Therefore the abundance of each species observed in a community sample, both herbaceous and woody, was measured on scale that encompassed a similar range of potential values and that permitted considerable resolution for distinguishing differences in abundance among community samples.

Community samples were inventoried during a six week period, from about the last of May to the second week of July, during the field seasons of 1990, 1991, and 1993. Altogether, 245 community samples were recorded. Species nomenclature follows Eilers and Roosa (1994).

Vegetation Analyses

Multivariate classification of the community samples was performed with two-way indicator species analysis using all the samples and species in the program TWINSPAN (Hill 1979a). TWINSPAN is a polythetic divisive classification method that uses repeated dichotomization to form groups. Two basic ordinations, one using reciprocal averaging and one using differential species, comprise each dichotomy. TWINSPAN identified species associations which were designated community types. Subsequent to the classification of community samples to a community type, the following four descriptive statistics of species occurrence within the various communities were calculated (Rosburg 1994):

1. The mean abundance of a species in a community is the average of all its abundance indices in the community samples that were classified as the community type. Rather than present rhe numerical

Table 2. Summary of environmental characteristics of community types in the Loess Hills, compiled from Rosburg and Glenn-Lewin (1996) and Rosburg (1994). The grassland communities considered to be natural communities are indicated with an asterisk (*).

COMMUNITY TYPE	CODE	NO. COMM. SAM.[a]	MEAN SLOPE ANGLE[b] (°)	SLOPE AZIMUTH[c]	INDEX OF RELATIVE ELEVATION[d] (m)	MEAN SOIL MOISTURE[e] (%)	MEAN THICKNESS OF SOIL A HORIZON (cm)	MEAN TOTAL SOIL NITROGEN (mg N/g soil)	MEAN DEPTH TO $CaCO_2$ (cm)	MEAN SOIL pH
MID-GRASS GROUP										
*Bluff Colluvium	BC	4	51.0	W	29	—	1.2	0.45	0.4	7.31
*Bluff Mid-grass	BM	15	41.2	W	45	—	4.3	0.51	0.3	7.34
*Dry Mid-grass	DM	17	34.1	SW	41	8.7	2.1	0.46	0.1	7.39
*Mid-grass	MG	79	21.0	S	40	10.3	11.1	0.65	1.4	7.23
TALLGRASS GROUP										
*Tall/Mid-grass	TM	45	17.7	NW, E	37	11.1	11.7	0.71	4.1	7.17
*Tallgrass	TG	37	22.1	none	32	12.5	18.8	0.95	5.3	7.12
Tallgrass Exotic	TX	13	10.5	NW	0	15.7	36.4	1.44	23.8	7.06
Tallgrass Edge	TE	11	24.8	N	28	15.8	21.9	1.14	12.7	7.04
WOODLAND/EDGE GROUP										
Shrub Edge	SE	6	12.7	S	13	13.3	56.3	1.60	7.9	7.10
Woodland Edge	WE	4	14.3	none	15	14.9	42.3	1.77	36.5	6.99
Red Cedar Woodland	RC	3	14.6	none	2	11.9	35.9	1.38	10.8	7.07
Dogwood/Elm Woodland	DE	6	18.8	N	0	16.0	38.4	1.99	43.3	6.98
Bur Oak Woodland	BO	5	22.4	none	37	—	17.6	1.12	14.9	7.04

[a]Number of community samples classified as the community type by TWINSPAN
[b]All means are calculated from measurements for all community samples classified as the community type
[c]Slope azimuths that exhibited a significant positive association with the community type
[d]Index of Relative Elevation = $[54 - \bar{d}]$, where $\bar{d}$ = mean distance (m) downslope from the ridgeline for the community type. The Index for the community type with the greatest mean distance downslope (i.e., lowest relative elevation, $\bar{d}$ = 54) was arbitrarily assigned 0
[e]Soil moisture in the top 20 cm of the soil profile; measured in a subset of community samples in the Loess Hills Wildlife Area on 10 July 1991 after 3 weeks of drought. Community types with (−) were not sampled

mean abundance for each species, categories representing ranges of mean abundance were utilized to make interpretation and comparison easier. The following six categories were used in the Appendix: (A)—abundant for species with mean abundance >35; (C)—common for species with mean abundance 21 to 35; (F)—frequent for mean abundance between 10.5 and 21; (O)—occasional for mean abundance between 3.5 and 10.5; (S)—sparse for species with mean abundance 1 to 3.5; and (T)—trace was used for mean abundance <1.

2. Community constancy is the percentage of community samples in which the species was present out of the number of samples that were classified as the community type.

3. The relative community affinity of species for a community type integrates mean abundance and constancy into a measure of importance, and calculates the percentage of a species' importance in a community type relative to its total importance in all 245 community samples. For each species, the sum of their relative community affinities in all community types is 100%. High values for relative community affinity, particularly those greater than 55%, indicate that the majority of observations of a species occurred in that community type.

4. Relative latitude affinity measures the distribution of abundance among three latitudinal regions. Plymouth and Woodbury Counties were assigned to the northern region, Monona, Harrison, and Pottawattamie Counties were assigned to the central region, and Mills and Fremont Counties were classified in the southern region. Relative latitude affinity in a region was the percentage of regional importance (an integrated measure of abundance and constancy at the county level) compared to total importance in all 245 community samples.

Species association was examined using the program DECORANA and the total abundance indices of species in the community samples. DECORANA produces a multi-dimensional ordination by detrended correspondence analysis, which reduces problems associated with arch effects in the calculation of second and higher axes in correspondence analysis and with the scaling of axes (Hill 1979b). It provided a species in sample-space ordination.

RESULTS AND DISCUSSION

Altogether 168 species were observed in the 245 community samples. An additional 21 species were encountered outside of community sample plots. Because the emphases of this study were the species inhabiting grassland communities, ecological information is presented on only those species that occurred in at least one of the six natural grassland community types (Table 2). A species checklist

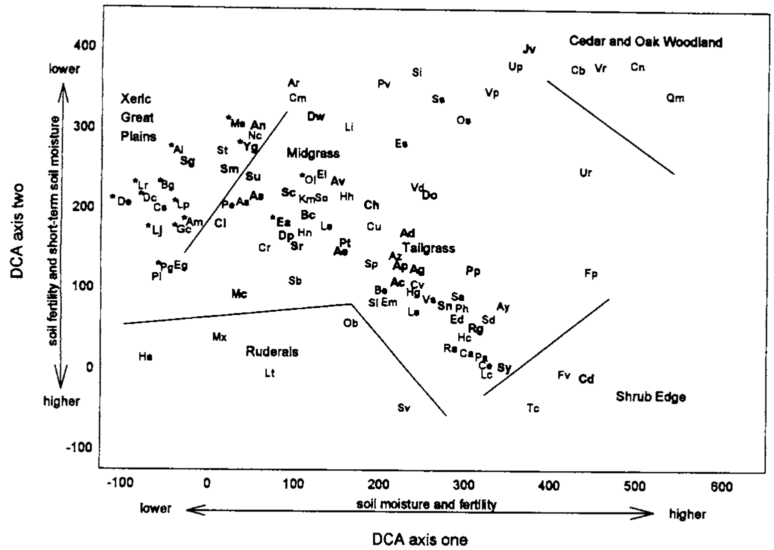

Fig. 2. DECORANA ordination of the 101 most common prairie species in habitat space. See Appendix for identification of the two-letter species codes. Species in boldface were among the 30 most abundant species (Table 3). Species identified with an (*) have high affinity for the mid-grass ecosystem in the Great Plains.

(Appendix) displays the distributions of species among Loess Hill habitats and latitudinal regions. The checklist includes 146 grassland species, including the 21 species observed outside of sample plots and for which only presence information is available. All of the prairie species which were observed are included because it is often just as important to know which species are uncommon as it is to know which ones are dominant.

Species associations and resource partitioning are addressed in an ordination of grassland species in habitat space (Fig. 2). Although all of the species observed in community samples were included in the analysis, only those that occurred in five or more community samples (i.e., 101 species) were plotted in the ordination.

It is intended that much of the inherent value of this paper is to served as a reference for information on a variety of ecological characteristics for a great number of Loess Hill species. Because a large number of species is included, discussions of individual species is not possible. Instead, ecological patterns are highlighted and discussed with individual examples.

Community Types

A detailed description of 13 community types identified by a TWINSPAN classification is available in Rosburg and Glenn-Lewin (1996) and Rosburg (1994). Variation in slope angle, slope azimuth, and relative elevation among the community types (Table 2) resulted in gradients that encompassed variation in soil moisture, soil fertility, and disturbance. South and southwestern slope azimuths and high relative elevation were associated with lower soil moisture and fertility. North and northeastern slope azimuths and low relative elevation were associated with higher soil moisture and fertility. Disturbance was associated with slope angles above 40° (Rosburg and Glenn-Lewin 1996, Rosburg 1994).

Three physiognomic groups were represented by the community types. Mid-grass communities occurred in habitats with relatively low soil moisture and fertility and were dominated by mid-grasses such as *Schizachyrium scoparium* (little bluestem), *Bouteloua curtipendula* (side-oats grama) or *Muhlenbergia cuspidata* (plains muhly). Tallgrass communities occupied habitats with medium soil moisture and fertility and were dominated by the native tallgrass species *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (Indiangrass). Woodland/edge communities occurred in habitats with relatively high soil moisture and fertility and were dominated by native woody species.

Overall Abundance

The prevalence of mid-grass vegetation in the extant Loess Hills is indicated by the high abundance of *Bouteloua curtipendula* and *Schizachyrium scoparium* (Table 3). *S. scoparium* was the most abundant in terms of the overall stem or tiller density, while *B. curtipendula* was the most abundant in terms of frequency in samples (i.e., more widespread). There were also several forbs with affinity to western mid-grass communities, for example *Lygodesmia juncea* (skeleton plant), *Yucca glauca* (yucca), and *Echinacea angustifolia* (purple coneflower), that were among the most abundant species in the Loess Hills (Table 3). Among the 30 most abundant species (Table 3), nine (30%) were in the Asteraceae and eight (27%) were in the Poaceae. The only other families with more than one representative were Fabaceae and Ranunculaceae, each with two species (7%).

The relative ranking of species overall abundance depended on how abundance was evaluated (Table 3). The two measures of abundance—stem or tiller density vs. presence in community samples—reflect differences in the distribution patterns of individuals. Species that ranked much higher in abundance in terms of overall density of stems or tillers than they did in terms of presence in community samples (Table 3) are species in which high local densities contributed relatively more to overall abundance than did consistent and widespread occurrence in community samples. Individuals of these species tended to be aggregated in relatively fewer large populations. Conversely, species that ranked much higher in terms of presence in community samples than they did in terms of overall density of stems or tillers are species in which consistent and widespread occurrence contributed relatively more to overall abundance than did high local density. Individuals of these species tended to be dispersed in many small populations throughout the Loess Hills.

An aggregated distribution would be most pronounced in species with a propensity for rhizomatous growth and/or relatively narrow seed dispersal. Among the 30 most abundant species in the Loess Hills (Table 3), those that exhibited the greatest tendency towards

Table 3. The most common plant species in the grassland communities of the Loess Hills measured two ways—with the abundance index, which is based on stem, root crown, or tiller densities (and also integrates basal area for woody species), and with presence in community samples.

COLUMN A — ABUNDANCE INDEX[a] — A(+) INDICATES SPECIES THAT RANK MUCH HIGHER IN COLUMN A THAN IN COLUMN B

SPECIES	TOTAL INDEX	AVE. INDEX
Andropogon scoparius	7,730	37.3
Bouteloua curtipendula	5,488	24.4
Andropogon gerardii	4,248	23.3
+*Cornus drummondii*	2,519	30.0
Carex heliophila	2,178	19.8
+*Poa pratensis*	1,695	19.7
Aster ericoides	1,632	9.7
Amorpha canescens	1,507	13.3
Lygodesmia juncea	1,146	10.8
Ambrosia psilostachya	1,059	11.3
Asclepias verticillata	1,008	8.7
+*Symphoricarpos* sp.	951	12.2
+*Comandra umbellata*	827	11.0
Sisyrinchium campestre	816	6.2
Anemone cylindrica	778	7.3
+*Juniperus virginiana*	735	19.9
+*Sorghastrum nutans*	680	10.5
Aster sericeus	679	6.7
Solidago missouriensis	632	5.5
Solidago nemoralis	595	7.6
Dichanthelium oligosanthes	588	4.6
+*Pulsatilla patens*	582	18.2
+*Antennaria neglecta*	566	8.4
Muhlenbergia cuspidata	553	5.0
Solidago rigida	490	5.1

COLUMN B — PRESENCE IN COMMUNITY SAMPLES — AN (*) INDICATES SPECIES THAT RANK MUCH HIGHER IN COLUMN B THAN IN COLUMN A

SPECIES	NO. PRESENT	% PRESENT
Bouteloua curtipendula	225	91.8
Andropogon scoparius	207	84.5
Andropogon gerardii	182	74.3
Aster ericoides	168	68.6
**Sisyrinchium campestre*	132	53.9
**Dichanthelium oligosanthes*	128	52.2
Asclepias verticillata	116	47.3
**Solidago missouriensis*	115	46.9
Amorpha canescens	113	46.1
**Muhlenbergia cuspidata*	111	45.3
Carex heliophila	110	44.9
Anemone cylindrica	107	43.7
Lygodesmia juncea	106	43.3
Aster sericeus	102	41.6
**Solidago rigida*	96	39.2
Ambrosia psilostachya	94	38.4
**Echinacea angustifolia*	87	35.5
Poa pratensis	86	35.2
Cornus drummondii	84	34.3
**Dalea purpurea*	80	32.7
**Rhus glabra*	80	32.7
Symphoricarpos sp.	78	31.8
Solidago nemoralis	78	31.8
Dichanthelium wilcoxianum	78	31.8
Yucca glauca	78	31.8

[a]Total Index is the sum of all the community sample indices; Average Index = (total index/no. community samples present); it indicates the relative amount of local abundance.

aggregation in fewer, large populations included *Cornus drummondii* (rough-leaved dogwood), *Poa pratensis* (Kentucky bluegrass), *Symphoricarpos* sp. (buckbrush), *Comandra umbellata* (bastard toadflax), *Juniperus virginiana* (eastern red cedar), *Sorghastrum nutans, Pulsatilla patens* (pasque flower), and *Antennaria neglecta* (pussytoes). All of these species, except *P. patens* and *J. virginiana,* exhibit either strong rhizomatous or stoloniferous growth (Great Plains Flora Association 1986, Weaver 1954). Their aggregated pattern likely results from strong clonal growth after an initial establishment. For *P. patens* and *J. virginiana,* high local dispersal of seed and establishment of individuals may be important factors causing a tendency for aggregation in relatively few, large populations.

A dispersed distribution would be most likely in species with a lack of rhizomatous growth and/or relatively wide seed dispersal. Among the 30 most abundant species (Table 3), those that exhibited the greatest tendency towards a distribution in many, small populations included *Sisyrinchium campestre* (blue-eyed grass), *Dichanthelium oligosanthes* var. *scribnerianum* (Scribner's panic grass), *Solidago missouriensis* (Missouri goldenrod), *Muhlenbergia cuspidata, Solidago rigida* (rigid goldenrod), *Echinacea angustifolia, Dalea purpurea* (purple prairie clover), and *Rhus glabra* (smooth sumac). All but two of these species (*S. missouriensis* and *R. glabra*) lack rhizomes or stolons (Great Plains Flora Association 1986, Weaver 1954) and their tendency towards a dispersed distribution could result from greater reliance on propagation from seed rather than clonal growth.

Species Distribution among Habitats

Loess Hill community types comprise compositional gradients associated with variation in the abiotic environment—soil moisture and fertility, and disturbance arising from high slope angles (Rosburg and Glenn-Lewin 1996). The distribution and abundance of a species changes in response to variation in the abiotic environment. However, the effect of the abiotic environment occurs within the context of a biotic environment. Thus community types represent habitats characterized by a range of soil moisture, soil fertility, and disturbance (i.e., the abiotic environment), and by changing associations of species (i.e., the biotic environment).

Although many species were observed in the same habitats (i.e., community types), species generally exhibited unique patterns of abundance among habitats. Although most species also occurred in several habitats, there was typically only one or two habitats where abundance was greatest (i.e., the habitat where a species was most successful).

Some species exhibited a wide distribution among community types and are therefore examples of highly adaptable and/or dispersed species. Two species, *Ambrosia psilostachya* (western ragweed) and *Symphoricarpos* sp., occurred in 12 of the 13 community types (Appendix). Four species, *Bouteloua curtipendula, Aster ericoides* (heath aster), *Poa pratensis,* and *Rhus glabra,* occurred in 11 of the 13 community types. Despite their widespread occurrence and apparent adaptability, high abundance of these species was limited to only a few habitats. For example, over half of all the total importance of *Symphoricarpos* occurred in the shrub edge community type, while sparse and/or trace amounts of *Symphoricarpos* occurred in seven of the 12 habitats. The widespread characteristic of these species occurred because at least small amounts were present in many of the habitats. Thus, high tolerance by these species to stressful environments may be as or more important as their adaptability.

A few species exhibited relatively narrow distributions among community types, and presumably represent species with more limited dispersal ability and/or more specialized life histories. *Echinacea angustifolia* was present in three community types. *Liatris punctata* (dotted blazing star), *Dalea enneandra* (big top prairie clover), and *Linum rigidum* (rigid flax) were present in four community types (Appendix). All four of these species are Great Plains species and two (*D. enneandra* and *L. rigidum*) are restricted in Iowa to the Loess Hills and/or to the extreme northwest corner of the state (Christiansen 1992). Their narrow distribution among Loess Hill community types is likely related to their specialization for xeric habitats.

Some of the Great Plains species occurred in a wider range of habitats than expected given their association with xeric habitat. For example, *Yucca glauca* and *Lygodesmia juncea* had the highest importance in the bluff mid-grass and dry mid-grass communities, respectively, and most observations of both species did occur within the mid-grass habitats (Appendix). However, both species also occurred in three of the communities in the tallgrass group, including the tallgrass exotic and tallgrass edge communities, which are typically associated with relatively lower and more mesic habitats. *Y. glauca* is apparently capable of competing with species in relatively mesic habitats, as indicated by several personal observations of it growing in roadsides dominated by *Bromus inermis* (smooth brome).

Some species exhibited a normal-like distribution among habitats. For example, *Aster sericeus* (silky aster) had the highest abundance in the tall/mid-grass community and decreased similarly in both directions along the community gradient (Appendix). Other species exhibited a skewed distribution. *Solidago nemoralis* (gray goldenrod) also had the highest importance in the tall/mid-grass community, but unlike *Aster sericeus* it decreased more rapidly in the mesic direction than in the xeric direction. Since the abiotic environment encompassed by both species is the same, the difference in the pattern of distribution between these two species suggests ecological differences in their response to the biotic environment. *Solidago nemoralis* may be less competitive with the species associated with more mesic habitats than is *Aster sericeus.*

Species Latitudinal Distribution

Relative latitude affinity of species among the south, central, and north regions of the Loess Hills identifies groups of species that are more abundant at either the north or south ends of the Loess Hills (Appendix). For some of these species, their northern or southern affinities are a consequence of their biogeography. Two of the northern species, *Carex heliophila* (sun-loving sedge) and *Pulsatilla patens* have distributions centered in the northern Great Plains, while four of the southern species—*Hedyotis nigricans* (bluets), *Aster azureus* (azure aster), *Strophostyles leiosperma* (slick-seed bean), and *Lespedeza capitata* (round-headed bush clover)—are more common in the southern Great Plains (Great Plains Flora Association 1977). For these species factors affecting their biogeography, such as their center of origin, Pleistocene migration routes and refugia, or climate preferences, have influenced their present distribution in the Central Grasslands. Their distribution in the Loess Hills simply reflects their larger continental distribution.

Migration routes of Great Plains species into the Loess Hills may also affect the latitudinal distribution of species. Two species, *Astragalus missouriensis* (Missouri milkvetch) and *Dalea enneandra,* both occur throughout the western Great Plains from North Dakota to Texas (Great Plains Flora Association 1977). Their northern distribution in the Loess Hills may be due to a migration route from the plains of South Dakota along upland bluffs and sandbars of the Missouri River into the northern Loess Hills (Novacek 1985). A northern migration route is especially explicative for *D. enneandra,* because it is more widespread in the southern Great Plains than in the northern Great Plains.

Other species with either northern or southern affinities are widely distributed throughout the Central Grasslands and an explanation for their northern or southern distribution in the Loess Hills is less evident. One possibility is related to the size of prairie remnants, which generally decreases from north to south because of increasing woody vegetation. Perhaps for some species with northern distributions, their lower abundance in the southern regions is related to an inability to maintain populations on smaller prairie remnants. Species that tend to be locally infrequent in small populations, such as *Pediomelum esculentum* (prairie turnip) and *Asclepias viridiflora* (green milkweed), should be more sensitive to size of remnants and may be good examples. Higher abundance of woody species, such as wild plum (*Prunus americana*), in the southern Loess Hills could result in part from higher precipitation.

Many species appear to be more common in the central region, but for most of these species their distribution is likely an artifact of sampling. Because intensive studies were completed in the Loess Hills Wildlife Area in Monona County (Rosburg 1994, Rosburg et al. 1994), there were far more community samples located in the central region than the other regions. Although the relative latitude affinity is standardized for the number of samples, the calculation does not account for the fact that much more area was sampled in the central region. Also, the Loess Hills Wildlife Area, an important study location in the central region, contains the largest prairie remnants included in the study. The larger remnants and the much greater amount of area sampled in the central region explain why some prairie species, for example *Gaura coccinea* (scarlet gaura), *Nothocalais cuspidata* (prairie dandelion) and *Lithospermum canescens* (hoary puccoon), appear to be more abundant in the central region. The central region also contained the majority of community samples of the bluffline community, thus the indication that bluffline species (e.g., *Lactuca tartarica* and *Helianthus annuus*) are most abundant in the central region is also an artifact of sampling.

Species Persistence under Woody Encroachment

The tail of the distribution of many prairie species extends into the communities in the woodland/edge group (Appendix), indicating some ability to persist during succession to woody vegetation. Among the graminoids with the highest persistence were *Bouteloua curtipendula, Schizachyrium scoparium, Andropogon gerardii, Dichanthelium oligosanthes,* and *Carex heliophila.* All of these species, except *C. heliophila,* were also present under the canopy of invading red cedar in prairie in eastern Nebraska (Gehring and Bragg 1992).

B. curtipendula had the highest mean frequency of any prairie grass in the red cedar woodland community, and in the study by Gehring and Bragg (1992) *B. curtipendula* was the only prairie grass to increase significantly in cover from open prairie to the crown edge of cedars before decreasing in cover under the canopy. Among the prairie gra-

Table 4. Pearson correlation coefficients for environmental and community variables with the first two axes of the DECORANA ordination of all 245 community samples. Coefficients are given for significant correlations (* $p \leq 0.01$, ** $p \leq 0.005$, *** $p \leq 0.0001$); "ns" indicates not significant (modified from Rosburg 1994).

VARIABLES	DCA AXIS ONE	DCA AXIS TWO
Geographical Variable		
Latitude	ns	ns
Topographic Variables		
Slope azimuth along a north (0) to south (180) gradient	−0.36***	ns
Slope angle	−0.18**	ns
Index of relative elevation	−0.46***	0.18*
Edaphic Variables		
Soil Moisture (from a soil core 40 cm deep):		
Upper 20 cm	0.68***	−0.44***
Lower 20 cm	0.49***	ns
Soil Fertility:		
Depth of soil A horizon	0.56***	−0.30***
Total soil nitrogen	0.73***	−0.31***
Depth to $CaCO_3$	0.63***	−0.27***
Soil pH	−0.71***	0.27***
Community Variables		
Total woody basal area	0.63***	0.25***
Species richness	ns	ns
Species diversity	−0.21**	ns

minoids, *B. curtipendula* appears to have relatively high shade tolerance and may actually benefit from a modest amount of shading that perhaps decreases competition from *Andropogon gerardii* and *Schizachyrium scoparium.*

The forbs with the highest persistence under woody vegetation included *Anemone cylindrica* (thimbleweed), *Pulsatilla patens,* and *Ambrosia psilostachya* (Appendix). *A. cylindrica* was observed in all but one of the communities in the woodland/edge group. Other prairie forbs that exhibited some persistence included *Aster ericoides, Sisyrinchium campestre, Solidago missouriensis, Amorpha canescens* (lead plant), *Solidago rigida, Dalea purpurea, Senecio plattensis* (prairie ragwort), and *Viola pedatifida* (prairie violet).

Species Associations

The species ordination (Fig. 2) locates 101 grassland species in sample space, that is species that tended to occur in the same community samples (i.e., habitat) are located close to one another in the ordination. Because of the large number of community samples collected, the habitat space is substantial and the ordination provides useful information about general species relationships, particularly the species that most often share similar habitats. DCA axis one was positively correlated with soil moisture and fertility, which increased on north-facing slopes and habitats at low relative elevation (Table 4). DCA axis two was negatively correlated with soil moisture and fertility, although not as strongly as axis one.

Twelve species with high affinity to the Great Plains ordinated closely together at the xeric end of the moisture gradient, while two additional Great Plains species, *Echinacea angustifolia* (Ea) and *Oxytropis lambertii* (Ol, locoweed), occurred in slightly more mesic habitats (Fig. 2). *Dalea candida* (Dc, white prairie clover) was among the group of species with high Great Plains affinity because it was the variety *oligophylla,* which is a western form sometimes classified as a separate species, *Petalostemon occidentale* (Great Plains Flora Association 1986).

Ruderal species such as *Helianthus annuus* (Ha, annual sunflower), *Lactuca tartarica* (Lt, blue lettuce), *Melilotus* sp. (Mx, sweet clover), *Oenothera biennis* (Ob, evening primrose), and *Setaria viridis* (Sv, green foxtail) occurred together in the bluff colluvium community (ordination space represented by low scores on both axes). These relatively dry and disturbed habitats occurred frequently on the steep slopes along the western bluffline, an abrupt wall of loess adjacent to the Missouri River floodplain.

Other general associations included edge species and oak woodland species. Both occupied the most mesic habitats sampled (Fig. 2), but edge species were associated with lower axis two scores, (i.e., higher soil fertility and moisture in the upper soil profile). Edge species represent ecotonal habitats, the site of the most recent woodland encroachment into prairie. The higher fertility in these habitats relative to the woodland could be a related to their more recent occupation by tallgrass prairie.

Much closer associations, which represent species most likely to be found together in patches within communities, can also be identified. Such information could be useful in prairie reconstruction to help design vegetation patches that more closely mimic natural patterns. For example, a group of three species, *Euphorbia glyptosperma* (Eg, ridge-seeded spurge), *Penstemon grandiflorus* (Pg, large flowered beardtongue) and silver leaf scurfpea (Pl, *Pediomelum argophyllum*), often occurred together in dry, semi-disturbed habitats (Fig. 2).

Resource Partitioning among Species

The positions of species along axes one and two are indicative of their relative positions along soil moisture and fertility gradients (Fig. 2). The ordination encloses a resource space, and the position of species in the ordination represents their realized niche and suggests how resources are partitioned. For example among the graminoids, *Schizachyrium scoparium* (Su) and *Muhlenbergia cuspidata* (Mc) exhibited the highest preference for xeric habitats (lowest scores on axis one), but *M. cuspidata* was more closely associated with disturbance (closer position to ruderal space). In order of increasing abundance with higher soil moisture and fertility (increasing axis one scores) were *Bouteloua curtipendula* (Bc) and *Koeleria macrantha* (Km, Junegrass), followed by *Dichanthelium oligosanthes* var. *wilcoxianum* (Dw, Wilcox panic grass), *Carex heliophila* (Ch), *Stipa spartea* (Si, porcupine grass), *Andropogon gerardii* (Ag), *Dichanthelium oligosanthes* (Do), *Sorghastrum nutans* (Sn) and *Poa pratensis* (Pp) (Fig. 2).

Resource partitioning in a group of forbs was demonstrated along the soil moisture and fertility gradient by the five species of *Solidago. S. nemoralis* (Sg) occupied the most xeric position of the gradient, and as soil moisture and fertility increased, *S. missouriensis* (Sm), *S. rigida* (Sr), *S. speciosa* (Ss, showy goldenrod), and finally *S. canadensis* (Sd, Canada goldenrod) were arranged sequentially along the gradient. *S. canadensis* was associated with edge species in the most mesic and highest fertility segment of the gradient (Fig. 2).

Endangered and Uncommon Species

Botrychium campestre (prairie moonwort) was discovered in the Loess Hills in Monona County in 1982 (Farrar and Johnson-Groh 1986, Wagner and Wagner 1986). It was observed in three community samples, all in Monona County. One sample was on a northwest aspect in a tall/mid-grass community. The other two samples were on an east-facing aspect under a canopy of red cedar in woodland edge and red cedar woodland community types.

Several species on the Iowa list of endangered and threatened species were encountered. *Penstemon cobaea* (cobaea penstemon) was recorded in one community sample of dry-mid-grass on a south-facing spur ridge in Fremont County. Many other individuals were observed on a privately-owned remnant prairie in Fremont County. Although the prairie on this formerly pastured site, the Baylor prairie, is primarily tallgrass exotic vegetation, it provides a rare example of prairie that occupied the lower valleys in the Loess Hills. *Sphaeralcea coccinea* (scarlet globemallow) was observed in one community sample of dry mid-grass on the bluffline in Pottawattamie County.

Other species were encountered outside of community samples. Several individuals of *Mentzelia decapetala* (ten petal blazingstar) were observed in the bluff mid-grass community in Harrison, Woodbury, and Plymouth Counties. A large population (perhaps the largest in Iowa) of *Asclepias stenophylla* (narrow-leaved milkweed) was observed in mid-grass habitat on private land in Mills County. A population of *Lomatium foeniculaceum* (prairie biscuit root) was observed in Fremont County along the base of the bluffline. The population contains several dozens of individuals, but nearly all are threatened by encroachment by *Juniperus virginiana.* Small populations of both *Penstemon albidus* and *Shepherdia argentea* were observed in Plymouth County; *P. albidus* occurred in dry mid-grass and *S. argentea* in tallgrass edge.

Euphorbia falcata (falcate spurge) was observed in four community samples, primarily from woodland edge communities, and in seed bank studies of woodland edge and red cedar woodland communities (Rosburg et al. 1994). These observations constituted a new record of this species for the Midwest (Rosburg 1992).

One orchid, previously unreported for the Loess Hills, was observed. *Spiranthes magnicamporum* (Great Plains ladies-tresses) was observed in low elevation tallgrass habitat at two locations in the southern Loess Hills. One of these was the aforementioned Baylor prairie, the valley remnant in Fremont County.

CONCLUSIONS

The 146 species included in the quantitative, floristic checklist represents about 77% of the 190 species listed by Novacek et al. (1985) as occurring on prairie in the Loess Hills. Some of the species listed by Novacek et al. (1985) but not represented in this study are either: 1) very uncommon species (e.g., *Asclepias lanuginosa*), 2) species that inhabit wet prairie more typical of the Missouri River floodplain (e.g., *Tradescantia bracteata*), or 3) species that have higher affinity for other habitats (e.g., *Erythronium albidum*).

The occurrence of many western species in the Loess Hills has been documented for well over a century. Many of these species, which occupy xeric habitats resulting from the effect of slope azimuth and elevation on microclimates, not only represent disjunct populations from the Great Plains, but also occur with high relative abundance and comprise a significant share of the biota in Loess Hill communities.

Numerous prairie species exhibited a conspicuous affinity for either the northern or southern portion of the Loss Hills. Species biogeography and migration is an important factor in some cases, while for other species ecological and environmental factors are likely more important.

Quantitative information on the distribution and abundance of prairie species in habitats representing a continuum of vegetation from dry and semi-disturbed prairie (bluff colluvium and bluff midgrass) to relatively mesic woodland (bur oak and dogwood/elm woodlands) is presented in a floristic checklist. Patterns of species associations and resource partitioning in habitat space representing gradients in soil moisture and fertility are illustrated in a species ordination. Both serve as a valuable reference on prairie species biology and ecology for prairie managers, restorationists, and ecologists.

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Appendix—Floristic Checklist

Distribution and abundance of Loess Hills grassland species among latitudinal regions and plant communities.

SPECIES ( ) DENOTE PROBABLE SPECIES	S[a]	N[b]	RLA (%)[c] S·C·N	ABUNDANCE OF SPECIES WITHIN COMMUNITY TYPES[d] MEAN ABUNDANCE INDEX[e]·RELATIVE COMMUNITY AFFINITY (%)[f]												
				MID-GRASS				TALLGRASS				WOODLAND/EDGE				
				BC	BM	DM	MG	TM	TG	TX	TE	SE	WE	RC	DE	BO
PTERIDOPHYTES																
EQUISETACEAE																
Equisetum laevigatum	El	39	32·52·16	—	—	—	T·5	S·69	T·4	T·16	—	—	T·5	—	—	—
OPHIOGLOSSACEAE																
Botrychium campestre	—	3	0·100·0	—	—	—	T·<1	—	—	—	—	—	T·39	T·60	—	—
GYMNOSPERMS																
CUPRESSACEAE																
Juniperus virginiana	Jv	37	17·81·2	—	T·<1	—	S·<1	S·1	T·<1	—	T·<1	—	C·17	A·65	F·14	S·2
DICOTYLEDONS																
ANACARDIACEAE																
Rhus glabra	Rg	80	22·32·46	T·2	S·8	T·2	T·3	T·2	S·9	S·7	O·22	O·44	T·2	—	T·1	—
Toxicodendron radicans	—	2	0·100·0	—	—	—	—	—	T·1	—	—	S·99	—	—	—	—
APIACEAE																
Lomatium foeniculaceum	—	—	P·0·0	—	—	—	P	—	P	—	—	—	—	—	—	—
ASCLEPIADACEAE																
Asclepias stenophylla	—	—	P·0·0	—	—	P	P	—	—	—	—	—	—	—	—	—
Asclepias syriaca	Ay	10	37·27·36	—	T·2	—	T·<1	—	T·<1	—	T·22	T·13	T·50	—	T·13	—
Asclepias tuberosa	—	—	P·0·0	—	—	—	—	—	P	—	P	—	—	—	—	—
Asclepias verticillata	Av	116	34·55·11	—	S·4	T·2	O·23	O·19	O·17	O·27	T·<1	—	S·8	—	—	—
Asclepias viridiflora	Ar	8	0·37·63	—	T·33	T·27	T·22	T·18	—	—	—	—	—	—	—	—
ASTERACEAE																
Ambrosia psilostachya	Ap	94	40·26·34	T·<1	O·8	O·10	S·4	S·2	S·4	C·44	T·<1	T·1	F·26	T·<1	—	T·<1
Antennaria neglecta	An	67	8·76·16	—	—	T·<1	T·4	F·92	T·1	T·3	—	—	—	—	—	—
Artemisisa ludoviciana	—	—	P·P·P	—	—	—	—	—	P	P	—	—	—	—	—	—
Aster azureuss	Az	25	94·6·0	—	—	—	S·24	—	T·8	S·50	T·15	—	—	—	T·4	—
Aster ericoides	Ae	168	31·32·37	T·<1	T·<1	O·6	O·16	F·25	O·24	O·21	S·6	T·1	T·<1	T·<1	—	—
Aster oblongifolius	—	2	100·0·0	—	—	—	T·100	—	—	—	—	—	—	—	—	—
Aster sericeus	As	102	6·32·62	—	T·<1	T·<1	S·13	O·77	S·5	T·4	T·<1	—	—	—	—	—
Brickellia eupatorioides	Be	7	86·14·0	—	—	T·38	T·11	—	T·12	T·40	—	—	—	—	—	—
Cacalia plantaginea	—	—	P·P·0	—	—	—	—	P	P	—	—	—	—	—	—	—
Cirsium undulatum	Cu	7	0·56·44	—	—	—	T·2	T·39	T·22	T·37	—	—	—	—	—	—
Coreopsis palmata	—	—	P·0·0	—	—	—	P	—	—	—	—	—	—	—	—	—
Echinacea angustifolia	Ea	87	6·50·43	—	—	—	S·38	S·41	S·21	—	—	—	—	—	—	—
Erigeron strigosus	Es	27	56·30·15	—	—	T·6	T·24	T·13	T·<1	T·15	T·4	—	—	—	T·38	—
Eupatorium altissimum	—	2	100·0·0	—	—	T·67	—	—	—	T·33	—	—	—	—	—	—
Grindelia squarrosa	—	—	0·0·P	—	—	—	P	—	—	—	—	—	—	—	—	—
Helianthus annuus	Ha	6	0·100·0	S·95	—	T·5	—	—	—	—	—	—	—	—	—	—
Helianthus rigidus	Hg	39	0·49·51	—	T·7	S·34	S·11	T·1	S·23	—	S·25	—	—	—	—	—
Latuca (serriola)	La	5	72·28·0	—	T·37	—	—	T·10	—	T·23	T·30	—	—	—	—	—
Lactuca tartarica	Lt	9	0·85·15	F·97	T·2	—	T·<1	T·<1	T·<1	T·<1	—	—	—	—	—	—
Liatris aspera	—	2	0·0·100	—	—	—	—	T·100	—	—	—	—	—	—	—	—
Liatris punctata	Lp	41	58·32·9	—	—	T·2	S·64	T·32	T·1	—	—	—	—	—	—	—
Lygodesmia juncea	Lj	106	19·54·27	O·14	O·13	F·49	O·15	O·8	S·2	—	T·<1	—	—	—	—	—
Machaeranthera spinulosa	Ms	19	0·100·0	S·62	T·1	T·17	T·5	T·3	—	—	—	—	—	T·11	—	—
Nothocalais cuspidata	Nc	7	0·100·0	—	—	—	T·37	T·63	—	—	—	—	—	—	—	—
Prenanthes aspera	—	—	0·P·0	—	—	—	—	P	—	—	—	—	—	—	—	—
Ratibida columnifera	—	—	0·P·P	—	—	—	—	P	—	—	—	—	—	—	—	—
Senecio plattensis	St	72	0·66·34	—	—	T·5	T·8	O·85	T·1	T·1	—	T·1	—	—	—	—
Silphium laciniatum	—	—	0·P·0	—	—	—	—	P	P	—	—	—	—	—	—	—
Solidago canadensis	Sd	9	21·26·53	T·16	—	—	T·<1	—	T·50	—	—	T·34	—	—	—	—

Appendix Continued

SPECIES () DENOTE PROBABLE SPECIES	S[a]	N[b]	RLA (%)[c]	ABUNDANCE OF SPECIES WITHIN COMMUNITY TYPES[d] MEAN ABUNDANCE INDEX[e]·RELATIVE COMMUNITY AFFINITY (%)[f]												
				MID-GRASS				TALLGRASS				WOODLAND/EDGE				
			S·C·N	BC	BM	DM	MG	TM	TG	TX	TE	SE	WE	RC	DE	BO
Solidago missouriensis	Sm	115	21·43·36	—	S·11	O·33	S·18	O·24	S·5	S·6	T·1	—	T·2	—	—	—
Solidago nemoralis	Sg	78	10·52·38	—	T·<1	T·3	S·18	O·78	T·<1	—	—	—	—	—	—	—
Solidago rigida	Sr	96	19·37·44	—	T·3	T·<1	S·37	S·31	S·20	T·3	T·2	T·3	—	—	T·1	—
Solidago speciosa	Ss	15	75·17·8	—	T·3	—	T·20	T·1	T·25	—	T·51	—	—	—	—	—
Vernonia baldwinii	—	4	100·0·0	—	—	T·46	—	—	T·20	T·34	—	—	—	—	—	—
BORAGINACEAE																
Lithospermum canescens	Lc	7	28·72·0	—	—	—	T·1	—	T·2	—	T·97	—	—	—	—	—
Lithospermum incisum	Li	37	37·15·48	—	—	T·16	T·16	T·28	T·<1	—	—	—	T·39	—	—	—
Onosmodium molle	—	—	0·P·0	—	—	—	—	—	P	—	P	—	—	—	—	—
BRASSICACEAE																
Arabis hirsuta	—	—	0·P·0	—	—	—	—	P	—	—	—	—	—	—	—	—
Lepidium virginicum	—	—	0·P·0	—	—	P	—	—	—	—	—	—	—	—	—	—
CAPRIFOLIACEAE																
Symphoricarpos species	Sy	78	22·55·23	S·1	—	T·<1	T·<1	T·<1	O·8	O·9	F·12	A·55	S·1	S·2	O·9	T·<1
CELASTRACEAE																
Celastrus scandens	Cn	15	48·35·19	—	—	T·1	—	—	T·<1	—	T·<1	T·6	T·4	S·41	S·27	S·21
CHENOPODIACEAE																
Chenopodium (album)	Ca	5	31·60·0	T·86	—	T·2	T·<1	—	—	—	—	—	—	—	T·11	—
Salsola iberica	Sb	8	0·56·44	T·56	—	T·39	T·1	T·4	—	—	—	—	—	—	—	—
CONVOLVULACEAE																
Calystegia sepium	—	2	71·29·0	—	—	—	—	T·9	—	T·91	—	—	—	—	—	—
CORNACEAE																
Cornus drummondii	Cd	84	32·40·29	—	T·<1	—	T·<1	T·<1	O·3	S·<1	A·22	A·28	C·6	—	A·21	A·21
ELAEAGNACEAE																
Sheperdia argentea	—	—	0·0·P	—	—	—	—	—	—	—	P	—	—	—	—	—
EUPHORBIACEAE																
Croton monanthogynus	Cm	10	0·100·0	—	T·92	—	T·6	T·1	T·1	—	—	—	—	—	—	—
Euphorbia corollata	—	3	100·0·0	—	—	T·70	T·30	—	—	—	—	—	—	—	—	—
Euphorbia dentata	Ed	7	0·100·0	S·97	—	—	T·<1	—	T·3	—	—	—	—	—	—	—
Euphorbia falcata	—	4	0·100·0	—	—	—	T·2	—	—	—	—	—	O·98	—	—	—
Euphorbia glyptosperma	Eg	14	31·34·36	T·12	T·3	S·78	T·<1	T·1	—	T·6	—	—	—	—	—	—
Euphorbia marginata	Em	38	25·47·28	T·16	T·8	T·15	T·2	T·1	T·3	T·24	—	T·16	T·17	—	—	—
FABACEAE																
Amorpha canescens	Ac	113	23·46·30	—	S·2	T·<1	O·15	O·8	F·37	T·<1	F·36	T·1	—	—	—	—
Astragalus crassicarpus	—	1	0·100·0	—	—	—	—	—	T·100	—	—	—	—	—	—	—
Astragalus lotiflorus	Al	52	19·61·20	—	T·3	S·75	T·15	T·7	—	T·1	—	—	—	—	—	—
Astragalus missouriensis	Am	5	0·0·100	—	—	—	T·51	T·49	—	—	—	—	—	—	—	—
Crotalaria sagittalis	—	—	0·P·0	—	—	—	P	—	—	—	—	—	—	—	—	—
Dalea candida	Dc	40	8·26·66	—	—	S·14	S·40	S·38	T·<1	T·5	T·2	—	—	—	—	—
Dalea enneandra	De	38	10·19·71	—	T·<1	S·73	S·19	T·8	—	—	—	—	—	—	—	—
Dalea purpurea	Dp	80	41·37·22	—	—	S·8	S·27	O·48	S·11	T·<1	T·3	T·2	—	—	—	—
Desmanthes illinoensis	—	—	0·P·0	—	—	—	—	P	P	—	—	—	—	—	—	—
Lespedeza capitata	—	4	100·0·0	—	—	—	T·2	—	—	S·98	—	—	—	—	—	—
Melilotus species	Mx	10	10·90·0	S·65	—	S·35	T·<1	T·<1	T·<1	—	—	—	—	—	—	—
Oxytropis lambertii	Ol	9	0·100·0	—	—	S·52	T·2	T·46	—	—	—	—	—	—	—	—
Pediomelum argophyllum	Pl	7	56·44·0	T·41	T·42	T·17	—	—	—	—	—	—	—	—	—	—
Pediomelum esculentum	Pe	19	0·36·64	—	—	T·14	T·50	T·24	T·2	T·10	—	—	—	—	—	—
Strophostyles leiosperma	Sl	5	89·11·0	—	T·20	T·69	T·2	—	T·10	—	—	—	—	—	—	—

Appendix Continued

SPECIES ( ) DENOTE PROBABLE SPECIES			RLA (%)[c]	ABUNDANCE OF SPECIES WITHIN COMMUNITY TYPES[d] MEAN ABUNDANCE INDEX[e]·RELATIVE COMMUNITY AFFINITY (%)[f]												
				MID-GRASS				TALLGRASS				WOODLAND/EDGE				
SPECIES	S[a]	N[b]	S·C·N	BC	BM	DM	MG	TM	TG	TX	TE	SE	WE	RC	DE	BO
FAGACEAE																
Quercus macrocarpa	Qm	9	54·1·45	—	—	—	T·<1	T·<1	T·1	—	—	—	—	—	—	C·99
Hedeoma hispidum	Hh	28	49·31·20	—	—	T·5	T·6	T·25	T·1	T·50	—	—	T·14	—	—	—
Salvia reflexa	—	—	0·P·0	P	—	—	—	—	—	—	—	—	—	—	—	—
Scutellaria parvula	Sp	6	0·100·0	—	—	—	—	T·18	T·6	T·76	—	—	—	—	—	—
Teucrium canadense	Tc	20	50·50·0	—	—	—	T·<1	—	S·2	O·10	T·1	C·78	S·4	—	S·7	—
LINACEAE																
Linum rigidum	Lr	32	10·48·41	—	—	T·33	T·24	T·42	T·1	—	—	—	—	—	—	—
Linum sulcatum	Ls	20	48·37·15	—	T·6	T·5	T·10	T·47	T·2	T·31	—	—	—	—	—	—
LOASACEAE																
Mentzelia decapetala	—	—	0·P·P	—	P	—	—	—	—	—	—	—	—	—	—	—
MALVACEAE																
Sphaeralcea coccinea	—	1	0·100·0	—	—	T·100	—	—	—	—	—	—	—	—	—	—
MORACEAE																
Cannabis sativa	—	2	0·100·0	S·100	—	—	—	—	—	—	—	—	—	—	—	—
OLEACEAE																
Fraxinus pennsylvanica	Fp	26	35·19·46	S·4	—	—	T·<1	—	T·<1	S·1	S·6	F·36	O·21	T·1	S·9	O·21
ONAGRACEAE																
Calylophus serrulatus	Cr	16	38·0·62	—	T·51	—	T·18	T·12	T·19	—	—	—	—	—	—	—
Gaura coccinea	Gc	33	0·86·14	—	T·<1	S·63	S·32	T·1	T·4	—	—	—	—	—	—	—
Oenothera biennis	Ob	11	42·42·17	T·39	T·46	T·2	T·<1	T·<1	—	T·13	—	—	—	—	—	—
OXALIDACEAE																
Oxalis stricta	Os	10	38·62·0	—	—	T·2	—	—	—	S·82	—	—	—	T·12	T·4	—
PLANTAGINACEAE																
Plantago patagonica	—	1	0·100·0	—	—	—	—	T·100	—	—	—	—	—	—	—	—
POLEMONIACEAE																
Phlox pilosa	—	—	0·P·0	—	—	—	—	—	P	—	P	—	—	—	—	—
POLYGALACEAE																
Polygala verticillata	Pv	10	65·35·0	—	T·56	—	T·27	T·3	T·15	—	—	—	—	—	—	—
RANUNCULACEAE																
Anemone cylindrica	Ad	107	13·44·43	—	—	—	T·1	F·43	S·6	O·21	O·11	T·1	O·13	—	S·3	T·1
Delphinium virescens	—	2	0·31·69	—	T·84	—	—	T·16	—	—	—	—	—	—	—	—
Pulsatilla patens	Pt	32	0·25·75	—	—	T·<1	T·1	O·60	S·2	S·12	—	—	O·23	—	—	—
RHAMNACEAE																
Ceanothus herbaceus	Ce	18	6·94·0	—	—	—	—	T·<1	S·17	—	O·83	—	—	—	—	—
ROSACEAE																
Fragaria virginiana	Fv	11	0·100·0	—	—	—	—	—	T·1	—	F·50	—	—	—	O·49	—
Potentilla arguta	—	4	0·0·100	—	—	—	—	T·55	—	T·45	—	—	—	—	—	—
Prunus americana	Pa	7	74·26·0	T·24	—	—	T·<1	—	T·22	—	—	T·53	—	—	—	—
Rosa arkansana	Ra	55	31·50·19	O·43	S·6	T·1	T·<1	T·2	S·13	T·2	O·31	T·2	—	—	—	—
RUBIACEAE																
Galium circaezens	—	4	68·0·32	—	—	—	T·<1	—	T·2	—	T·9	—	—	—	—	T·89
Hedyotis nigricans	Hn	52	55·45·0	—	S·38	S·13	T·8	S·26	T·6	—	S·11	—	—	—	—	—
SALICACEAE																
Salix humilis	—	4	0·100·0	—	—	—	—	T·1	T·2	—	S·97	—	—	—	—	—
SANTALACEAE																
Comandra umbellata	Cl	75	41·13·47	—	T·<1	O·38	O·32	O·17	S·12	T·1	—	—	—	—	—	—
SAXIFRAGACEAE																
Heuchera richardsonii	Hc	12	0·100·0	—	—	—	—	T·12	T·11	T·19	S·58	—	—	—	—	—

Appendix Continued

SPECIES ( ) DENOTE PROBABLE SPECIES	S[a]	N[b]	RLA (%)[c]	ABUNDANCE OF SPECIES WITHIN COMMUNITY TYPES[d] MEAN ABUNDANCE INDEX[e]·RELATIVE COMMUNITY AFFINITY (%)[f]												
				MID-GRASS				TALLGRASS				WOODLAND/EDGE				
			S·C·N	BC	BM	DM	MG	TM	TG	TX	TE	SE	WE	RC	DE	BO
SCROPHULARIACEAE																
Agalinis aspera	Aa	15	30·31·39	—	—	T·68	T·16	T·14	T·2	—	—	—	—	—	—	—
Castilleja sessiliflora	Cs	19	0·100·0	—	—	T·13	T·25	T·60	T·2	—	—	—	—	—	—	—
Penstemon albidus	—	—	0·0·P	—	—	P	—	—	—	—	—	—	—	—	—	—
Penstemon cobaea	—	1	100·0·0	—	—	T·100	—	—	—	—	—	—	—	—	—	—
Penstemon grandiflorus	Pg	25	27·37·36	S·30	S·61	T·7	T·1	—	T·<1	—	—	—	—	—	—	—
SOLANACEAE																
Physalis virginiana	Ph	47	10·44·46	—	—	T·<1	T·<1	T·2	S·25	S·15	S·13	T·2	S·38	T·4	—	—
THYMELAEACEAE																
Thymelaea passerina	—	—	0·P·P	—	P	P	—	—	—	—	—	—	—	—	—	—
ULMACEAE																
Ulmus pumila	Up	5	0·100·0	—	—	—	—	T·<1	T·2	T·5	—	—	O·53	—	S·41	—
Ulmus rubra	Ur	57	13·47·40	—	—	—	T·<1	T·<1	T·1	S·1	F·19	O·11	O·10	—	C·52	O·5
VERBENACEAE																
Verbena stricta	Vs	44	17·49·34	—	T·3	T·9	T·2	T·2	T·10	S·63	T·9	T·3	—	—	—	—
VIOLACEAE																
Viola pedatifida	Vd	50	27·37·36	—	—	—	T·1	S·24	T·10	S·47	T·13	—	T·7	—	—	—
Viola pratincola	Vp	40	23·46·31	—	—	—	T·<1	T·2	T·1	S·16	T·<1	O·31	O·36	S·9	S·4	T·1
VITACEAE																
Vitis riparia	Vr	11	14·26·60	—	—	—	—	—	T·1	—	T·4	—	S·34	S·21	S·33	T·7
MONOCOTYLEDONS																
AGAVACEAE																
Yucca glauca	Yg	78	34·37·29	S·27	O·43	S·10	S·13	T·4	T·1	T·<1	T·<1	—	—	—	—	—
CYPERACEAE																
Carex blanda	Cb	24	5·62·32	—	—	—	T·<1	T·<1	—	T·1	T·2	S·9	O·42	S·7	O·32	S·6
Carex brevior	Cv	11	60·23·16	—	T·3	—	T·3	T·1	—	O·93	—	—	—	—	—	—
Carex heliophila	Ch	110	4·38·58	—	—	—	S·2	C·39	F·14	F·24	S·2	O·3	F·16	T·<1	T·<1	T·<1
IRIDACEAE																
Sisyrinchium campestre	Sc	132	30·35·35	—	—	S·4	O·22	O·47	S·11	S·14	—	T·2	T·1	—	—	—
ORCHIDACEAE																
Spiranthes (magnicamporum)	—	—	P·0·0	—	—	—	—	—	P	—	—	—	—	—	—	—
POACEAE																
Andropogon gerardii	Ag	182	37·35·28	—	F·6	S·<1	F·9	F·12	C·23	C·23	C·19	O·5	O·4	—	—	T·<1
Bouteloua (gracilis)	Bg	9	0·54·46	—	—	—	T·50	T·50	—	—	—	—	—	—	—	—
Bouteloua curtipendula	Bc	225	29·30·42	O·4	F·12	C·19	C·19	C·18	F·12	F·10	S·2	S·2	O·4	S·<1	—	—
Calamovilfa longifolia	—	2	37·63·0	—	T·30	T·70	—	—	—	—	—	—	—	—	—	—
Dichanthelium oligosanthes var. *scribnerianum*	Do	128	20·34·46	—	—	T·1	S·7	S·8	O·15	O·34	T·3	S·15	O·17	T·1	—	—
Dichanthelium oligosanthes var. *wilcoxianum*	Dw	78	0·50·50	—	T·1	T·2	T·8	O·80	T·2	T·1	—	—	T·6	—	—	—
Eragrostis spectabilis	—	4	0·100·0	—	—	—	—	T·100	—	—	—	—	—	—	—	—
Koeleria macrantha	Km	21	0·25·75	—	—	—	—	S·83	T·3	T·7	T·1	—	T·6	—	—	—
Muhlenbergia cuspidata	Mc	111	32·45·23	C·60	F·27	S·3	S·2	S·5	S·2	T·<1	T·<1	—	—	—	—	—
Panicum capillare	—	1	0·0·100	—	—	—	—	T·100	—	—	—	—	—	—	—	—
Poa pratensis	Pp	86	20·37·43	—	T·<1	—	T·<1	O·7	O·3	A·30	C·16	T·<1	C·29	S·1	F·11	O·3
Schizachyrium scoparium	Su	207	30·37·33	—	F·9	A·24	A·28	A·24	F·7	O·5	T·<1	S·1	O·2	T·<1	—	—
Setaria glauca	—	1	0·100·0	—	T·100	—	—	—	—	—	—	—	—	—	—	—
Setaria viridis	Sv	7	0·100·0	F·99	T·1	T·<1	—	—	—	—	—	—	—	—	—	—
Sorghastrum nutans	Sn	65	36·34·30	—	T·<1	T·<1	T·2	S·5	F·57	T·<1	O·30	T·2	S·4	—	—	—
Sporobolus asper	Sa	46	49·24·27	—	—	T·1	T·4	T·<1	S·32	O·34	S·8	S·19	T·2	—	—	—
Sporobolus cryptandrus	So	32	0·100·0	S·27	S·28	O·42	T·2	T·<1	—	—	—	—	—	—	—	—
Stipa spartea	Si	14	0·86·14	—	S·82	—	T·2	T·4	—	—	T·12	—	—	—	—	—

[a]Two letter code that identifies species in the species ordination (Fig. 2)

[b]Number of community samples in which the species was present (out of 245 possible)

[c]Relative Latitude Affinity by region: S (southern)—Fremont and Mills Counties; C (central)—Pottawattamie, Harrison, and Monona Counties; N (northern)—Woodbury and Plymouth Counties. Occurrence of species outside of sample plots is indicated with (P)

[d]Community types are grouped into three physiognomic classes. Symbols for community types are identified in Table 2. Occurrence of species outside of sample plots is indicated with (P). For species where N ≥ 5, boldface entries indicate the community type where species abundance was highest

[e]See Methods section for classification of mean abundance categories

[f]Relative Community Affinity is the proportion of species importance (combining abundance and constancy) accounted for by each community type