

Ecological Restoration

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Plant Communities of the Chicago Region

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Establishment Success of Native Bunchgrasses In California

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The Prairie-Wetland Vegetation Continuum in the Chicago Region of Northeastern Illinois

by Marlin Bowles and Michael Jones

ABSTRACT

We conducted a floristic ordination and gradient analysis of plant communities extending from prairie through graminoid-dominated wetlands in the Chicago region of northeastern Illinois. Data represented about 450 species from 103 stands sampled across a gradient of six soil moisture classes ranging from dry to hydric, and included sand, gravel, dolomite, and loam prairies as well as fen, sedge meadow, floating mat, marsh, and bog. As found in other Midwestern grassland studies, vegetation aligned most strongly along a soil moisture gradient with individualistic species distributions forming a hierarchical continuum, and lower species richness at the dry and wet extremes of the moisture gradient. Most species were infrequent, with about 70 percent occurring at less than 20-percent frequency and present in less than five communities. Species that were more frequent within communities were also more widespread among communities, fitting the niche-based model of species distribution. Moreover, less than 20 percent of all species sampled were significant indicators of soil moisture gradient classes, with most representing mesic and hydric habitats. Dominant prairie grasses extended from dry to wet habitats, merging with wetland species in graminoid fen, calcareous seep and sedge meadow habitats. Hydric habitat, represented by calcareous floating mat, marsh and bog, had fewer dominant prairie species and was dominated by a wetland flora. These results provide compositional and structural models for managing and restoring vegetation across the prairie-wetland vegetation gradient of the Chicago region.

Keywords: Chicago region flora, floristic ordination, gradient analysis, prairies, wetlands

The eastern tallgrass prairie and its associated wetlands are one of North America's most highly fragmented ecosystems (Robertson and Schwartz 1994, Samson and Knopf 1994). This vegetation constituted about 80 percent of the pre-European settlement landscape of the Chicago region of northeastern Illinois, covering about 1.6 million acres (647,000 hectares) (McBride and Bowles 2001). Today, less than 0.2 percent of this vegetation remains in high-quality condition (White 1978), and there is little specific information available on the extent to which it intergrades along an edaphic gradient ranging from dry to hydric. This information is

important because the great interest in managing and restoring tallgrass prairie and wetlands in the Chicago region (Betz 1986, Packard and Mutel 1997, Betz and others 2000) requires knowledge of how species are distributed across environmental gradients.

Soil moisture, as controlled by drainage, is considered the primary environmental factor affecting the distribution of prairie vegetation. Curtis (1959) used a compositional index based on indicator species for different drainage types to describe the distribution of Wisconsin prairie species along a one-dimensional soil moisture gradient ranging from dry to wet. Dix and Smeins (1967) also used soil moisture as the primary ecological gradient for a landscape-scale analysis of North Dakota prairie vegetation. However, soil texture, degree of internal drainage, and soil depth

also have important secondary effects on species distribution (Whitford 1958, Nelson and Anderson 1982). For example, White and Glenn-Lewin (1984) found a multidimensional relationship among Iowa prairie stands based on direct gradient analysis of species distribution in relation to soil drainage and textural differences. Faber-Langendoen and Maycock (1994) found a similar relationship across prairie vegetation gradients in Ontario. In Illinois, Corbett and Anderson (2001) also demonstrated that soil texture and topographic position interact with soil moisture to affect the distribution of prairie vegetation.

In addition to expected edaphic effects on vegetation, multiple models have been applied to the landscape scale distribution of prairie species. Using data from Betz and Lamp (1989), Collins and Glenn (1991)

demonstrated that regional prairie species distribution fits the niche-based species distribution model of Brown (1984). In this model, common species (species occurring at high frequencies within communities) also have broad habitat niches, occurring across multiple communities. Conversely, rare species that occur at low frequencies also tend to have more narrow niches, occurring across fewer communities. Plant species are also expected to have individualistic distributions that form a continuum across environmental gradients (Gleason 1926). Based on this model, plant communities can be described according to overlapping distributions of dominant species, although no species will have identical patterns (Curtis 1959). With a broad gradient, this pattern also may be nested and hierarchical (Collins and others 1993). A third model can be developed according to the expected distribution of species richness, which usually peaks at intermediate resource levels (Mittlebach and others 2001). In accordance, species richness in Midwest prairies has been found to be unimodal across a landscape soil moisture gradient, with lower richness in dry or wet habitat extremes (Curtis 1959, Bliss and Cox 1964, Dix and Smeins 1967, Crist and Glen-Lewin 1978).

In this paper, we use historic data to conduct a floristic gradient analysis in relation to soil moisture drainage classes and substrate types for prairie and graminoid wetland vegetation of the Chicago region of northeastern Illinois. We sought to determine how plant species and communities are distributed across a landscape soil moisture gradient, and to describe the ecological distribution of dominant prairie and graminoid wetland vegetation in the Chicago region. We also determined how species and species richness are distributed across this ecological gradient in relation to the niche-based, continuum and unimodal models, and the extent to which indicator species could be identified for differ-

ent habitats based on moisture gradient categories.

Study Area

The surficial geology of the Chicago region of Illinois represents Woodfordian-aged glacial material, which was deposited in the last 20,000 years. The northern, western, and southern portions of the region are primarily glacial drift represented as end moraines, till plains and outwash, while the east central part of the region occupies the former bed of glacial Lake Chicago, which formed about 14,000 years ago after the retreat of the last glacier (Willman 1971). Predominant substrates include fine-textured silt-loams and clay-loams developed from glacial till and lake bed deposits; sands in glacial outwash, lake plain deposits, and beach ridges; coarse-textured gravels in kames, eskers, and valley train deposits; and dolomite bedrock exposed along the major river valleys. Soil chemistry and fertility vary across these habitats (Fehrenbacher and others 1984). Fine-textured prairie soils tend to be neutral in pH, with about 10 percent organic matter. Sand soils are usually acidic with less organic content, but become alkaline near Lake Michigan, while gravel and dolomite soils are usually alkaline and calcareous but with low organic matter (Bowles and others 2005a). Wetlands range from acid to alkaline, depending upon groundwater characteristics, with up to 50 percent or more organic matter in bogs and fens and over 20,000 ppm calcium in strongly calcareous sites (Bowles and others 2005b).

The Chicago region is located along the northeastern boundary of the "prairie peninsula," a biogeographic zone of North America located at the east edge of the rain shadow of the Rocky Mountains (Transeau 1935). This eastern extension of prairie has cold winters and warm, humid summers that are characterized by unpredictable precipita-

tion and occasionally severe summer drought (Weaver 1954). These periodic droughts acted in concert with frequent lightning- and Indian-set prairie fires to maintain tallgrass prairie and savanna in a region in which annual rainfall is capable of supporting forest development (Gleason 1913, Curtis 1959, Anderson 1990, Anderson and Bowles 1999).

Methods

To ensure that our analyses represented naturally occurring vegetation that had not been substantially altered by human intervention, we used data collected by the Illinois Natural Areas Inventory (INAI) in 1976 (White 1978). This statewide survey sampled almost 100 groundlayer vegetation transects representing high-quality prairie, savanna, and graminoid wetland natural areas identified in the Chicago region of Illinois (Figure 1). These remnants tend to be distributed either by chance or by local occurrences of specialized habitats, such as sand-and-gravel deposits or wetlands. The natural quality of each site was graded in the INAI according to its stage of plant succession following human-caused disturbance. In this system, Grade A vegetation was defined as stable or undisturbed, Grade B as late-successional following human disturbance, Grade C as heavily disturbed and mid-successional, and Grade D as very heavily disturbed early-successional (White 1978). Some ecologists would assign late-, mid-, and early successional to Grades A, B, and C, respectively. The INAI used a natural community classification system based on *xeric*, *dry*, *dry-mesic*, *mesic*, *wet-mesic*, *wet*, and *hydric* soil-drainage classes defined by the U.S. Department of Agriculture (White and Madany 1981), a method similar to that used by Dix and Smeins (1967). In addition, loam, sand, gravel, and dolomite soil substrates were used in combination with drainage modifiers to further define communities, such as "dry-mesic sand

prairie.” Loam, the finest texture, was considered typical and was not used as a modifier, such as a “dry-mesic (silt-, clay-, or sand-loam) prairie.” The Chicago region INAI data also included a single sand shrub prairie and six black oak (*Quercus velutina*) sand savannas, which were defined by having 10-80 percent tree canopy cover. We included the shrub prairie and sand savanna data sets in our analysis as well as wetland data sets collected from sedge meadow, graminoid fen, calcareous seep, calcareous floating mat, marsh, and graminoid bog vegetation. Nomenclature for scientific names follows *Plants of the Chicago Region* (Swink and Wilhelm 1994). Common names follow USDA, NRCS (2006).

The INAI surveyors usually sampled Grade A or B sites, using 20 to 30 circular 0.25-m² plots randomly distributed along transects within natural community types. We re-sampled the Chicago region sites in 2001-2002 by re-surveying original transect locations that had been mapped on 1:7,920-scale aerial photos. Our sampling indicated that many vegetation types had deteriorated with time due to fire exclusion (Bowles and Jones 2004, Bowles and Jones 2006a), but our data had more precise identification of difficult graminoid species. As a result, we used the 1976 data as the reference for undisturbed composition, and our data to correct for dominant grasses and sedges that were identified to the genus level in 1976. We also added recent data from a single foredune transect, as well as from six transects in INAI wet prairie stands that were not originally sampled, resulting in 103 data sets used for this study (Table 1). Each sampling data set was organized into a species by plot matrix from which we calculated species frequencies. These frequencies were then averaged across the replicate data sets for each community type and entered in a new matrix used for ordination and classification analysis. Seven rare habitat types (foredune, dune, dry

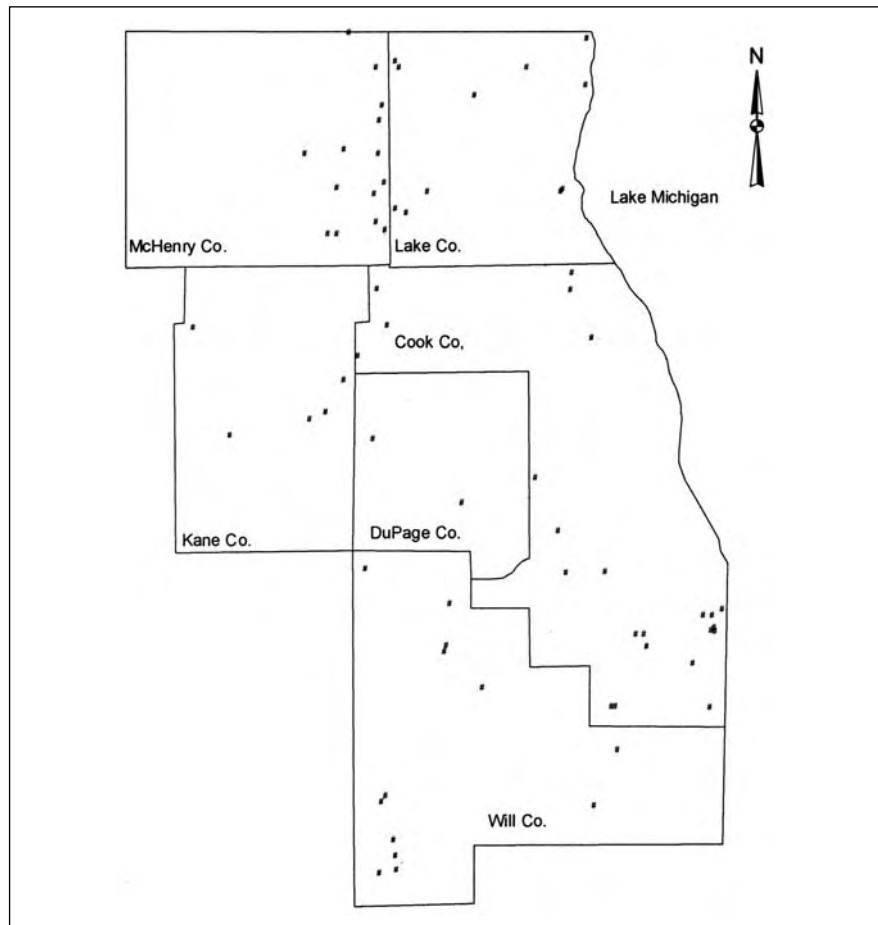


Figure 1. Locations of Chicago region prairie, savanna, and wetland natural areas from which Illinois Natural Areas Inventory sampling data were analyzed. Some sites represent multiple communities.

sand prairie, dry sand savanna, sand shrub prairie, graminoid bog and calcareous seep) were represented by single data sets in this average matrix. Consequently, they would tend to have comparatively low total richness and unreplicated estimates of average species frequencies—factors that could affect subsequent analyses.

We ordinated community types using Non-metric Multi-dimensional Scaling (NMS) with mean species frequencies as metrics and a Sorenson (Bray-Curtis) distance measure on PC-ORD (McCune and Mefford 1997). They were also clustered on PC-ORD using Ward’s method with a Relative Euclidean distance measure. The soil moisture classes assigned to each community, as well as substrate types, allowed a direct gradient analysis of the ordination and avoided the circularity that otherwise would have resulted from inter-

preting species composition from a species-based classification. To assess species distribution across the moisture gradient, we averaged mean species frequencies from each community within each of the six moisture classes. Communities were assigned to these classes based on their alignment on the first ordination axis. We combined sand shrub prairie data with dry-mesic prairie data. Graminoid fen and calcareous seep data were averaged with wet-mesic prairie data, while sedge meadow data were averaged with wet prairie data, and graminoid bog, marsh and calcareous floating mat data were averaged as hydric data. We also used Indicator Species Analysis (Dufrene and Legendre 1997) on PC-ORD to determine abundance of indicator species for different soil moisture classes, with a Monte Carlo test of significance at $p < 0.05$ with 1,000 runs.

Table 1. Number and grade of Illinois Natural Areas Inventory plant community transects analyzed for the Chicago region of northeastern Illinois. Zeros (0) indicate that sampling data were unavailable. Data collected in 1976, or in 2001 as indicated by asterisks (*).

INAI Community classification		A	B	Total
PRIMARY				
Lakeshore	Foredune	1*	0	1
	Dune	1	0	1
PRAIRIE				
Loam prairie	Dry-mesic	4	3	7
	Mesic	7	7	14
	Wet-mesic	0	2	2
	Wet	0	2*	2
Sand prairie	Dry	1	0	1
	Dry-mesic	2	1	3
	Mesic	2	7	9
	Wet-mesic	2	3	5
	Wet	2*	1*	3
Gravel prairie	Dry	2	3	5
	Dry-mesic	1	2	3
	Mesic	2	1	3
Dolomite prairie	Wet	0	1*	1
	Dry-mesic	1	1	2
	Wet-mesic	0	3	3
Shrub prairie	Sand	0	1	1
SAVANNA				
Sand savanna	Dry	1	0	1
	Dry-mesic	2	3	5
WETLAND				
Marsh		1	2	3
Graminoid bog		1	0	1
Fen	Graminoid fen	8	3	11
	Calcareous floating mat	4	0	4
	Sedge meadow	6	5	11
Seep & spring	Calcareous seep	1	0	1
TOTAL		52	51	103

We took total species richness from each original transect data set to avoid inflated values caused by pooling replicate transects. This measure represents an estimate of species richness based on the species accumulation curve for each transect. There was no significant variation ($F = 0.74$, $p = 0.592$) in sample size among soil moisture classes in this study ($\bar{x} = 21.87 \pm 0.41$ se plots/transect), which would avoid bias in this estimate of richness. From the same data, we also calculated the average number of native species sampled per 0.25-m² plot, which is a scale-dependent measure of α diversity or species density. We then used ANOVA in a general linear model to

test whether these metrics differed across the INAI soil moisture gradient classes described above, and also whether these values differed between Grade A and B data sets. We used two approaches to assess whether species distribution patterns fit the niche-based model of Brown (1984). We first used linear regression to test whether the frequencies of species averaged across all communities in which they occurred were dependent upon their niche breadth (the number of communities they occupied). We conducted this analysis using all communities, as well as a subset from which unreplicated rare communities had been eliminated.

In the second analysis, we tested whether rare species had more narrow niche breadths than common species. For this test, we defined rare species as having less than 10 percent average frequency ($n = 282$ species) and common species as having greater than 20 percent frequency ($n = 142$). We then calculated species niche-breadths for these groups as the mean number of communities occupied. We used these arbitrary thresholds for rare and common, because average plot frequency ($\bar{x} = 11.5\% \pm 15.4$ std. dev.) for all species fell between these values. We also compared niche breadth and frequency between graminoid and woody species groups in both rare and common categories. Woody vegetation occurrences were too infrequent for a statistical comparison.

Results and Discussion

Community Gradients

The first and second NMS ordination axes contained more information than expected by chance, with the first axis accounting for more than three times as much variation and corresponding to the INAI soil moisture categories (Figure 2). The dry extreme of the ordination consisted of vegetation with low first axis scores. Fore-dune, dry sand prairie, and dune vegetation had the lowest scores, while dry sand savanna and dry gravel prairie tended to separate by higher first axis scores and lower second axis scores. Hydric vegetation, represented by calcareous floating mat, marsh and graminoid bog, had the highest first axis scores, and also separated from sedge meadow and wet prairie vegetation by higher second axis scores. Mesic and wet-mesic prairies were centrally located, with intermediate first axis scores, while dry-mesic prairies and dry-mesic savanna had lower first axis scores. Calcareous seep and sand shrub prairie had extremely high and low second axis scores, respectively.

Ward's cluster analysis corresponded closely to the NMS ordination (Figure 2). With about 50 percent of the in-

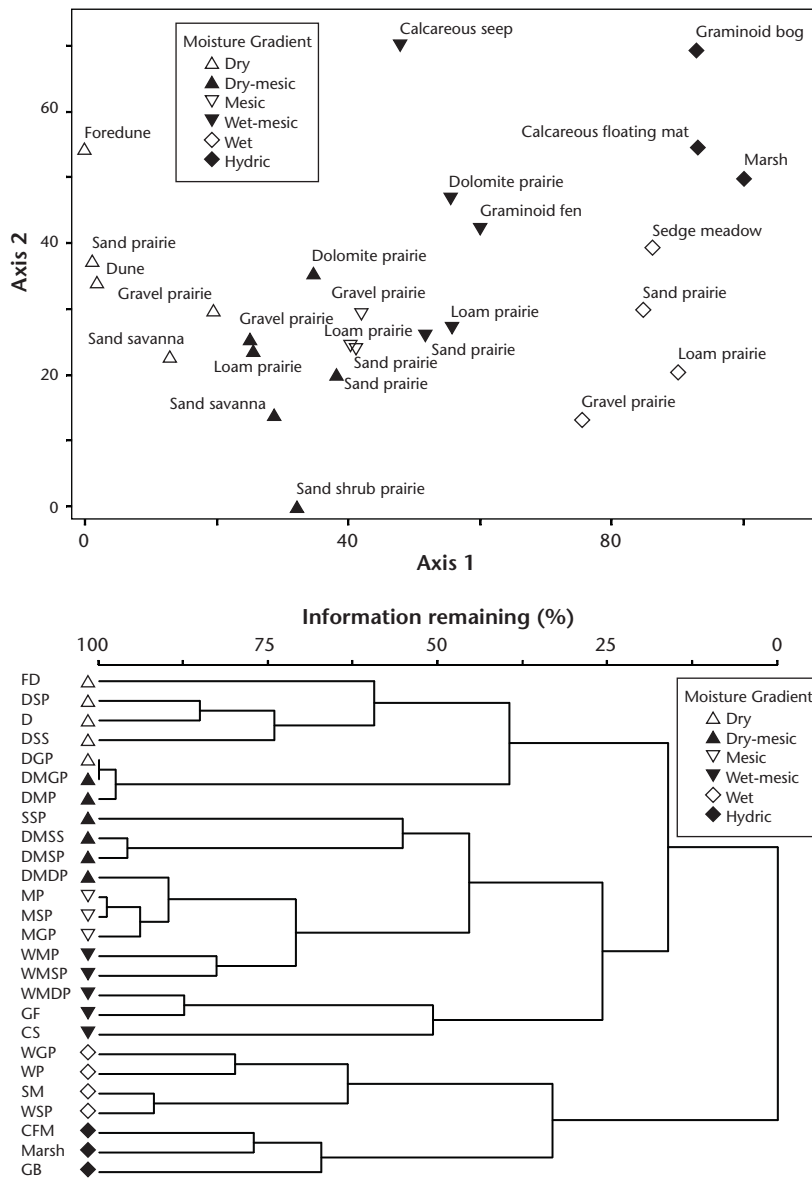


Figure 2. Non-metric, Multi-dimensional Scaling (NMS) ordination (upper) and Flexible Beta Cluster Analysis (lower) of Chicago region prairie and wetland vegetation. NMS: Less than 5 percent of 20 random runs with stress less than observed stress for a two-dimensional solution; cumulative r^2 between ordination distances and original distances = 0.611 (Axis I), = 0.771 (Axis II). Flexible Beta: Less than 5-percent chaining.

formation retained, six cluster groups had 77 percent correspondence to our initial assignment of communities into six INAI drainage classes. With about 25 percent information remaining, two cluster groups corresponded to wetland and upland vegetation categories. Our hydric and wet prairie drainage classes formed separate groups in the wetland category. Among the upland cluster groups, one included five of the six communities assigned to the dry drainage class. Our dry-mesic and wet-mesic communities were more diver-

gent between multiple cluster groups. Subgroups representing graminoid fen, calcareous seep, and wet dolomite prairie as well as graminoid bog, calcareous floating mat, and marsh also corresponded to their separations on the second NMS axis. The INAI classified calcareous floating mat differently—as a type of fen.

Ordination of Chicago region prairie and wetland plant communities suggests that a soil moisture gradient is the strongest environmental factor affecting the distribution of this

vegetation, which supports the one-dimensional species distribution model of Curtis (1959). The clustering of different substrates within similar moisture classes shows the overriding importance of drainage. However, the soil moisture gradient is also linked with substrate and topographic effects. Dry sites are primarily on sand or gravel substrates, which are easily drained, especially on slopes. Meanwhile, hydric sites usually occupy low landscape positions and tend to be strongly organic because water saturation retards decomposition. Vegetation alignment on the second NMS ordination axis could reflect substrate effects, such as greater alkalinity and calcium content in fen, dolomite prairie and calcareous seep vegetation (Bowles and others 2005b). Other secondary effects are less clear, but could include differences in organic and nutrient content among sand, gravel and loam soils (Bowles and others 2005a). Such differences would support contentions that substrate effects are important in understanding multivariate vegetation patterns (Whitford 1958, Nelson and Anderson 1982, Faber-Langendoen and Maycock 1994, White and Glenn-Lewin 1984, Corbett and Anderson 2001). Because our data represent drainage and substrate classes that lack exact environmental measures, specific effects are unknown. However, our data appear to be most strongly influenced by drainage as they represent broad hydrological gradients within different substrate types—effects that are rarely detected in other vegetation studies.

Species Distribution

Species Richness and Spatial Abundance

More than 450 species were sampled across all communities. Graminoid species represented 22 percent of these species, forbs 68 percent, and woody species 10 percent. As found by Curtis (1959) and by Dix and Smeins (1967), species richness was lowest at

Table 2. Niche differentiation of common and rare species in high-quality prairie and graminoid wetland vegetation in the Chicago region of northeastern Illinois. Niche width = number of communities occupied, frequency = average mean frequency across occupied communities. Data = average + std. error.

Metric	Category		Mann-Whitney Z	Probability
All species	common (n = 142)	rare (n = 230)		
Niche width	6.54 + 0.37	2.10 + 0.11	12.1254	< 0.001
Common species	graminoid (n = 35)	forb (n = 97)		
Niche width	6.11 + 0.90	6.93 + 0.39	-1.9119	0.0559
Frequency	26.38 + 3.36	16.99 + 0.93	3.3480	0.0009
Rare species	graminoid (n = 51)	forb (n = 153)		
Niche width	2.08 + 0.23	2.12 + 0.13	-0.1586	0.8741
Frequency	3.02 + 0.32	2.61 + 0.14	0.8358	0.4032

the dry and wet extremes of the moisture gradient, with average total richness exceeding 40 species in mesic and wet-mesic habitat (Figure 3). Mean plot species richness corresponded similarly ($F = 8.99$, $p < 0.001$), with highest values in mesic and wet-mesic habitats, which exceeded 10 species per 0.25 m². As a result, total richness and plot species richness were significantly correlated ($r = 0.556$, $p < 0.001$). This tendency for greater species richness in mesic habitat is apparently regulated by multiple factors, including levels of biomass, nutrients, and competition as well as the pool of species available to colonize this habitat (Grace 2001). Grade A prairies had higher total richness ($F = 4.91$, $p = 0.029$) and higher plot species richness ($F = 12.0$, $p < 0.001$) than Grade B prairies. This indicates that species richness can be an important factor in ranking vegetation quality (Bowles and Jones 2006b).

Most species were rare at the landscape level, with 33 percent occurring in single communities and 70 percent found in less than five communities (Figure 4). Most species were also infrequent within communities, with 50 percent occurring at less than 10-percent average plot frequency and 70 percent occurring at 20 percent or less average plot frequency. There was a significant positive correlation ($p < 0.001$, $r^2 = 0.054$) between average species frequencies and their

niche breadth (measured by the number of communities occupied) across all communities and a stronger correlation ($p < 0.001$, $r^2 = 0.182$) across communities represented by multiple replicates.

Niche differences also occurred between rare and common vegetation (Table 2). Among all species, common species had greater niche breadth than rare species. However, neither common nor rare species (both graminoids and forbs) showed any difference in terms of niche width. Thus, few species were widely distributed, and species that were more frequent within communities had broader niche distributions, fitting the niche-based regional species distribution model of Brown (1984). Collins and Glenn (1991), using data from Betz and Lamp (1989), verified this same pattern. However, because their site data was based on species lists, within-habitat species frequencies were not available to test whether widespread species also were more frequent within habitats.) Graminoid species represented only 25 percent of all common species, but averaged greater plot frequency than forbs (Table 2). This indicates that prairies and graminoid wetlands tend to be dominated by comparatively few graminoid species that occur at relatively high frequencies, but that species richness is dependent upon a larger number of less-frequent forbs.

Shrubs were the most infrequent components of these communities, with only 46 species sampled, 5.38 (± 0.87 se) species occurrences per community—an overall average frequency of 10.24 percent (± 2.51 se) and an average niche width of 3.08 (± 0.37 se).

Species Distribution in Relation to Soil Moisture Classes

Dominant graminoid and forb species showed strong individualistic but overlapping distribution patterns along the soil moisture gradient (Figure 5). Individual species distributions by plant community are in the appendices. These unique distributions along a moisture gradient are consistent with Curtis's findings (1959) that species form a vegetational continuum. This pattern is most clear with forbs. Graminoid species tend to form a hierarchical nested continuum, which would be expected when dominant species, such as grasses, are present (Collins and others 1993). Our lack of data from intermediate drainage positions (midway between dry and dry-mesic) as well as the potential for use of dominant grasses to help identify moisture classes may affect this distribution. Nevertheless, dominant prairie grasses are well known as indicators of soil drainage characteristics because they are organized by β -level competition (Parrish and Bazzaz 1979). Our data indicate that dry to dry-mesic habitats tend to be dominated by graminoid species with broad niches, while wet-mesic to hydric habitats tend to have dominants with more narrow niches. Upland sites are also dominated by prairie grasses, while sedges and grasses dominate wetlands.

Indicator Species Analysis (Dufrene and Legendre 1997) produced a total of 89 species (less than 20 percent of all species) that were significant indicators (at $p \leq 0.05$) of one of the six moisture gradient categories. These species were also unevenly distributed

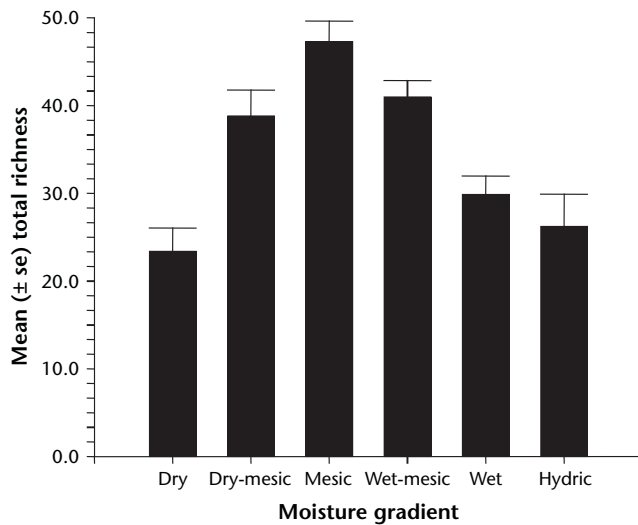


Figure 3. Unimodal distribution of species richness across a prairie-wetland soil-moisture gradient in the Chicago region of northeastern Illinois. ANOVA: $F = 12.29$, $p < 0.001$.

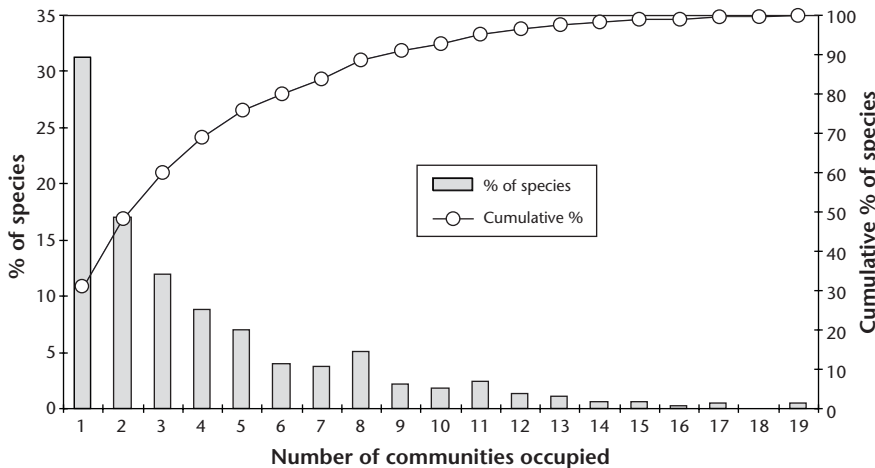


Figure 4. Proportional species abundance in relation to number of communities among high-quality prairie and wetland plant communities in the Chicago region of northeastern Illinois.

($X^2 = 56.97$, $p < 0.001$) with 66 percent representing hydric or mesic habitats, 26 percent representing wet or wet-mesic habitats, and 8 percent representing dry or dry-mesic habitats. More than half (54 percent) of the indicator species were common species and were primarily forbs. As indicated by Corbett and Anderson (2001), the tendency for dominant species to be widespread prevents them from being good indicators of specific habitats. The rarity of most species also precludes them from being sampled or detected as potential indicators, a condition observed for modal species by Curtis (1959).

Vegetation Types

Dry Habitats: Fore-dune, Dune, Prairie, and Savanna

Dry habitats are restricted to somewhat excessively drained gravel and sand substrates, with sand habitats occurring primarily along Lake Michigan. Little bluestem (*Schizachryium scoparium*) was dominant or co-dominant across all dry habitats. However, Indiangrass (*Sorghastrum nutans*) and needlegrass (*Stipa spartea*) were abundant, and absent only from dunes. Other dominant grasses were more restricted to specific substrates. These included American beachgrass (*Ammophila breviligulata*) on fore-dune habitat, prairie sandreed (*Cal-*

movilfa longifolia) in dry sand prairies, and Junegrass (*Koeleria cristata*) on sand dunes. Dry gravel prairies differed by having prairie dropseed (*Sporobolus heterolepis*) as a co-dominant grass, with side-oats grama (*Bouteloua curtipendula*) an important secondary species. Dry sand savannas had needlegrass as a co-dominant. Pennsylvania sedge (*Carex pennsylvanica*) also reached its greatest abundance in dry-sand savanna.

No single forb species was most abundant across all dry habitats, although oldfield goldenrod (*Solidago nemoralis*) was present at comparatively high frequencies throughout. Leading forbs were oldfield goldenrod and sage (*Artemisia caudata*) on fore-dunes, lance-leaved coreopsis (*Coreopsis lanceolata*) and sage in dry sand prairie, rough blazingstar (*Liatris aspera*) and stichwort (*Arenaria stricta*) on dunes, western sunflower (*Helianthus occidentalis*) and flowering spurge (*Euphorbia corollata*) in dry sand savanna, and purple prairie clover (*Petalostemum purpureum*) and smooth blue aster (*Aster laevis*) in dry gravel prairie. Shrubs were more restricted in distribution, and were not sampled on fore-dunes. The trailing shrubs, kinnikinnick (*Arctostaphylos uva-ursi*) and horizontal juniper (*Juniperus horizontalis*), were dominant and co-dominant on dune habitats. Early wild rose (*Rosa blanda*) was the most abundant shrub in dry sand prairie. Carolina rose (*Rosa carolina*) was the leading shrub in dry sand savanna, occurring with kinnikinnick and black oak (*Quercus velutina*), and in dry gravel prairie with leadplant (*Amorpha canescens*). Some areas of the Lake Michigan dunes had an open canopy of white pine (*Pinus strobus*) in the early 1900s (Pepoon 1927), probably in association with trailing shrubs, which might have allowed for their classification as a pine forest or pine barrens. The occurrence of black oak in groundlayer vegetation in sand savanna may represent post-fire sprouting from tree bases, as these

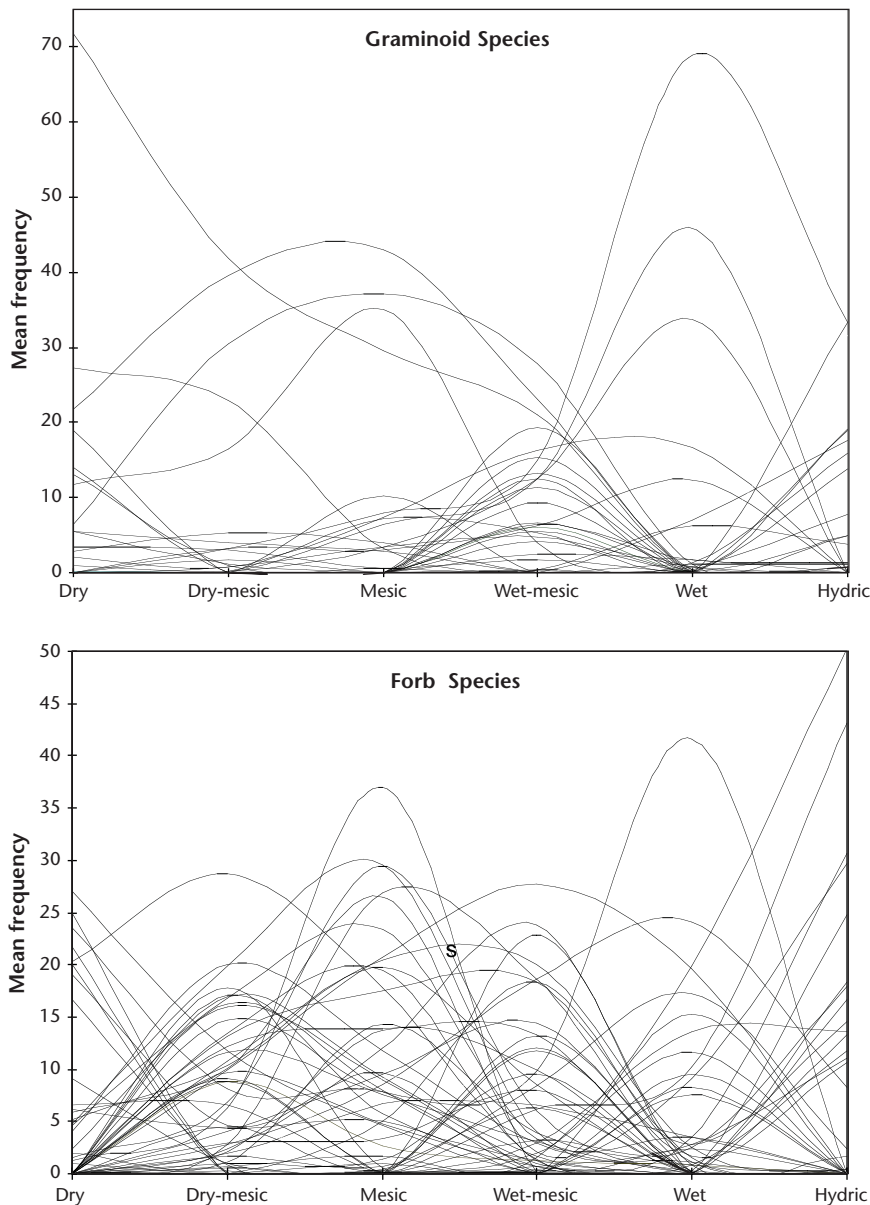


Figure 5. Frequencies of dominant graminoid (greater than 15 percent frequency) and forb (greater than 30 percent frequency) species across a prairie-wetland soil-moisture gradient in the Chicago region of northeastern Illinois. See Appendices for species frequency by community.

sites had high fire frequencies at the time of the INAI.

Dry-mesic Habitats: Prairie and Savanna

Dry-mesic habitats occur across a wide range of well-drained substrates, and consequently they support many different dominant species. Little bluestem and Indiangrass were dominant grasses across most habitats, with greater abundance of prairie dropseed and needlegrass in both gravel and loam prairies. Big bluestem (*Andro-*

pogon gerardii) was dominant in sand shrub prairie and present in lower frequencies in other communities. Flowering spurge, bee balm (*Monarda fistulosa*) and heath aster (*Aster ericoides*) were the most widespread abundant forbs, but neither was most frequent in more than two habitats. Spiderwort (*Tradescantia ohiensis*) was the dominant forb in sand prairie and sand savanna, followed by sky-blue aster (*Aster azureus*) in sand prairie and arrow-leaved violet (*Viola sagittata*) and woodland sunflower (*Helianthus divaricatus*) in savanna.

Flowering spurge, bee balm, and cylindrical blazingstar (*Liatris cylindracea*) were dominant forbs in gravel prairie, heath aster and bee balm in dolomite prairie, and flowering spurge and heath aster in loam prairie. In sand shrub prairie, ashy sunflower (*Helianthus mollis*) and smooth Solomon's seal (*Polygonatum canaliculatum*) were the most frequent forbs. Leadplant and Carolina rose were the most common shrubs in most dry-mesic habitats, with New Jersey tea (*Ceanothus americanus*) reaching secondary abundance in sand prairie. Stepplebush (*Spiraea tomentosa*) and blackberry (*Rubus setosus*) were the dominant woody species in sand shrub prairie. The blueberries, *Vaccinium angustifolium* and *V. pallidum*, were restricted to sand savanna, possibly due to their tolerance of acid sand soils as well as the partial shade in these communities.

Mesic Prairie Habitats

Mesic prairie vegetation occupies moderately well-drained habitats. Big bluestem, Indiangrass, and prairie dropseed were the most widespread, dominant grasses in mesic prairie habitats, although prairie dropseed tended to be less abundant in sand prairies. Little bluestem was subdominant in these habitats. No forb species were most important across all mesic habitats. Heath aster was the dominant forb in mesic loam prairie, followed in abundance by nodding wild onion (*Allium cernuum*), prairie dock (*Silphium terebinthenaceum*), and yellow coneflower (*Ratibida pinnata*). Virginia mountain mint (*Pycnanthemum virginianum*) was the most frequent forb in mesic sand prairie, followed in abundance by heath aster, nodding wild onion, and starry false Solomon's seal (*Smilacina stellata*) were dominant forbs in mesic gravel prairie, with secondary abundance of yellow coneflower. Carolina rose was the most abundant shrub in all mesic habitats. Gray dogwood (*Cornus racemosa*) and leadplant were

important secondary shrubs in loam and gravel prairie, while bristly dewberry (*Rubus hispidus*) was also important in mesic sand prairie.

Wet-mesic Habitats: Prairie, Calcareous Seep, and Graminoid Fen

Wet-mesic prairie, seep, and fen communities are transitional between wet prairie and wetland habitats due to their imperfectly or somewhat poorly drained conditions. Dolomite prairie, seep and fen habitats are also strongly calcareous. As a result, wet-mesic habitats support both prairie and wetland species, as well as calcicolous species. The prairie grasses, little bluestem and Indiangrass, were abundant across all habitats, reaching subdominance in sand prairie. Big bluestem was absent only from seep habitat, and was dominant in graminoid fen and co-dominant in loam prairie. The wetland species—wooly sedge (*Carex pellita*) and prairie cordgrass (*Spartina pectinata*)—dominated loam prairie, while bluejoint grass (*Calamagrostis canadensis*) was the leading dominant in sand prairie. Hayden's sedge (*Carex haydenii*) and tufted hairgrass (*Deschampsia cespitosa*) dominated dolomite prairie. Smallhead rush (*Juncus brachycephalus*) dominated seep habitat with secondary dominance by needle beaksedge (*Rhynchospora capillacea*) and Hayden's sedge. Spiked mulhy (*Muhlenbergia glomerata*) and dioecious sedge (*Carex sterilis*) were co-dominant in graminoid fen.

Among forbs, Virginia mountain mint and balsam ragwort (*Senecio pauperculus*) were dominant in wet-mesic sand prairie, prairie dock and wild strawberry (*Fragaria virginiana*) in loam prairie, and Ohio goldenrod (*Solidago ohioensis*) and Riddell's goldenrod (*Solidago riddellii*) in dolomite prairie. In graminoid fen, Ohio goldenrod and Virginia mountain mint were the most frequent forbs. The most abundant forbs in calcareous seep vegetation were Kalm's lobelia (*Lobelia kalmii*) and bog goldenrod (*Solidago uliginosa*), although prairie dock was not infre-

quent. There were few abundant shrubs in wet-mesic habitats. Gray dogwood was the most abundant shrub in loam prairie, but was less frequent than shrubby cinquefoil (*Potentilla fruticosa*) in graminoid fen and calcareous seep habitat. Bristly dewberry was the leading shrub in wet-mesic sand prairie, while bayberry willow (*Salix glaucophylloides*) was the most frequent shrub in dolomite prairie.

Wet Habitats: Prairie and Sedge Meadow

Wet prairie and sedge meadow vegetation occupy poorly drained habitats, and had strong similarity among their dominant graminoid species. Bluejoint grass was a leading dominant in all wet prairies and secondary to upright sedge (*Carex stricta*) in sedge meadows. Woolly sedge and prairie cordgrass were co-dominant in wet prairies, but were absent or infrequent in sedge meadows. Only hedge false bindweed (*Convolvulus sepium*) was a co-dominant forb in both habitats. Eastern marsh fern (*Dryopteris thelypteris*) and northern bugleweed (*Lycopus uniflorus*) were the most frequent forbs in wet sand prairie, while large goldenrod (*Solidago gigantea*), hedge false bindweed, and stiff marsh bedstraw (*Galium obtusum*) were dominant forbs in wet gravel prairie. White-panicle aster (*Aster simplex*) and American bugleweed (*Lycopus americanus*) were most frequent in wet prairie. Virginia mountain mint was the leading forb in sedge meadow, followed by spotted Joe-Pye weed (*Eupatorium maculatum*), Virginia water horehound (*Lycopus virginicus*), and eastern marsh fern. Shrubs were infrequent, with sandbar willow (*Salix interior*) most important in wet prairie and sageleaf willow (*Salix candida*) in sedge meadow.

Hydric Habitats: Marsh, Floating Mat and Bog

Hydric habitats are very poorly drained, with the water table at or

above the surface the greater amount of the time. Marsh vegetation shared only a single dominant species with prairie vegetation—bluejoint grass. Co-dominant graminoid species in marshes were hairy sedge (*Carex lacustris*), cattail (*Typha latifolia*), narrow-leaved cattail (*T. angustifolia*), and woollyfruit sedge (*Carex lasiocarpa*). The most abundant marsh forbs were skullcap (*Scutellaria epilobiifolia*), Virginia water horehound, and tufted loosestrife (*Lysimachia thyrsoiflora*). Red-osier dogwood (*Cornus stolonifera*) was the only frequent shrub in marsh vegetation. In calcareous floating mat vegetation, woollyfruit sedge and bluejoint grass were the dominant graminoid species, while softstem bulrush (*Scirpus validus*) and water sedge (*Carex aquatilis*) were also abundant. Virginia water horehound, tufted loosestrife, northern bog aster (*Aster borealis*) and eastern marsh fern were the most abundant forbs, while bog willow (*Salix pedicellaris*), white meadowsweet (*Spiraea alba*), and sageleaf willow were dominant shrubs.

Graminoid bog vegetation had the most distinctive assemblage of species among all vegetation types and is known from only a single site. The dominant graminoid species was tall cottongrass (*Eriophorum angustifolium*), with minor representation of spiked muhly and bluejoint grass. Eastern marsh fern was the dominant forb, while pitcherplant (*Sarracenia purpurea*), Virginia water horehound, and roundleaf sundew (*Drosera rotundifolia*) were also abundant. Bog willow and bog birch (*Betula pumila*) were the most frequent shrubs.

Summary and Conclusions

Our ordination indicates that soil drainage is the primary environmental factor affecting the distribution of prairie- and graminoid-dominated wetland plant communities in the Chicago region. This vegetation supports multiple models that have been demonstrated in other studies of

prairie vegetation. As established by Curtis (1959), plant species formed an individualistic distribution comprising a continuum. Graminoid species also formed a nested hierarchical continuum, a pattern expected for dominant species (Collins and others 1993). The overlapping distributions of these species allow characterization of communities based on their compositional differences across differing substrate and moisture classes. Common graminoid and forb species were also more abundant among communities than rare species, supporting the niche-based regional species distribution model of Brown (1984).

Species richness was greatest at the midpoint of the soil moisture gradient, which apparently represents optimum resources for a greater pool of species available to colonize these intermediate habitats. Most species were rare within and among communities, with less than 20% of all species significant indicators of moisture gradient categories. These species were not evenly distributed, with greater abundance in hydric and mesic habitats.

Species that are commonly thought of as comprising prairie vegetation occurred across the entire dry to hydric soil moisture gradient, but were better represented in dry than in wet or hydric habitats. Prairie grasses also appear to have broader niches in upland sites than dominant grasses or sedges in wetlands. Little bluestem was the dominant grass in dry and dry-mesic habitats, and was less abundant in mesic and wet-mesic habitats. Needlegrass, Junegrass, and side-oats grama were most abundant in drier habitats. Indiangrass, big bluestem, and prairie dropseed were the most abundant grasses in mesic habitats, and were replaced by increasing abundances of bluejoint grass and prairie cordgrass in wet-mesic and wet habitats. These grasses, as well as some prairie forbs also extended into sedge meadow and graminoid fen, where they associate with wetland and calci-

colous sedge and grass species. However, only bluejoint grass continued as an important grass in hydric habitats. Although some sedge species characterized upland habitats, many tended to become more abundant than grasses primarily in lower points of the soil-moisture gradient. These species include upright sedge, Hayden's sedge, and woolly sedge in wet-mesic to wet habitats, hairy sedge and woollyfruit sedge in wet habitats, and water sedge in hydric habitats.

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Marlin Bowles is a plant conservation biologist at The Morton Arboretum, Route 53, Lisle, IL 60532; mbowles@mortonarb.org.

Michael Jones is a botanist at Christopher B. Burke Engineering, Ltd., Rosemont, IL 60018.
