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

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## 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% occurring at less than 20% 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% 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

## Introduction

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% of the pre-European settlement landscape of the Chicago region of northeastern Illinois, covering about 1,598,090 acres (647,000 hectares) (e.g., McBride and Bowles 2001). Today, less than 0.2% 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 impor-

tant 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 (i.e., 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 based on overlapping distributions of dominant species, but 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 based on 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).

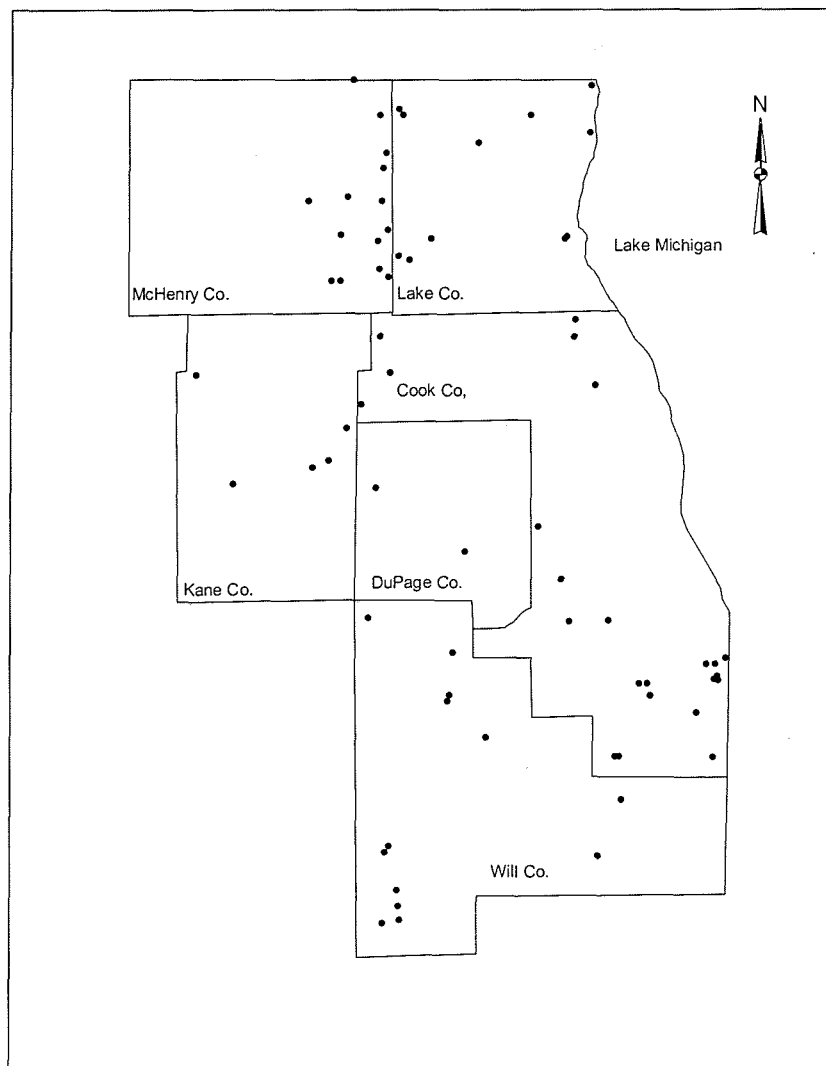
In this paper, we use historic data to conduct a floristic gradient analysis in relation to soil moisture drainage classes and substrate types for prairie and graminoid wetland vegetation of the Chicago region of northeastern Illinois. We sought to determine how plant species and communities are distributed 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 different 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, formed about 14,000 years ago after the retreat of the last glacier (Willman 1971). Predominant substrates include fine-textured silt- 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% organic matter; sand soils are usually acidic with less organic content, but become alkaline near Lake Michigan; 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% 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 precipitation 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 where annual rainfall is capable of supporting forest development (Gleason 1913, Curtis 1959, Anderson 1990, Anderson and Bowles 1999).



**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 plant communities.

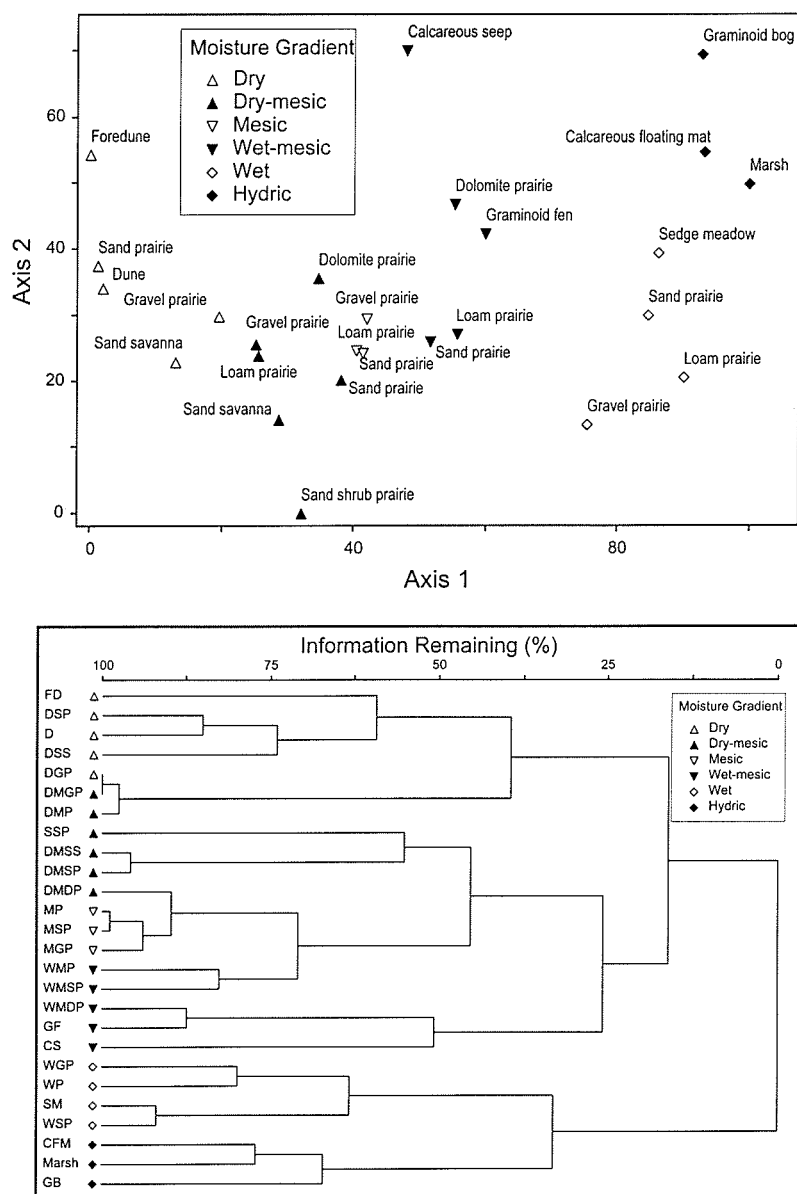
## Methods

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 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 by the INAI based on 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% 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

**Table 1.** Number and grade of INAI 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
<b>PRIMARY</b>				
Lakeshore	Foredune	1*	0	1
	Dune	1	0	1
<b>PRAIRIE</b>				
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
Gravel prairie	Wet	2*	1*	3
	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
<b>SAVANNA</b>				
Sand savanna	Dry	1	0	1
	Dry-mesic	2	3	5
<b>WETLAND</b>				
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
<b>TOTAL</b>		<b>52</b>	<b>51</b>	<b>103</b>



**Figure 2.** Non Metric Multi-dimensional Scaling ordination (upper) and Ward's Cluster Analysis (lower) of Chicago region prairie and wetland vegetation. NMS: < 5 % of 20 random runs with stress < observed stress for a two-dimensional solution; cumulative  $r^2$  between ordination distances and original distances = 0.611 (Axis I), 0.771 (Axis II). Cluster analysis: < 5 % chaining.

graminoid bog vegetation. Nomenclature follows *Plants of the Chicago Region* (Swink and Wilhelm 1994).

The INAI usually sampled Grade A or B sites, using 20 to 30 circular 0.25-m<sup>2</sup> plots randomly distributed along transects within natural community types. We re-sampled the Chicago region sites in 2001–2003 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 over time with fire exclusion (Bowles and Jones 2004), 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 species frequencies were calculated. 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 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.

Community types were ordinated 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 interpreting species composition from a species-based classification. To assess species distribution across the moisture gradient, mean species frequencies from each community were averaged within each of the six moisture classes. Communities were assigned to these classes based on their alignment on the first ordination axis. Sand shrub prairie data were combined with dry-mesic prairie data, graminoid fen and calcareous seep data were averaged with wet-mesic prairie data, 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.

Total species richness was taken 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-m<sup>2</sup> plot, which is a scale-dependent measure of  $\alpha$  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 frequencies of species averaged across all communities in which they occurred were dependent upon their niche breadth, (i.e., 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% average frequency ( $N = 282$  species) and common species as having greater than 20% frequency ( $N = 142$ ), and 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. Foredune, 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% information retained, six cluster groups had 77% correspondence to our *a priori* assignment of communities into six INAI drainage classes. With about 25% 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 divergent 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 overriding importance of drainage is also shown by the clustering of different substrates within similar moisture classes. 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, while 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, White and Glenn-Lewin 1984, Faber-Langendoen and Maycock 1994, 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

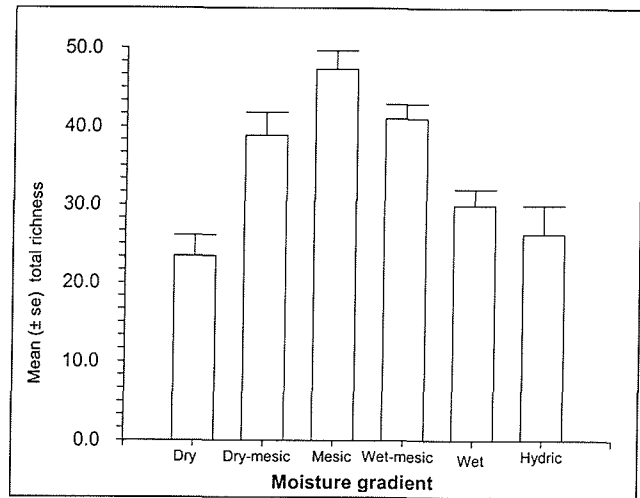
#### Species Richness and Spatial Abundance

More than 450 species were sampled across all communities. Graminoid species represented 22% of these species, forbs 68%, and woody species 10%. As found by Curtis (1959) and by Dix and Smeins (1967), species richness was lowest at 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 ten species per 0.25 m<sup>2</sup>. 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

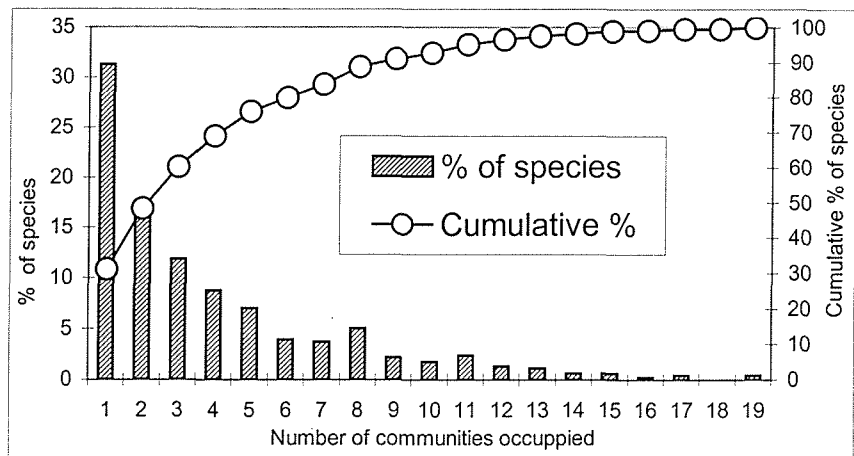
higher total richness ( $F = 4.91, P = 0.029$ ) and higher plot species richness ( $F = 12.0, P < 0.001$ ) than Grade B prairies. This indicates that species richness can be an important factor in ranking vegetation quality (Bowles and Jones 2006).

Most species were rare at the landscape level, with 33% occurring in single communities and 70% found in less than five communities (Figure 4). Most species were also infrequent within communities with 50% occurring at less than 10% average plot frequency and 70% occurring at 20% or less 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 only 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. There was no difference in niche width between common or rare graminoid and forb species. 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% 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 infre-



**Figure 3.** Unimodal distribution of plant species richness sampled 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.

**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. err.

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	0.0589
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

quent components of these communities, with only 46 species sampled, 5.38 ( $\pm$  0.87 se) species occurrences per community, an overall average frequency of 10.24% ( $\pm$  2.51 se) and an average niche width of 3.08 ( $\pm$  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 (Appendices I and II). 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 (e.g., 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  $\beta$ -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 (< 20% 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 ( $\chi^2 = 56.97$ ,  $P < 0.001$ ) with 66% representing hydric or mesic habitats, 26% representing wet or wet-mesic habitats, and 8% representing dry or dry-mesic habitats. More than half (54%) of the indicator species were common species (i.e., with > 20% plot frequencies in at least one community) 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: Dune, Prairie, and Savanna

Dry habitats are restricted to somewhat excessively drained gravel and sand substrates, with sand habitats occurring primarily along Lake Michigan. *Schizachryium scoparium* was dominant or co-dominant across all dry habitats. However, *Sorghastrum nutans* and *Stipa spartea* were abundant and absent only from dunes. Other dominant grasses were more restricted to specific substrates. These included *Ammophila breviligulata* on fordune habitat, *Calamovilfa longifolia* in dry sand prairies, and *Koeleria cristata* on sand dunes. Dry gravel prairies differed by having *Sporobolus heterolepis* as a co-dominant grass, with

*Bouteloua curtipendula* an important secondary species. Dry sand savannas had *Stipa spartea* as a co-dominant. *Carex pennsylvanica* also reached its greatest abundance in dry-sand savanna.

No single forb species was most abundant across all dry habitats, although *Solidago nemoralis* was present at comparatively high frequencies throughout. *Solidago nemoralis* and *Artemisia caudata* were the most abundant forbs on foredunes, *Coreopsis lanceolata* and *Artemisia caudata* in dry sand prairie, *Liatris aspera* and *Arenaria stricta* on dunes, *Helianthus occidentalis* and *Euphorbia corollata* in dry sand savanna, and *Petalostemum purpureum* and *Aster laevis* in dry gravel prairie. Shrubs were more restricted in distribution, and were not sampled in foredunes. The trailing shrubs *Arctostaphylos uva-ursi* and *Juniperus horizontalis* were dominant and co-dominant species on dune habitats. *Rosa blanda* was the most abundant shrub in dry sand prairie, while *Rosa carolina* was the leading shrub in dry sand savanna (with *Arctostaphylos uva-ursi* and *Quercus velutina*) and in dry gravel prairie (with *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 their classification as a pine forest or pine barrens. The occurrence of *Quercus velutina* in groundlayer vegetation in sand savanna may represent post-fire sprouting from tree bases, as these 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. Among grasses, *Andropogon scoparius* and *Sorghastrum nutans* were dominant across most habitats, with greater abundance of *Sporobolus heterolepis* and *Stipa spartea* in both gravel and loam prairies. *Andropogon gerardii* was dominant in sand shrub prairie and present in lower frequencies in other communities. *Euphorbia corollata*, *Monarda fistulosa* and *Aster ericoides* were the most widespread abundant forbs, but neither was most frequent in more than two habitats. *Tradescantia ohiensis* was the dominant forb in sand prairie and sand savanna, followed by *Aster azureus* in sand prairie and *Viola sagittata* and *Helianthus divaricatus* in savanna. *Euphorbia corollata*, *Monarda fistulosa*, and *Liatris cylindracea* were dominant forbs in gravel prairie, *Aster ericoides* and *Monarda fistulosa* in dolomite prairie, and *Euphorbia corollata* and *Aster ericoides* in loam prairie. In sand shrub prairie, *Helianthus mollis* and *Polygonatum canaliculatum* were the most frequent forbs. *Amorpha canescens* and *Rosa carolina* were the most common shrubs in most dry-mesic habitats, with *Ceanothus americanus* reaching secondary abundance in sand prairie. The shrubs *Spiraea tomentosa* and *Rubus setosus* were dominant species in sand shrub prairie. The blueberries *Vaccinium angustifolium* and *Vaccinium pallidum* were restricted to sand savanna, possibly due to presence of acid sand soils as well as partial shade tolerance.



### Mesic Prairie Habitats

Mesic prairie vegetation occupies moderately well-drained habitats. *Andropogon gerardii*, *Sorghastrum nutans*, and *Sporobolus heterolepis* were the most widespread dominant grasses in mesic prairie habitats, although *Sporobolus heterolepis* tended to be less abundant in sand prairies. *Schizachyrium scoparium* was subdominant in these habitats. No forb species were most important across all mesic habitats. *Aster ericoides* was the dominant forb in mesic loam prairie, followed in abundance by *Allium cernuum*, *Silphium terebinthinaceum*, and *Ratibida pinnata*. *Pycnanthemum virginianum* was the most frequent forb in mesic sand prairie, followed in abundance by *Aster ericoides*. *Allium cernuum* and *Smilacina stellata* were dominant forbs in mesic gravel prairie, with secondary abundance of *Ratibida pinnata*. *Rosa carolina* was the most abundant shrub in all mesic habitats. *Cornus racemosa* and *Amorpha canescens* were important secondary shrubs in loam and gravel prairie, while *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 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 *Schizachyrium scoparium* and *Sorghastrum nutans* were abundant across all habitats, reaching subdominance in sand prairie, while *Andropogon gerardii* was absent only from seep habitat, and was dominant or co-dominant in graminoid fen and loam prairie, respectively. The wetland species *Carex pellita* and *Spartina pectinata* dominated loam prairie, while *Calamagrostis canadensis* was the leading dominant in sand prairie. *Carex haydenii* and *Deschampsia cespitosa* dominated dolomite prairie, while *Juncus brachycephalus* dominated seep habitat with secondary dominance by *Rhynchospora capillacea* and *Carex haydenii*. *Muhlenbergia glomerata* and *Carex sterilis* were co-dominant in graminoid fen.

Among forbs, *Pycnanthemum virginianum* and *Senecio pauperculus* were dominant in wet-mesic sand prairie, *Silphium terebinthinaceum* and *Fragaria virginiana* in loam prairie, and *Solidago ohioensis* and *Solidago riddellii* in dolomite prairie. In graminoid fen, *Solidago ohioensis* and *Pycnanthemum virginianum* were the most frequent forbs. The most abundant forbs in calcareous seep vegetation were *Lobelia kalmii* and *Solidago uliginosa*, although *Silphium terebinthinaceum* was not infrequent. There were few abundant shrubs in wet-mesic habitats. *Cornus racemosa* was most abundant shrub in loam prairie, but was less frequent than *Potentilla fruticosa* in graminoid fen and calcareous seep habitat. *Rubus hispidus* was the leading shrub in wet-mesic sand prairie, while *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. *Calamagrostis canadensis* and *Carex stricta* were abundant in all habitats, with the former being the leading dominant in all wet prairies and secondary to *Carex stricta* in sedge meadows. *Carex pellita* and *Spartina pectinata* were co-dominant in wet prairies, but were absent or infrequent in sedge meadows. Only *Convolvulus sepium* was a co-dominant forb in both habitats. *Dryopteris thelypteris* and *Lycopus uniflorus* were the most frequent forbs in wet sand prairie, while *Solidago gigantea*, *Convolvulus sepium* and *Galium obtusum* were dominant forbs in wet gravel prairie, and *Aster simplex* and *Lycopus americanus* most frequent in wet prairie. *Pycnanthemum virginianum* was the leading forb in sedge meadow, followed by *Eupatorium maculatum*, *Lycopus virginicus*, and *Dryopteris thelypteris*. Shrubs were infrequent, with *Salix interior* the most important shrub species in wet prairie and *Rosa blanda* 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—*Calamagrostis canadensis*. Co-dominant graminoid species in marshes were *Carex lacustris*, *Typha latifolia*, *Typha angustifolia*, and *Carex lasiocarpa*. The most abundant forbs were *Scutellaria epilobiifolia*, *Lycopus virginicus*, and *Lysimachia thysiflora*. *Cornus stolonifera* was the only frequent shrub in marsh vegetation. In calcareous floating mat vegetation, *Carex lasiocarpa* and *Calamagrostis canadensis* were the dominant graminoid species, while *Scirpus validus* and *Carex aquatilis* were also abundant. *Lycopus virginicus*, *Lysimachia thysiflora*, *Aster borealis* and *Dryopteris thelypteris* were the most abundant forbs, while *Salix pedicellaris*, *Spiraea alba*, and *Salix candida* 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 *Eriophorum angustiolium*, with minor representation of *Muhlenbergia glomerata* and *Calamagrostis canadensis*. *Dryopteris thelypteris* was the dominant forb, while *Sarracenia purpurea*, *Lycopus virginicus*, and *Drosera rotundifolia* were also abundant. *Salix pedicellaris* and *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. *Schizachyrium scoparium* was the dominant grass in dry and dry-mesic habitats, and was less abundant in mesic and wet-mesic habitats. *Stipa spartea*, *Koeleria cristata*, and *Bouteloua curtipendula* were most abundant in drier habitats. *Sorghastrum nutans*, *Andropogon gerardii*, and *Sporobolus heterolepis* were the most abundant grasses in mesic habitats, and were replaced by increasing abundances of *Calamagrostis canadensis* and *Spartina pectinata* 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 calcicolous sedge and grass species. However, only *Calamagrostis canadensis* continued as an important grass in hydric habitats. Although some sedge species characterize upland habitats, many tend to become more abundant than grasses primarily in lower points of the soil moisture gradient. These species include *Carex stricta*, *Carex haydenii* and *Carex pellita* in wet-mesic to wet habitats, *Carex lacustris* and *Carex lasiocarpa* in wet habitats, and *Carex aquatilis* in hydric habitats.

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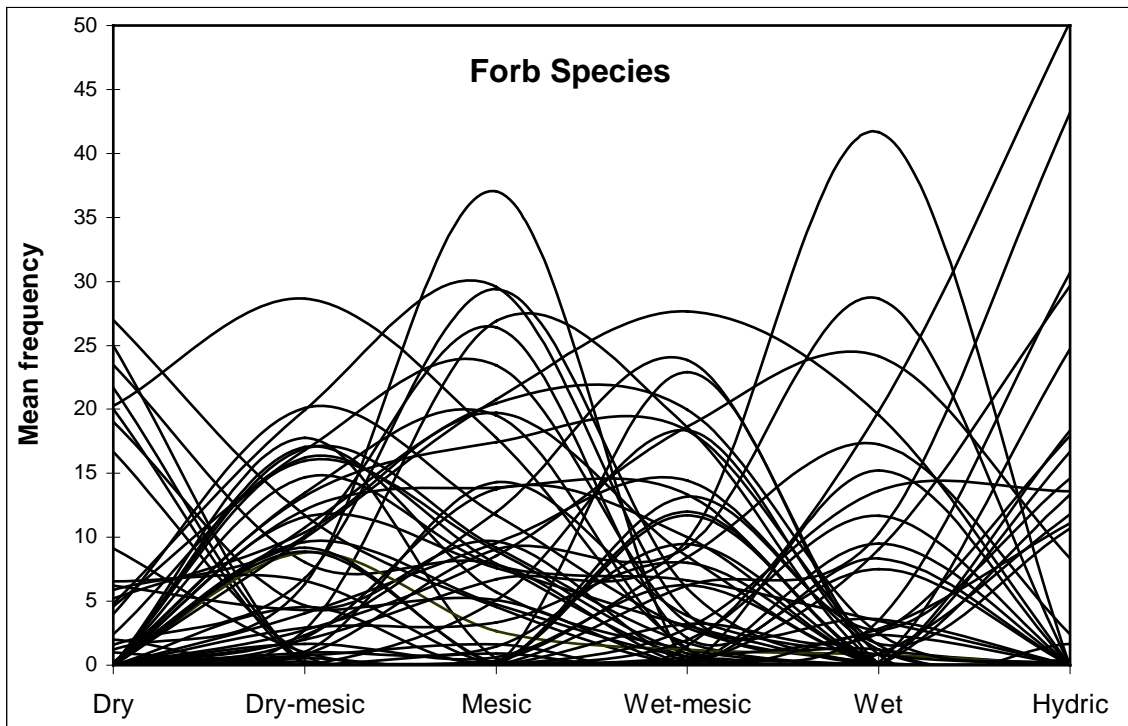
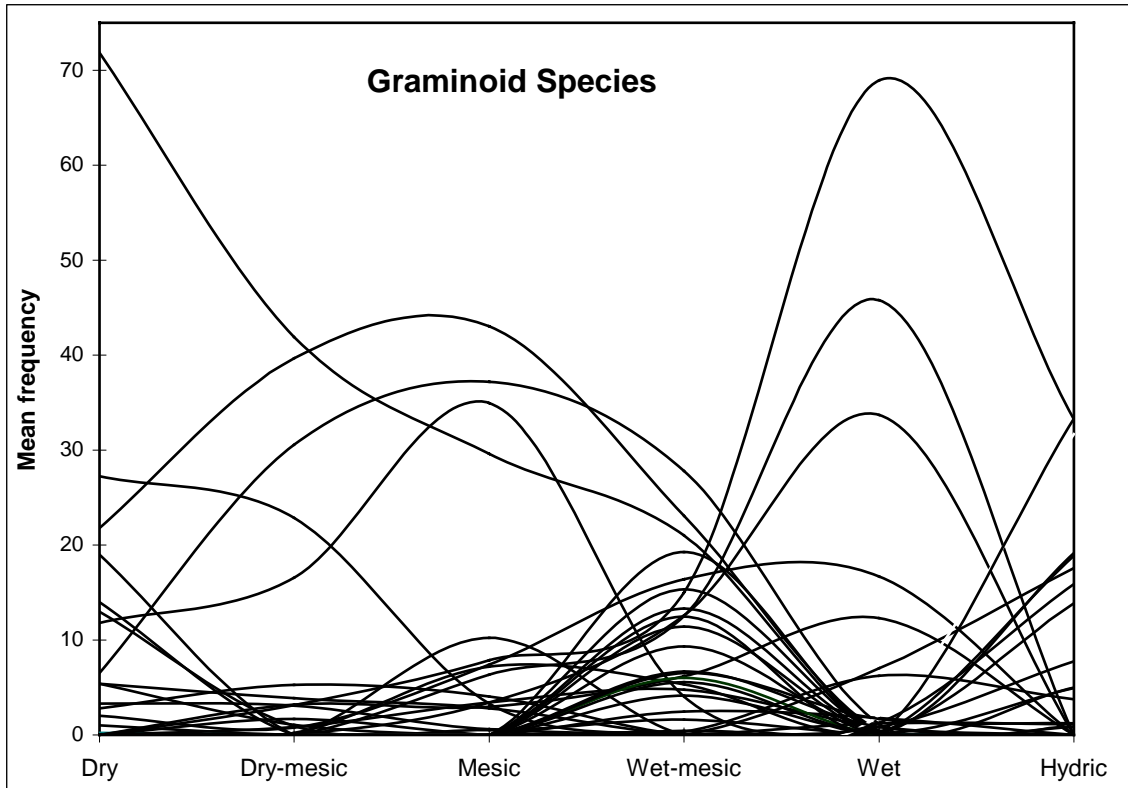
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**Appendix figure.** Frequencies of dominant graminoid (>15% mean frequency) and forb (> 30% mean frequency) species across a prairie-wetland soil moisture gradient in the Chicago region of northeastern Illinois. See Appendices I and II for species frequencies by community.



Appendix I. Average frequencies of grass and sedge species occurring at 15% average frequency in at least one community. Ordered by abundance across the first NMS ordination axis.

Abbreviations: FD = Foredune, DSP = Dry sand prairie, D = Dune, DSS = Dry sand savanna, DGP = Dry gravel prairie, DMGP = Dry-mesic gravel prairie, DMP = Dry-mesic prairie, DMSP = Dry-mesic sand savanna, DMDP = Dry-mesic dolomite prairie, DMSP = Dry-mesic sand prairie, MP = Mesic Prairie, MGP = Mesic gravel prairie, MSP = Mesic sand prairie, WMP = Wet-mesic prairie, WMSP = Wet-mesic sand prairie, WMDP = Wet-mesic dolomite prairie, CS = Calcareous seep, GF = Graminoid fen, WGP = Wet gravel prairie, SM = Sedge meadow, WSP = Wet prairie, CEM = Calcareous floating mat, M = Marsh, GB = Graminoid bog.

Species	FD	DSP	D	DSS	DGP	DMGP	DMP	DSS	DMSP	DMGP	DMP	MGP	MSP	WMP	WMSP	WMDP	CS	GF	WGP	SM	WSP	WP	CFM	M	GB
<i>Amnophila breviflora</i>	95.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Calamovilfa longifolia</i>	10.0	55.0	5.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Koeleria cristata</i>	—	25.0	40.0	—	—	—	—	—	5.7	—	—	—	1.5	—	—	—	—	—	—	—	—	—	—	—	—
<i>Carex meadii</i>	—	5.0	—	—	22.0	23.3	—	—	—	—	2.4	—	6.1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Bouteloua curtipendula</i>	—	—	—	—	27.0	2.2	4.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Stipa spartea</i>	—	45.0	15.0	43.3	33.0	49.4	50.7	—	25.3	5.0	6.7	3.2	5.0	1.7	—	—	—	—	—	—	—	—	—	—	—
<i>Andropogon scoparius</i>	85.0	65.0	80.0	53.3	76.0	43.3	33.6	35.0	30.3	62.5	46.7	23.3	35.0	30.6	22.5	28.7	13.3	6.7	33.9	—	—	—	—	—	—
<i>Panicum oligosanthes</i> v. <i>scrib.</i>	—	—	—	—	14.0	21.7	10.0	—	—	—	10.5	—	1.7	—	—	—	—	—	—	—	—	—	—	—	—
<i>Sporobolus heterolepis</i>	—	—	—	—	59.0	62.2	37.1	—	—	—	46.5	38.3	20.0	15.0	—	—	—	5.3	—	—	—	—	—	—	—
<i>Sorghastrum nutans</i>	—	20.0	30.0	20.0	39.0	60.0	14.3	40.0	14.0	62.5	47.2	33.8	61.7	33.7	30.0	22.0	23.3	16.8	—	—	1.7	—	—	—	—
<i>Andropogon gerardi</i>	—	—	—	6.7	26.0	18.3	31.4	70.0	10.3	50.0	3.3	33.1	45.2	47.5	13.7	18.3	—	59.5	4.8	—	—	—	2.5	—	—
<i>Panicum villosissimum</i> v. <i>pseu.</i>	—	—	—	—	—	—	—	17.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Carex pennsylvanica</i>	—	—	16.7	—	—	—	—	—	13.3	—	5.1	1.9	—	—	8.1	—	—	—	—	—	—	—	—	—	—
<i>Panicum implicatum</i>	—	—	—	—	—	—	5.0	—	—	—	7.0	3.3	—	2.5	16.0	—	—	5.5	—	—	3.3	—	—	—	—
<i>Eleocharis compressa</i>	—	—	—	—	—	—	—	—	12.5	6.7	2.9	5.0	1.1	—	13.0	15.0	—	3.0	—	0.9	3.3	45.0	—	—	—
<i>Carex buxbaumii</i>	—	—	—	—	—	—	—	—	—	—	14.4	4.6	2.6	2.5	5.1	—	—	19.1	—	—	—	1.7	—	40.0	1.7
<i>Carex pellita</i>	—	—	—	—	—	—	—	—	—	—	6.0	—	4.3	62.5	—	—	—	0.3	85.7	—	—	3.3	45.8	—	—
<i>Carex tetanica</i>	—	—	—	—	—	—	—	—	—	—	—	23.8	6.9	—	—	—	—	—	—	—	—	—	—	—	—
<i>Panicum implicatum</i>	—	—	—	—	—	—	—	—	—	—	7.1	3.3	—	2.5	16	—	—	5.5	—	—	—	3.3	—	—	—
<i>Spartina pectinata</i>	—	—	10.0	—	—	—	0.7	—	0.7	—	3.3	5.0	13.5	45.0	11.0	25.0	—	0.9	—	5.0	28.3	33.3	—	—	
<i>Calamagrostis canadensis</i>	—	—	—	—	—	—	—	—	1.7	—	17.2	2.1	15.0	6.5	25.0	39.0	—	10.9	95.2	47.1	88.3	45.0	70.0	25.0	5.0
<i>Carex stricta</i>	—	—	—	—	—	—	—	—	—	—	18.8	—	0.4	—	11.0	28.3	—	23.2	19.0	95.0	55.0	14.2	—	—	—
<i>Rhynchospora capillacea</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	56.7	0.5	—	—	—	—	—	—	—
<i>Panicum flexile</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16.7	—	4.1	—	—	—	—	—	—	—
<i>Juncus brachycephalus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.7	20.0	50.0	—	0.9	—	—	—	—	—
<i>Carex sterilis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	43.3	23.3	—	—	—	—	—	—	—	—
<i>Deschampsia cespitosa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	40.0	30.0	26.4	—	1.8	—	—	—	—	—
<i>Carex haydenii</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16.7	—	4.1	—	0.9	—	—	—	15.0	—
<i>Panicum flexile</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16.7	45.6	—	—	0.9	—	—	—	—	—
<i>Muhlenbergia glomerata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	7.9	—	11.4	—	16.7	3.8	11.1	—
<i>Scirpus validus</i> v. <i>erber</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	20	—	—	—	—	—	—	—	—
<i>Carex lacustris</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Carex lasiocarpa</i> v. <i>americana</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Juncus canadensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Typha angustifolia</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cladium mariscoides</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Eleocharis rostellata</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Scirpus pungens</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Scirpus validus</i> var. <i>erber</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Typha latifolia</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Carex atherodes</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Carex aquatilis</i> v. <i>altior</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Eriophorum angustifolium</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
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Appendix II. Average frequencies of forbs occurring at > 30% frequency in at least one community. Ordered by abundance across the first NMS ordination axis. See Appendix I for key to community abbreviations.

Species	FD	DSP	D	DSS	DGP	DMGP	DMP	SSP	DMSS	DMDDP	DMSP	MP	MGP	MSP	WMP	WMSP	WMDDP	CS	GF	WGP	SM	WSP	WP	CFM	M	GB
<i>Arenaria caudata</i>	30.0	65.0	30.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Coreopsis lanceolata</i>	—	75.0	—	33.3	—	—	—	—	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Arenaria stricta</i>	—	55.0	45.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Helianthus occidentalis</i>	—	10.0	30.0	43.3	—	1.1	—	—	3.7	—	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Petalostemum purpureum</i>	—	60.0	10.0	—	25.0	12.8	7.9	—	7.5	—	6.8	20.0	2.2	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Liatris aspera</i>	—	60.0	75.0	—	14.4	25.0	—	18.7	12.2	6.1	5.0	2.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Solidago nemoralis</i>	45.0	10.0	25.0	13.3	24.0	8.9	7.9	5.0	6.7	20.0	8.1	5.0	10.6	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Euphorbia corollata</i>	—	40.0	43.3	18.0	55.0	37.1	30.0	15.3	34.4	20.8	13.3	19.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Smilacina stellata</i>	—	5.0	—	23.3	1.0	25.0	0.7	—	3.7	—	31.1	9.0	66.7	3.5	3.0	—	—	6.7	0.9	33.3	—	—	—	—	—	—
<i>Parthenium integrifolium</i>	—	—	—	—	12.0	2.8	14.3	60.0	—	18.9	11.2	—	15.6	4.7	—	—	—	—	—	—	—	—	—	—	—	—
<i>Helianthus mollis</i>	—	—	—	—	6.7	—	—	90.0	0.7	—	3.2	—	20.6	3.3	—	—	—	—	—	—	—	—	—	—	—	—
<i>Potentilla simplex</i>	—	—	—	—	1.4	55.0	7.7	—	5.6	8.3	—	14.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Solidago juncea</i>	—	—	—	—	0.7	65.0	14.3	—	22.2	12.1	—	—	5.0	6.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tridactenaria ohioensis</i>	—	—	—	—	5.7	—	48.0	5.0	42.8	10.7	1.7	15.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Polygonatum canadicalatum</i>	—	—	—	—	3.3	2.1	90.0	10.0	—	1.1	—	—	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Anemone cylindrica</i>	—	—	36.7	9.0	1.1	5.0	—	—	—	0.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Aster azureus</i>	5.0	—	—	—	18.0	8.3	7.1	—	11.7	17.5	56.1	19.4	38.3	12.6	7.5	5.3	3.3	—	0.5	14.3	—	—	—	—	—	—
<i>Aster erioideus</i>	—	—	—	—	24.0	17.8	30.0	—	1.0	62.5	8.3	31.9	30.0	26.9	2.5	14.3	3.3	—	—	4.8	—	—	—	—	—	—
<i>Ratibida pinnata</i>	—	—	—	—	8.0	13.3	25.0	—	—	2.5	—	28.8	51.7	7.8	30.0	—	—	26.7	—	—	—	—	—	—	—	—
<i>Silphium terebinthinaceum</i>	—	—	—	—	—	—	—	—	—	—	2.2	26.8	43.3	10.6	55.0	11.3	—	—	—	—	—	—	—	—	—	—
<i>Eupatorium altissimum</i>	—	—	—	—	—	—	—	—	—	—	1.0	2.5	1.1	3.8	—	—	—	—	—	—	—	—	—	—	—	—
<i>Allium cernuum</i>	—	—	—	—	6.0	—	—	—	—	25.0	1.7	30.5	75.0	5.6	—	—	—	—	—	—	—	—	—	—	—	—
<i>Liatris spicata</i>	—	—	—	—	—	—	—	35.0	4.0	—	33.9	15.4	8.3	18.0	7.5	29.7	3.3	—	0.5	—	—	—	—	—	—	—
<i>Monarda fistulosa</i>	—	—	—	—	20.0	33.3	11.4	—	13.0	55.0	7.8	15.5	10.0	9.6	—	—	—	—	—	—	—	—	—	—	—	—
<i>Senecio pauperculus</i>	—	—	—	—	—	—	—	—	—	17.5	6.7	8.7	18.3	1.7	5.0	33.3	18.3	—	—	—	—	—	—	—	—	—
<i>Satureja arkansana</i>	—	—	—	—	—	—	—	—	—	17.5	—	—	10.0	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Solidago ohioensis</i>	—	—	—	—	—	—	—	—	—	—	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Aster laevis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Coreopsis tripteris</i>	—	31.0	—	—	—	—	—	—	—	—	13.6	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Helianthus divaricatus</i>	—	—	—	—	—	—	—	—	—	—	34.4	14.9	25.0	18.7	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lespedeza capitata</i>	—	—	—	—	—	—	—	—	—	—	31.1	—	—	0.4	—	—	—	—	—	—	—	—	—	—	—	—
<i>Liatris cylindracea</i>	—	—	—	—	—	—	—	—	—	—	19.4	1.0	—	13.3	—	—	—	—	—	—	—	—	—	—	—	—
<i>Phlox pilosa</i>	—	—	16.7	16.0	39.4	—	—	—	—	—	22.8	19.9	25.0	14.3	37.5	5.0	—	—	—	—	—	—	—	—	—	—
<i>Physostegia virginiana</i>	—	—	20.0	6.0	10.0	22.9	—	—	6.7	—	1.1	7.7	33.3	1.9	7.5	11.0	—	—	—	—	—	—	—	—	—	—
<i>Rudbeckia hirta</i>	—	—	—	—	1.0	3.3	6.4	—	17.7	15.0	22.2	21.4	28.3	11.7	20.0	27.3	15.0	—	—	—	—	—	—	—	—	—
<i>Senecio aureus</i>	—	—	—	—	—	—	—	—	—	—	10.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Spiraea tomentosa</i> v. <i>rosea</i>	—	—	—	—	—	—	—	55.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Thalictrum dasycarpum</i>	—	—	—	—	—	—	—	0.7	5.0	—	—	2.7	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Zizia aurea</i>	—	—	—	—	—	—	—	5.0	—	—	7.8	19.6	8.3	13.3	42.5	7.0	—	—	—	—	—	—	—	—	—	—
<i>Convolvulus sepium</i>	—	—	—	—	—	—	—	—	—	—	2.5	1.1	3.0	16.7	0.6	22.5	11.7	3.3	—	—	—	—	—	—	—	—
<i>Lycopus uniflorus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Aster dumosus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pycnanthemum virginianum</i>	—	—	—	—	—	—	—	—	—	—	45.0	14.4	19.3	10.0	33.0	37.5	34.0	20.0	3.3	43.5	9.5	47.0	21.7	—	—	—
<i>Galium obtusum</i>	—	—	—	—	—	—	—	—	—	—	5.0	11.5	8.3	7.2	25.0	17.0	—	—	—	—	—	—	—	—	—	—
<i>Solidago gymnospermoides</i>	—	—	—	—	—	—	—	60.0	17.0	—	11.1	2.9	—	20.6	—	29.0	3.3	—	—	—	—	—	—	—	—	—
<i>Fragaria virginiana</i>	—	—	—	—	1.0	5.0	9.3	—	7.0	32.5	25.6	26.4	8.3	17.6	50.0	27.0	13.3	—	—	—	—	—	—	—	—	—
<i>Aster simplex</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Viola sagittata</i>	—	—	—	—	—	—	—	—	—	—	21.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Camparula uliginosa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lysimachia quadriflora</i>	—	—	—	—	—	—	—	—	—	—	—	6.4	6.7	2.2	10.0	2.0	38.3	10.0	31.4	—	—	—	—	—	—	—
<i>Lycopus americanus</i>	—	—	—	—	—	—	—	—	—	—	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Solidago riddellii</i>	—	—	—	—	—	—	—	—	—	—	12.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lobelia kalnit</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Galium boreale</i>	—	—	—	—	—	—	—	—	—	—	15.0	12.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Solidago gigantea</i>	—	—	—	—	—	—	—	—	—	—	2.5	3.3	2.5	15.0	8.1	22.5	30.7	25.0	—	—	—	—	—	—	—	—
<i>Hypericum virginicum</i> v. <i>fraseri</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—



Appendix II, Continued. See Appendix I for key to community abbreviations.

Species	FD	DSP	D	DSS	DGP	DMGP	DMP	SSP	DMSS	DMDP	DMSP	MP	MGP	MSP	WMP	WMSP	WMDP	CS	GF	WGP	SM	WSP	WP	CFM	M	GB
<i>Aster borealis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16.1	10.0	—	—	—	43.8	5.0	5.0
<i>Eupatorium maculatum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14.4	37.9	16.7	—	—	12.5	13.3	15.0
<i>Solidago uliginosa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	46.7	19.2	11.1	—	—	28.8	—	15.0	
<i>Scutellaria epithimifolia</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7.9	28.3	—	—	35.0	38.9	15.0
<i>Dryopteris thelypteris</i> v. <i>pub.</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	0.6	—	—	—	—	5.2	22.7	56.7	—	—	42.5	18.3	90.0
<i>Lycopodium virginicum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24.1	23.6	—	17.5	—	54.6	20.0	55.0
<i>Lysimachia thyrsiflora</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.5	12.3	1.7	—	—	38.8	23.3	30.0
<i>Viola pallens</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10.0	30.0
<i>Potentilla palustris</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.9	—	—	25.8	3.3	45.0
<i>Sarracenia purpurea</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	55.0
<i>Drosera rotundifolia</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Appendix III. Average frequencies of woody vegetation occurring at 5% frequency in at least one community. Ordered by abundance across the first NMS ordination axis. See Appendix I for key to community abbreviations.

Species	FD	DSP	D	DSS	DGP	DMGP	DMP	SSP	DMSS	DMDP	DMSP	MP	MGP	MSP	WMP	WMSP	WMDP	CS	GF	WGP	SM	WSP	WP	CFM	M	GB
<i>Prunus pumila</i>	—	10	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Arcostaphylos uva-ursae</i>	—	10	100	33.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Juniperus horizontalis</i>	—	—	45	3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ceanothus herbaceus</i>	—	—	—	6.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Quercus velutina</i>	—	—	—	10	—	—	—	5	9.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rhus radicans</i>	—	—	50	—	—	—	—	—	—	—	—	—	—	3.3	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rosa carolina</i>	—	30	73.3	23	47.2	13.6	—	—	20.7	17.5	—	28.1	18.3	7.9	—	—	—	—	—	—	—	—	—	—	—	—
<i>Salix glaucophylloides</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ceanothus americanus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Amorpha canescens</i>	—	—	—	—	21	20.6	17.9	—	3.7	—	8.3	5.4	1.7	0.4	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rubus hispida</i>	—	—	—	—	—	—	—	—	7	—	—	—	—	11.1	—	—	—	—	—	—	—	—	—	—	—	—
<i>Salix humilis</i>	—	—	—	—	—	6.7	2.1	—	7.3	—	10	1.4	—	2.6	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cornus racemosa</i>	—	—	—	—	—	1	5	—	2	—	1.1	7	3.3	3.3	15	0.7	—	—	—	—	—	—	—	—	—	—
<i>Rosa blanda</i>	—	65	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Spiraea tomentosa</i> v. <i>rosea</i>	—	—	—	—	—	—	—	55.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Vaccinium pallidum</i>	—	—	—	—	—	—	—	—	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Vaccinium angustifolium</i>	—	—	—	—	—	—	—	—	10	—	7.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Salix interior</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	0.6	—	—	—	—	—	—	—	10	—	—	—	—
<i>Salix eriocephala</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rubus setosus</i>	—	—	—	—	—	—	—	95	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ribes americana</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Spiraea alba</i>	—	—	—	—	—	—	—	—	—	0.7	—	1.1	0.2	—	—	—	—	—	—	—	—	—	—	—	5	—
<i>Potentilla fruticosa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Corsum stolonifera</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Salix pedicularis</i> var. <i>hypoglauca</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Betula pumila</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Decodon verticillatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Salix candida</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—