

Landscape analysis of Illinois and Wisconsin remnant prairies¹

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CORBETT, E. A. (Department of Biological Sciences, Southeastern Oklahoma State University, Durant, OK 74701-0609) AND R. C. ANDERSON (Behavior, Ecology, Evolution and Systematics Section, Department of Biological Sciences 4120, Illinois State University, Normal, IL 61790-4120). Landscape analysis of Illinois and Wisconsin remnant prairies. *J. Torrey Bot. Soc.* 133(2): 267–279. 2006.—We examined Illinois and Wisconsin remnant prairie data to determine regional patterns of species composition as influenced by landforms with different topographic positions and soil properties resulting from glacial history. Three data sets were used, including 84 sites from Wisconsin sampled in the 1950s; 216 sites from Illinois sampled as part of the Illinois Natural Areas Inventory (INAI) in the 1970s; and a subset of 29 INAI sites resampled in 1998. These data sets are the best characterization of remnant prairie vegetation in the two states after most of the original prairies were lost. Data were analyzed using detrended correspondence analysis (DCA), principal components analysis (PCA), and canonical correspondence analysis (CCA). CCA was used only for the INAI sites resampled in 1998 that had a complete set of soils data. Results from all analyses were similar. We determined that an interaction between topographic position and soil texture, which affected moisture availability, was most important in influencing species composition and abundance in Illinois and Wisconsin remnant prairies. Separation of dominant prairie species in Illinois and Wisconsin followed similar patterns, if differences in community designation for similar vegetation types were considered. However, Wisconsin and Illinois sites separated on DCA axis 2, which was negatively correlated with calcium and phosphorus. The first DCA ordination axis for INAI prairie sites was correlated with a topographically-based Integrated Moisture Index (IMI). For the 1998 INAI data, PCA was used to reduce soil variables to fewer dimensions and resulting axis 1 scores were used in stepwise multiple regression analysis to determine relationships between environmental variables and DCA ordination axis scores. The IMI was the first variable entered in the stepwise multiple regression model; however, PCA axis 1 stand scores based on soil variables did not meet criteria for entry into the model. For all data sets, including the CCA ordination of the resampled INAI sites, there was a secondary separation at the dry end of the moisture gradient between hill prairies and dry sand prairies, which was related to differences in soil texture and availability of calcium and phosphorus. In general, soil nutrients and texture were less important than topographically controlled moisture availability in determining prairie species composition and abundance at this scale of analysis.

Key words: canonical correspondence analysis, detrended correspondence analysis, Illinois prairie, inorganic nutrients, moisture gradient, remnant prairie, vegetation analysis, Wisconsin prairie.

The importance of ecological and historical factors is often dependent upon the spatial scale of the investigation (Allen and Starr 1982, Stoll and Prati 2001, Symstad et al. 2003). However, the mechanisms affecting ecological patterns op-

erate at different scales. To understand local-scale phenomena and fit them into a larger, more general framework, it is necessary to examine patterns at the regional and global scale (Levin 1992). As spatial scale changes from small to large, the factors affecting species diversity, number of rare species, and general patterns of abundance change (Willis and Whittaker 2002, Fleishman et al. 2003, Cavender-Bares et al. 2004). Additionally, it is often easier to detect general patterns at a larger spatial scale than at a small spatial scale, because random effects play a greater role at smaller spatial scales (Levin 1992). Fleishman et al. (2003) suggested that the results of studies carried out at different spatial scales may not be strictly comparable because the environmental factors which are important differ as a function of spatial scales.

Studies of large-scale vegetation patterns are

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important because they provide insight into ecological processes on spatial vegetation patterns on higher level of aggregation (Haines-Young and Chopping 1996, Anderson et al. 2000, Bollinger et al. 2004). However, large scale analyses of prairie vegetation data are relatively rare. On the continental scale, Diamond and Smeins (1988) examined remnant prairie in sites that ranged from Manitoba to the Gulf Coast of Texas. Species composition varied most in response to a north-south latitudinal gradient (related to differences in precipitation), with a secondary separation of Texas prairies that was related to soils. In Wisconsin, Curtis (1971) determined that moisture availability was the most important factor that affected prairie species composition. Soil nutrient data were also available but showed little influence on species composition. Umbanhowar (1992) reanalyzed these data using detrended correspondence analysis (DCA), determining that in addition to the moisture gradient on axis 1 (the most important factor), sand prairies and prairies on finer-textured soils separated on axis 2. Umbanhowar (1992) concluded that both ordination axes were necessary to represent patterns of prairie vegetation adequately, but he found no clear evidence for a complex gradient where nutrient levels interacted with moisture on axis 1, as some researchers found with data collected across a smaller spatial scale (Nelson and Anderson 1983, Anderson et al. 1984). While large-scale studies of prairies are relatively rare, studies of prairie vegetation at a single site in Illinois demonstrated topographically-influenced moisture-nutrient gradients as well as moisture gradients. At Goose Lake Prairie State Park (GLP) in Grundy County, northeastern Illinois, Nelson and Anderson (1983) determined that moisture changes along a topographic gradient were the most important factor affecting species composition. Anderson et al. (1984) expanded this work at GLP and reported significant correlations between soil moisture and availability of inorganic nutrients. Further, they demonstrated that the best determinant of differences in prairie species composition and abundance was position on a topographically controlled soil moisture-nutrient gradient. Bazzaz and Parrish (1982) suggested that topographic position is the major factor controlling water availability, but that soil texture, depth and bulk density are also important.

Even though numerous studies have examined Illinois prairies (e.g. Evers 1955, Anderson 1970, Nelson and Anderson 1983, Anderson et

al. 1984, Robertson et al. 1997, Corbett and Anderson 2001) none was a comprehensive study of prairies state-wide. In this paper, we ask the following questions: (1) Is the landscape distribution of Illinois prairies controlled by factors related to soil moisture such as soil texture and topography? (2) What is the relationship between soil inorganic nutrients and the occurrence and abundance of prairie species? (3) Is there a continuum of prairie communities across Wisconsin and Illinois at the eastern edge of the prairie peninsula (Transeau 1935)?

Materials and Methods. STUDY AREAS. *Illinois Prairie.* Illinois is popularly called “the Prairie State,” and although historically 60% of the state was tallgrass prairie (Fig. 1), less than 0.01% of the original nearly 9 million hectares of prairie remain (Anderson 1991). Landforms and soils vary across the state, largely as a result of Illinois’ glacial history (Fig. 2A), and these differences have given rise to a diversity of prairie types. Unglaciaded areas in the south, west-central and northwest parts of the state have highly dissected topography, whereas most of the recently glaciaded area (Wisconsinan glaciation, 12,000–10,000 YBP) is relatively flat (Fehrenbacher et al. 1967, Willman and Frye 1970). The Illinoian till plain is older (300,000–125,000 YBP), more dissected, and historically had a smaller percentage of its area covered by prairie than the portion of the state covered by Wisconsinan-age ice. Glaciation also affected drainage patterns within the state and deposited material that contributed to soil formation, including till and alluvial deposits (Risser et al. 1981). Soils vary across the state but most formed in loess, a silty windblown parent material that developed in Pleistocene river valleys (Fehrenbacher et al. 1967, Willman and Frye 1970). Other soils, particularly in the northwestern, west-central, and east-central portion of the state, formed from Pleistocene sand deposits (Hart and Gleason 1907, Willman and Frye 1970).

The prairies of Illinois were distributed in the northern three-quarters of the state, with most of the prairies occurring on the Illinoian and Wisconsinan glacial till plains, Fig. 2A. The roughly 930 hectares of prairie remaining in Illinois represent diverse habitat types differing in topography and substrate. Mesic or “black soil prairie” that occurred on fine-textured, deep soils derived from loess or glacial till on upland sites was historically the dominant prairie type in Il-

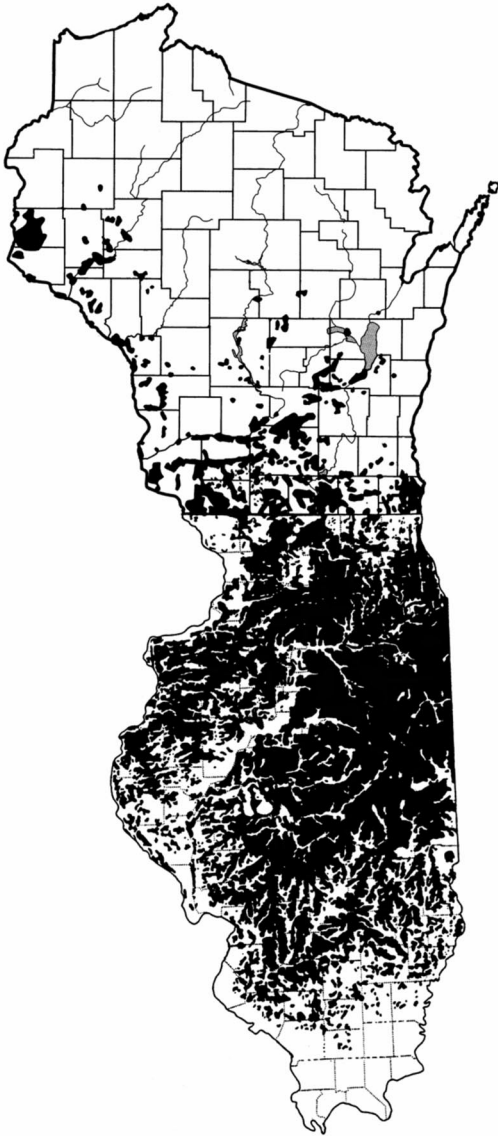


FIG. 1. Location of prairie in Illinois and Wisconsin. Illinois prairies after Anderson 1970 and Wisconsin prairies after Curtis 1971.

Illinois (White 1978, Robertson et al. 1997, Corbett and Anderson 2001). *Andropogon gerardii* is the leading grass species on these prairies that grade into wet-prairies that are dominated by *Calamagrostis canadensis* and *Spartina pectinata*. Pioneer cemeteries and railroad rights-of-way support remnant prairies that tend to be more mesic, although some of these sites have a sand substrate. Illinois prairie includes xeric hill prairies that are dominated by drought adapted species including grasses such as and *Schizachyr-*

ium scoparium and *Bouteloua curtipendula*, and *Sorghastrum nutans* and important forbs include *Dalea purpureum*, *Echinacea pallida*, and *Euphoibia corollata* (Evers 1955, Robertson et al. 1995, Corbett and Anderson 2001). Hill prairies are small (<2 ha) and generally have south-to-west-facing aspects, steep slopes, well-drained soils, and exposure to dry prevailing winds and are most common along the Mississippi and Illinois rivers in the western part of the state but they are found in other locations (Schwartz et al. 1997, Corbett and Anderson 2001). They occur on loess bluffs, sand and gravel substrates, or on steep slopes of glacial drift but most are loess hill prairies (Illinois Department of Energy and Natural Resources 1994).

Sand prairies formed on deep Pleistocene sand deposits in northwestern, west-central, and northeastern portion of the state where they extend into Indiana and support similar vegetation. They have droughty, coarse-textured soils that tend to be lower in organic matter, and potassium than other prairie soils, but they may have higher phosphorus (Dickman et al. 1984). Sand prairies in Illinois have xeric adapted species, including grasses such as *Schizachyrium scoparium*, *Eragrostis trichoides*, and *Bouteloua hirsuta* and forbs such as *Ambrosia psilostachya* and *Optunia humifusa* (Dhillion and Anderson 1994). Depending upon topographic position, some sand prairies are mesic or even wet and have species compositions like those found on sites of similar moisture conditions but with finer textured soils (Corbett and Anderson 2001).

Wisconsin Prairie. Original prairie in Wisconsin occupied 850,000 hectares, or about 5.5%, of the area of the state, and was concentrated in the southwestern portion of the state. Prairies along the southern border of Wisconsin were continuous with those of northern Illinois (Fig. 1). Only 0.1% of the original Wisconsin prairie remains (Cochran and Iltis 2000). A diversity of prairie types remained at the time of Curtis' research, including xeric prairies, "high lime prairies," mesic prairies, and wet prairies (Curtis 1971). These sites, like Illinois prairies, are found on a diversity of substrates, including loess, till, outwash, and limestone-influenced soils.

Much of Wisconsin experienced Wisconsin-ian-era glaciation and presents a level-to-rolling topography with low relief (Curtis 1971). The majority of the state's land surface has a 5% to 18% slope, with the rest of the state having less-

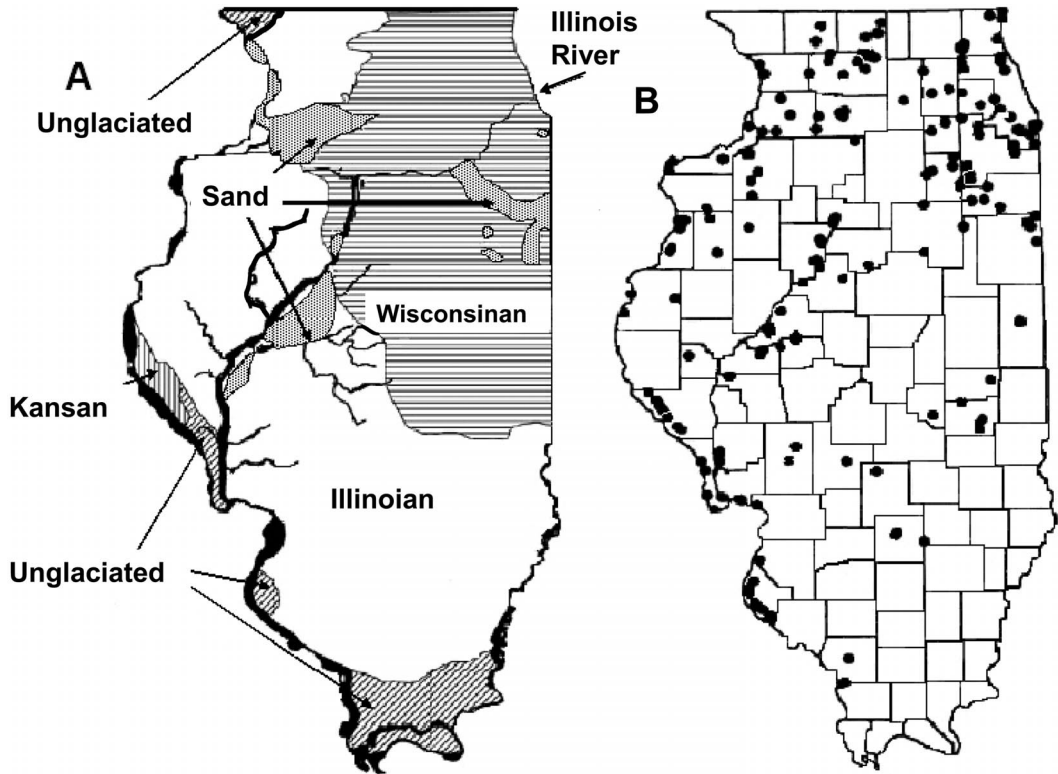


FIG. 2. A. Map of Illinois glacial deposits of various ages, sand deposits, and location of the Mississippi and Illinois Rivers in Illinois. B. Map of Illinois indicating locations of Illinois Natural Areas Inventory sites.

er slopes (Hole 1976). Unlike Illinois, there are no large exposures of glacial deposits from earlier in the Pleistocene. In general, Illinois has a greater variety of glacial exposure than Wisconsin. However, a large driftless area in southwestern Wisconsin (roughly 35,000 km²) provides the greatest amount of topographic variability within the state.

The soil parent materials in Wisconsin reflect its glacial history. About 40% of Wisconsin's soils formed in loess, with the remaining soils derived from outwash deposits, till, and some residual bedrock—especially in the Driftless Area (Hole 1976). In areas where glacial-era lakes were present, the parent material for soils may be sand (from wave action) or lacustrine clay deposits (Curtis 1971). Some sites had thin soils, or soils over limestone (Umbanhowar 1992).

As in Illinois, much of Wisconsin's original prairie has been lost, and the remaining sites are in danger of losing biodiversity. Leach and Givnish (1996) re-examined some of the remnant prairies sampled by Curtis (1971). They determined that in the highly-fragmented remnant

prairies, there was a tendency for short-statured species, early-flowering species, and legumes to be lost from the sites over time (Leach and Givnish 1996). Consequently, data from Wisconsin remnant prairies sampled in the 1950s (Curtis 1971) represent the best characterization of original Wisconsin prairies.

DATA SETS. We developed a combined data set using information from three sources: the Illinois Natural Areas Inventory (INAI; this was the principal source of data) conducted between 1975 and 1978, the Wisconsin Plant Ecology Laboratory (PEL) data, which were collected by J.T. Curtis and students in the 1950s and are described by Umbanhowar (1992, 1993) and a subset of the INAI sites resampled in summer 1998.

These data sets characterize remnant prairie vegetation after most of the original prairies in Illinois or Wisconsin were lost. The goals of the INAI were to locate the remaining undisturbed natural communities in Illinois and to encourage their protection. Woodland, prairie and wetland areas were surveyed, but a special effort was made to locate remnant prairie areas. Generally,

the researchers preferred to select sites larger than 2 ha, but included prairie sites as small as 0.1 ha. A total of 953 ha of prairie were identified in Illinois. Locations of the original INAI sites are shown in Fig. 2B. Most of these sites were sampled for frequency of herbaceous species in 20 to 30, 0.25 m² circular quadrats per site. Some environmental/geographic data (e.g., elevation, soil association and physiographic unit) were provided for each site (White 1978). However, detailed information about soils, slope degree and aspect, or site matrix (the type of land use surrounding the site) was not collected. Based on observations made by the authors when resampling the sites in 1998, the majority of the remnant prairies were isolated fragments in an agricultural matrix (corn, soybeans, and some grazed land). Other sites (mostly hill prairies) were in a forest or disturbed-forest matrix and those in the Chicago region and near other major urban areas were in a residential or urbanized matrix. However, it is possible that the matrix for some sites was different 20 years previously when the original INAI data were collected.

From the Wisconsin data, only 84 sites with vegetation quadrat data (as opposed to simple species lists) were used. Of those sites, 57 had soils data available. The soil samples were most likely collected to a depth of 10 cm and were analyzed using colorimetric tests on standard soil extracts (Curtis 1971). The soil information available for these sites included pH, P, K, Ca, Mg, and nitrate.

We converted all vegetative data to relative frequency values by dividing the number of quadrat occurrences of a species at a site by the sum of all quadrat occurrences of all species at that site. Soil nutrient data were not available for the original INAI data set, so we collected new vegetation and soils data from 29 of the original 216 INAI sites in 1998. The sites selected were located in Illinois State Parks or dedicated Illinois Nature Preserves, which were protected from disturbance since the original survey. These sites were selected to provide a broad representation of the geographic area prairies occupied within the state and a good representation of different site types.

To the extent possible, we replicated the sampling techniques used in the original INAI. At most sites, 30 circular, 0.25 m² quadrats were sampled (10 quadrats per each of three transects, individual quadrats were separated by either 5 or 10 meters depending on site size). However,

twelve of the sites were too small for this sampling scheme. For these sites, we collected between 15 and 25 samples per site, but four of the sites were so small that it was only possible to sample ten points and maintain quadrat spacing.

For the 29 INAI sites sampled in 1998, we collected fifteen soil cores (15 cm deep by 2.5 cm diameter). Generally, soil cores were collected adjacent to every other quadrat sampled. All soil cores from a site were combined, giving a sample of approximately 1 kg from each site. These soils were transported to a laboratory at Illinois State University, air-dried and sent to the University of Wisconsin Extension Service Soil Laboratory, where they were tested for pH, percent organic matter (measured as loss on ignition) available soil P, K, Ca, Mg and texture (percent sand, silt and clay).

ORDINATION ANALYSIS. We used PC-ORD (McCune and Mefford 1997) to run Detrended Correspondence Analysis (DCA) on the 1970s INAI data, the 1998 resampling of the INAI sites, and a combined data set consisting of the original INAI data, the 1998 resampling, and the Wisconsin PEL data. The default settings in PC-ORD were used for each of these analyses. We chose DCA despite some author's objections (e.g., Minchin 1987), because it is commonly used with field data (Cavender-Bares et al. 2004, Hong et al. 2004, Lazarova et al. 2004) and it generally works well with landscape-scale data, which can include gradients encompassing a wide range of environmental variation (Gauch 1982, Digby and Kempton 1987, Peet et al. 1988). Data were also analyzed using Non-Metric Multidimensional Scaling (NMDS) analysis and the results were similar to those from the DCA, but were less interpretable.

We calculated an Integrated Moisture Index (IMI) for INAI sites using a modification of methods described by Iverson et al. (1996). Iverson et al. (1996) based their IMI calculation on hillshade (40% weight in the model), flow accumulation of water downslope (30% weight), total Available Water Capacity (20% weight), and landscape curvature (10% weight). We downloaded Digital Elevation Models (DEM files) for the locations of the INAI prairie sites. We then calculated flow accumulation, curvature, and hillshade using Arc-View (ESRI 1998). These factors were then fed into the formula $(0.4 * \text{hillshade}) + (0.3 * \text{flow accumulation}) + (0.1 * \text{curvature})$. This is similar to the model used

by Iverson et al. (1996), with the omission of data on available water capacity of the soil, which was not available for the INAI sites. Additionally, because of errors in the DEM files or high variability, we had to drop about one-quarter of the sites, leaving 162 sites in the final analysis. To determine vegetation response to moisture we ran Pearson product-moment correlations between Integrated Moisture Index values and ordination axis scores for the 1970s INAI sites (SAS Institute 1989).

Pearson product moment correlations (SAS Institute 1989) between soil parameters and site ordination scores were performed for sites that had soils data available. Soil texture data were only available for the INAI sites sampled in 1998 and nitrate data were only available for Wisconsin sites. We tested the relationship between the soil variables and site axis score for each of the three ordination axes. We used the axis scores from the analysis of the combined data sets. The INAI sites resampled in 1998 with soils data were fairly evenly spread throughout the ordination space, therefore, correlation analyses are meaningful for the gradient as a whole. In addition, we compared ordination axis scores of the INAI sites resampled in 1998 to the scores of the same sites from the 1970s sampling, to determine if the 1998 samples were comparable to the 1970s samples using Pearson product-moment correlations.

To explore the relationship between soil variables and the IMI in determining species distribution we used only the data from the resampled INAI sites because this was the only data set linked with both soils and IMI data. We reduced the number of dimensions expressed by soil variables by using Principal Components Analysis (PCA) to order the sites using soil variables (% organic matter, and available Ca, Mg, K, and P). The axis 1 PCA scores from this ordination and the Integrated Moisture Index were used as independent variables in a stepwise multiple regression of the axis 1 DCA scores using species data. Only 19 sites resampled in 1998 had both IMI and soils data and were included in the regression analysis. We additionally ran a DCA ordination using soil variables and a PCA ordination using species data. Thus, the sites were ordinated using PCA and DCA for species data and again using soils data. Axis 1 scores from the PCAs and DCAs using species and soils data were compared to each other using Pearson product moment correlations

The 1998 INAI data were also analyzed sep-

arately using Canonical Correspondence Analysis (CCA) in PCORD version 4 (1999). This method is similar in concept to DCA, except that is a direct ordination technique that performs multivariate regressions to explicitly test environmental data against ordination scores (ter Braak 1986, Palmer 1993). For a CCA, a complete set of environmental data is necessary for every site, so we were only able to perform the analysis on the 1998 INAI data. We removed silt from the set of variables to be considered, as it showed a high level of correlation with sand ($r = -0.983$) and was moderately correlated with clay ($r = 0.382$). We also performed Monte Carlo simulation analyses on the data to test for the significance of the axes. Only the p-value for the first axis is reported because using a simple randomization test for axes two and three may bias the p-value for these axes (P. Legendre, Personal Communication, 9 May 2005). For the Monte Carlo tests, the null hypothesis was no linear relationship between matrices scores and time of day was used for random number seeds. One thousand runs were made. We used weighted-average (WA) scores because these have been generally used in the past with field data. There are also some concerns about the effect of noise in the data on the LC (linear combination) scores (McCune 1997).

Results. INAI SITES. The 1970s samples of the INAI sites separated into six groups of sites on the first two axes of the ordination (Fig. 3). These groups generally support the substrate/topographic categories that INAI sites were placed into by the Illinois Natural Area Inventory: blacksoil, sand, gravel, dolomite and hill prairies. Axis 1 represented a moisture gradient and was significantly correlated with the Integrated Moisture Index calculated from topographic data ($r^2 = 0.35$, $P < 0.0001$, $df = 160$). Dry sand prairies were separated from hill prairies on axis 2. The separation of sites into six groups also generally reflected a topographic gradient within the state, with upland sites receiving low axis 1 scores and lowland sites receiving high axis 1 scores.

The six substrate/prairie groups from the driest to the wettest grouping were: (1) dry sand prairies, (2) transitional sites, including gravel and sand prairies, (3) loess and glacial drift hill prairies, (4) transitional sites including gravel and dry dolomite, loess hill, and dry-mesic prairies, (5) dry-mesic to mesic prairie sites on loess or glacial till blacksoil or sand substrates, and

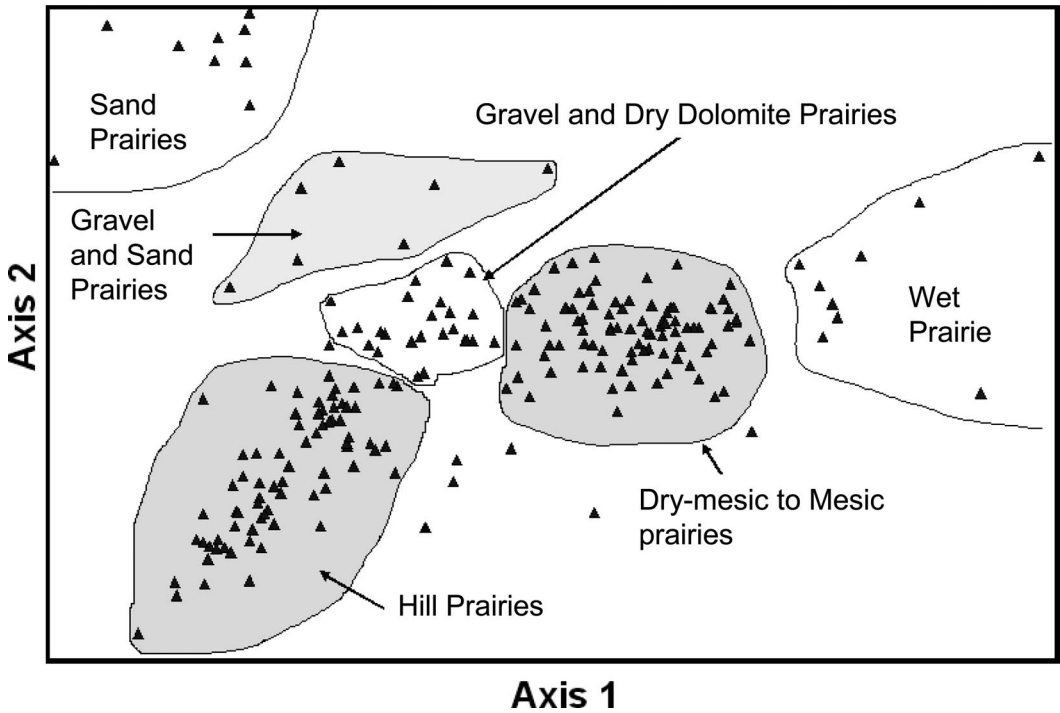


FIG. 3. DCA axes 1 and 2 for of Illinois Natural Areas Inventory sites, modified from Corbett and Anderson (2001).

(6) wet, wet-mesic and wet dolomite prairies. Outliers are most closely related to group five.

Even though *Schizachyrium scoparium* is the leading species in 4 of 6 community types, historically it was not the most abundant prairie species in Illinois (Table 1). Mesic and wet prairies were the most common prairie types and may have covered as much as 55% of the state (Fehrenbacher et al. 1968) and other species dominate these communities. Comparing these results to what is known about Wisconsin prairie (Curtis 1971, Umbanhowar 1992, 1993, Cochran and Iltis 2000) demonstrated that the separation of dominant prairie species in Illinois and Wisconsin follow similar patterns, if differences in community designation for similar vegetation types are considered.

In Table 1, species are listed from those occupying the most xeric sites to species dominating wet prairie and wet dolomite prairies in Illinois. Most of the species listed in Table 1 were prevalent species in one or more of the prairie communities delineated by Curtis (1971). However, Curtis' designations for Wisconsin were different from patterns observed in Illinois for several species. Curtis indicated *Calamovilfa longifolia* (Hook.) was a dune modal. In Illinois

sand prairies, *Calamovilfa* usually occurs on dunes within the prairie. *Opuntia humifusa* (Raf.), *Ambrosia psilostachya* (DC), *Tephrosia virginiana* (L.), and *Lithospermum carolinense* (J. F. Gmel.), which occur in Illinois sand prairies, were modal in cedar glades, sand barrens, or oak barrens. The oak barrens and sand barrens of Wisconsin (Curtis 1971, Will-Wolf and Stearns 1999) are similar to Illinois sand prairies, which often grade into sand savannas, and Wisconsin cedar glades have a ground layer similar to dry prairie (Curtis 1971). In Wisconsin, *Solidago riddellii* (Frank.) and *Carex stricta* (Lam.) were modal in fen and southern sedge meadow communities, respectively, and occurred in Illinois wet and wet dolomite prairies. Curtis (1971) indicated that some investigators consider fens to be variants of wet prairies that have an internally flowing supply of bicarbonate-rich water. Sedge meadows have many species in common with wet prairie, but they are dominated by members of the Cyperaceae instead of members of Poaceae (Curtis 1971). Thus, the leading species in prairies in the two states are similar and they occupy similar habitats (Curtis 1971, Cochran and Iltis 2000).

Table 1. Leading species in six community types for species with mean (\pm SE) quadrat frequency of at least 2.0%. Letters after species names indicate its modal community in Wisconsin (Curtis 1971), PD = dry prairie, PDM = dry mesic prairie, PM = mesic prairie, PWM = wet mesic prairie, PW = wet prairie, DUN = dune, OB = oak barren, CG = cedar glade, SB = sand barren, FN = fen, SS = southern sedge meadow (modified from Corbett and Anderson 2001).

Species	Community type					
	Dry Sand	Gravel/Sand	Hill Prairie	Gravel/Dry Dolomite	Mesic/Dry Mesic	Wet/Wet Dolomite
<i>Schizachyrium scoparium</i> PD	16.1 \pm 1.5	17.3 \pm 2.9	15.4 \pm 0.7	11.6 \pm 1.4	3.6 \pm 1.4	
<i>Opuntia humifusa</i> CG	8.4 \pm 1.8					
<i>Ambrosia psilostachya</i> SB	6.7 \pm 2.2					
<i>Calamovilfa longifolia</i> DUN	3.9 \pm 2.0					
<i>Panicum oligosanthos</i> PDM	3.3 \pm 1.7	2.4 \pm 1.6				
<i>Tephrosia virginiana</i> OB	3.3 \pm 1.7					
<i>Bouteloua hirsuta</i> CG	2.3 \pm 1.5					
<i>Stipa spartea</i> PDM	2.0 \pm 1.0	4.2 \pm 2.4		4.5 \pm 1.0		
<i>Euphorbia corollata</i> OB		5.4 \pm 2.0			3.6 \pm 0.4	
<i>Echinacea Echinacea pallida</i> PM		3.1 \pm 2.0		3.4 \pm 2.6		
<i>Lithospermum carolinense</i> SB		2.7 \pm 2.2				
<i>Koeleria cristata</i> SB		2.5 \pm 2.0				
<i>Callirhoe triangulata</i> PDM		2.3 \pm 1.6				
<i>Bouteloua curtipendula</i> PD			9.1 \pm 0.8	3.8 \pm 0.8		
<i>Sorghastrum nutans</i> DMP			4.5 \pm 0.7		4.4 \pm 0.4	
<i>Dalea purpurea</i> DP		2.2 \pm 2.2	4.5 \pm 0.4			
<i>Euphorbia corollata</i> OB			4.1 \pm 0.4	4.6 \pm 0.7		
<i>Solidago nemoralis</i> DP			3.6 \pm 0.5			
<i>Psoralea tenuiflora</i>			2.8 \pm 0.4			
<i>Aster azureus</i> DMP			2.5 \pm 0.5			
<i>Amorpha canescens</i> DP			2.3 \pm 0.4	3.6 \pm 0.7		
<i>Sporobolus heterolepis</i> DP				3.0 \pm 0.6	3.0 \pm 0.4	
<i>Rosa caroliniana</i>				2.5 \pm 0.6	2.4 \pm 0.3	
<i>Aster ericoides</i> PDM				2.3 \pm 0.6	3.6 \pm 0.4	
<i>Andropogon gerardii</i> PM					5.0 \pm 0.5	2.5 \pm 0.7
<i>Fragaria virginiana</i> ND					2.2 \pm 0.3	2.7 \pm 0.8
<i>Carex</i> spp.						6.3 \pm 1.8
<i>Solidago gigantea</i> PW						4.3 \pm 0.9
<i>Pycnanthemum virginianum</i> PWM						3.7 \pm 0.8
<i>Calamagrostis canadensis</i> FN						3.5 \pm 1.5
<i>Spartina pectinata</i> PW						3.2 \pm 0.8
<i>Carex stricta</i> SS						2.2 \pm 2.1
<i>Helianthus grossuserratus</i> PWM						2.7 \pm 1.1
<i>Solidago riddellii</i> FN						2.7 \pm 0.9

COMBINED INAI AND WISCONSIN SITES. For the combined data set (Fig. 4), based on published species distribution across moisture gradients (Curtis 1971, Bazzaz and Parrish 1982, Nelson and Anderson 1982, Anderson et al. 1983), we determined that DCA axis 1 represented a moisture gradient from dry (sites with low axis 1 scores) to wet (sites with high axis 1 scores). Sites from Illinois and Wisconsin were fairly evenly spread across the axes and formed a continuum. The second ordination axis separated most Wisconsin and Illinois sites. The separation of Wisconsin and Illinois sites on DCA axis 2 is due in part to differences in species relative frequencies between Wisconsin and Illinois sites and some species being present in the Wisconsin data set that were absent from the Illinois set

and *vice versa* (Corbett 1999). That does not mean these species are absent from the flora of either state; they were merely not recorded in these data sets. The third ordination axis (Fig. 4) separated hill prairies from dry sand sites. The first and third axes are the most interesting axes, as they represent regional environmental patterns.

The first ordination axis showed positive correlations with soil organic matter, potassium, and negative correlations with phosphorus and pH (Table 2) and nitrate ($r^2 = 0.18$, $P < .001$), which was only available for the Wisconsin data, is not shown in Table 2.

The second ordination axis, which separated Illinois and Wisconsin sites, was positively correlated with calcium and phosphorus. A com-

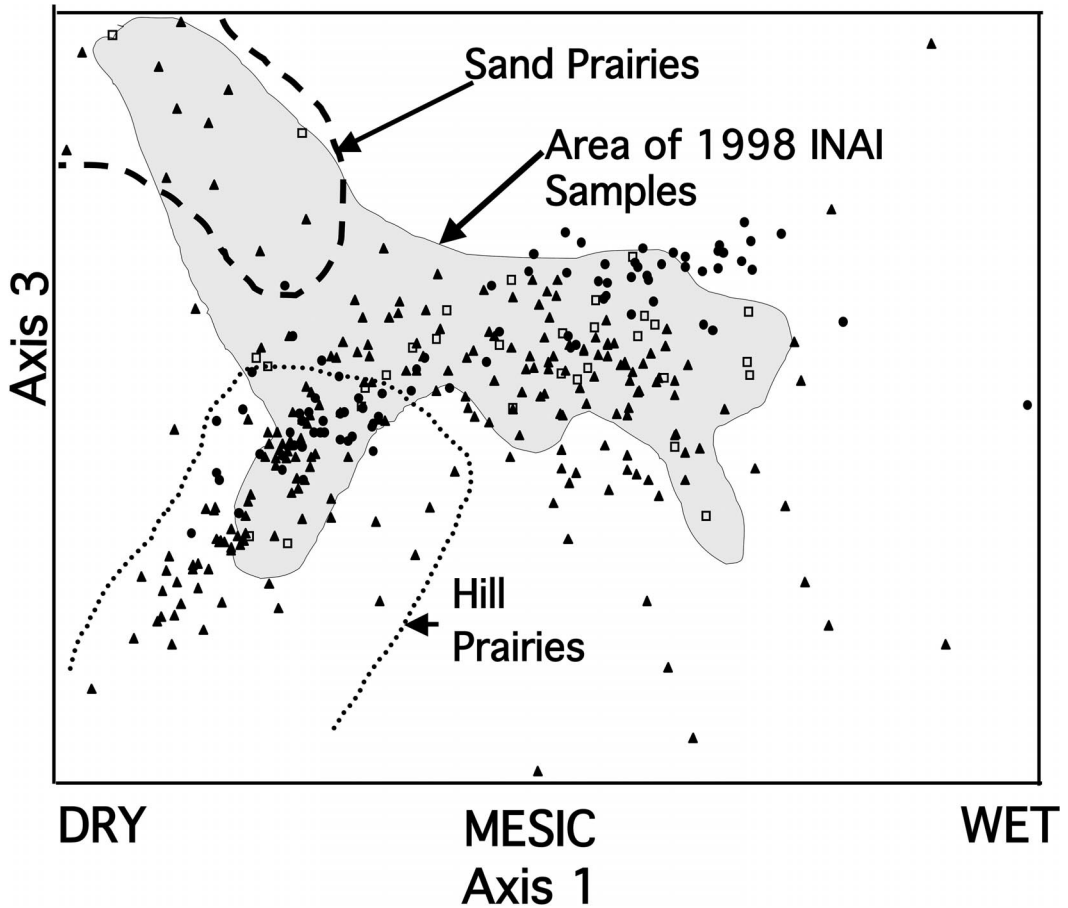


FIG. 4. First and third axes from ordination analysis of combined data set (INAI, PEL, and summer 1998 sampling). Solid triangles represent original Illinois Natural Areas Inventory sites, solid circles represent Wisconsin sites, and open squares represent summer 1998 resampled INAI sites. The first ordination axis corresponds to a moisture gradient from dry (left side) to wet (right side). The third ordination axis separates hill prairies from dry sand sites, with sand sites having higher axis 3 scores than hill prairies.

parison of average P and Ca values between both states demonstrated that Wisconsin sites were higher in both phosphorus (34.8 ppm P for Wisconsin vs. 8.6 ppm P for Illinois, $P = 0.0017$, $df = 86$) and calcium (4252 ppm Ca for Wisconsin vs. 2798 ppm Ca for Illinois, $P <$

0.0001, $df = 86$). (Phosphorus was tested using Kruskal-Wallis, as the data did not have equal variances; calcium was tested using a Student's t -test). A few dry sand areas in Illinois with relatively high levels of phosphorus received axis 2 scores similar to those of Wisconsin sites. Cor-

Table 2. Pearson product-moment r^2 -values between axis scores and soil parameters. Correlations marked with an * are significant and other correlations are not statistically significant.

Soil parameter	Axis 1	Axis 2	Axis 3
Organic matter	0.55* (direct)	n.s.	n.s.
Potassium	0.37* (direct)	n.s.	0.32* (inverse)
Phosphorus	0.47* (inverse)	0.31* (direct)	n.s.
pH	0.33 (inverse)	n.s.	n.s.
Calcium	n.s.	0.45* (direct)	0.49* (inverse)
Magnesium	n.s.	n.s.	n.s.
Sand	n.s.	n.s.	0.59* (direct)
Silt	n.s.	n.s.	0.58* (direct)

Table 3. Interest correlations from Canonical Correspondence Analysis of summer 1998 data. Interest correlations represent the r^2 values between the environmental values and the site scores.

Soil parameter	Axis 1	Axis 2	Axis 3
pH	-0.439	-0.532	0.393
Organic matter	0.679	0.081	0.179
Phosphorus	-0.011	0.413	-0.414
Potassium	0.562	-0.346	-0.476
Calcium	0.154	-0.435	0.598
Magnesium	0.565	-0.167	0.099
Sand	-0.121	0.820	0.031
Clay	0.317	-0.391	0.134

relations with other soil variables were not significant.

The third ordination axis showed greatest separation between dry sand (high axis 1 scores) and hill prairies (low axis 1 scores). This axis was positively correlated with sand content and negatively correlated with silt content, reflecting differences in soil texture and parent materials (sand or loess) between sand prairies and hill prairies, respectively. The third ordination axis was also negatively correlated with potassium and calcium, suggesting that hill prairie soils are higher in these nutrients than are soils of dry sand prairies.

RESAMPLED INAI SITES. We compared the DCA ordination scores for the 1998 and 1970s INAI samples using Pearson correlation. Correlation of axis 1 and axis 2 scores were statistically significant, with r^2 values of 0.94 for axis 1 and 0.93 for axis 2, respectively, indicating that the 1998 samples are comparable to and representative of the original 1970s samples. This does not mean the prairies have not changed between the time of the INAI and when we sampled them. Rather these results indicate that the areas we sampled in the prairie in 1998 were like those sampled by the INAI even though the overall size of some prairies may have declined. Additionally, portions of the prairies that we did not sample in 1998 may have been sampled during the INAI and undergone compositional change since 1970s.

The results of the Canonical Correspondence Analysis of the 1998 INAI data were similar to those of the DCA analyses, in that axis 1 corresponded to a moisture gradient. Based on interest correlations (Table 3), Axis 1 is most strongly positively correlated with organic matter, potassium, magnesium, and clay. It shows negative correlations with pH, and weakly, with

sand. The second CCA axis was positively correlated with sand and phosphorus, and most strongly negatively correlated with pH and calcium. Typically, this axis separated high-calcium sites (the dolomite prairie and also some of the sand sites) from other sites in the analysis. The third axis was most strongly correlated to calcium (positive correlation) and to potassium and phosphorus (negative correlation). This axis separated sand prairies (typically higher in calcium) from hill prairies (typically higher in phosphorus). For the three axes, eigenvalues were as follows: Axis 1: 0.476 ($P = 0.009$), Axis 2: 0.414, and Axis 3: 0.321. The species-environment correlation is 0.947 ($P = 0.02$, $n = 29$). The total variation explained by the three axes is 21.4%, which is fairly low, but that may reflect the importance of moisture availability, which was not included in the second matrix for the CCA, in affecting species composition.

For the PCA ordination of the resampled INAI sites using soils data, the first and second eigenvalues accounted for 53 and 26 percent of the variance, respectively. Eigenvectors for Mg, organic matter, Ca, K, and P on the first axis were 0.57, 0.56, 0.46, 0.32, and -0.17, respectively. In the stepwise forward multiple regression, using the species based DCA axis 1 scores as the dependent variable, the first independent variable entered into the equation was IMI with a partial R^2 of 0.53, ($F = 19.55$, $P = 0.004$). Adding PCA axis 1 scores into the model increased the R^2 to 0.60 but this did not result in a significant increase in variance accounted for by the regression ($F = 2.94$, $P = 0.105$). These results suggest that species distributions are more responsive to variation in moisture than variation in availability of inorganic nutrients.

To demonstrate that the insignificant contribution of PCA axis 1 scores to the multiple regression R^2 -value was not related to the dependent variable being generated using DCA and the axis one scores resulting from a PCA ordination, we compared DCA and PCA ordinations using soils or species data. There were no significant correlations when PCA axis 1 site scores that were generated using soil data were compared with axis 1 site scores using species data (PCA soils vs. DCA species, $r = 0.38$, $P = 0.06$, $df = 27$; or PCA soils vs. PCA species, $r = 0.13$, $P = 0.47$, $df = 27$). However, DCA and PCA axis one scores using species data were significantly correlated ($r = -0.66$, $P < 0.0001$, $df = 27$) as were DCA and PCA scores using soils data ($r = 0.79$, $P < 0.0001$, $df = 27$). These

results emphasize that ordinations using species or soils data result in different patterns, suggesting the variations in soils are not the primary factor affecting plant species distributions.

Discussion. Ordination analysis of the Wisconsin and Illinois data demonstrated a vegetation continuum on the first DCA ordination axis that corresponded to a moisture gradient with significant correlations with some soil variables (organic matter, K, nitrate, and P). In Illinois, this gradient is related to topographic patterns among sites within the state, as shown by the Integrated Moisture Index correlation with axis 1. In western and southwestern Illinois, there is a greater degree of topographic variability than in northeastern Illinois and most prairies occurred on south or southwest facing slopes or sandy upland sites and received low axis 1 scores. Prairie sites on the fairly flat and low-lying Wisconsinan till plain in northeastern Illinois received high axis 1 scores. In Wisconsin, Curtis (1971) described general topographic patterns and notes that xeric prairies tend to be found on uplands, mesic prairies on flat to rolling plains, and wetter prairies in lowland areas. Thus, at a regional scale examining most of the eastern 1/3 of the Prairie Peninsula, a major environmental influence on prairie species composition is soil moisture availability as affected by topographic conditions. Other studies have demonstrated that variation in prairie vegetation is continuous and is primarily influenced by moisture availability at a variety of spatial scales (e.g., Curtis and Greene 1949, Bazzaz and Parrish 1982, Nelson and Anderson 1983, Anderson et al. 1984, and Umbanhowar 1992). However, none of these studies explicitly addressed topography on a regional scale.

Using the 1998 INAI data set, we assessed the effects of moisture and soil nutrients on species composition. The strongest environmental influence on the first DCA axis was the Integrated Moisture Index, which is topographically-based. In the stepwise multiple regression, it was the first variable to enter the model, and it explained 53% of the variation on the first axis. Adding nutrient results (from the PCA of nutrient data) did not significantly improve the model's fit. These results suggest that the primary factor affecting prairie plant species distribution on a state-wide scale is soil moisture availability as influenced by topography.

Nevertheless, on specific sectors of the moisture gradient we found differences between

communities related to soil texture and availability of inorganic nutrients. Dickman et al. (1984) reported that sand prairies have coarser textured soils and higher levels of phosphorus but lower levels of calcium than hill prairies. These results are consistent with the distribution of hill prairies and sand prairies on the axes of two ordinations. For example, on the third ordination axis of the combined regional data set and the 1970s and 1998 INAI data sets, sand prairies were separated from hill prairies. The third ordination axis of the regional data was positively correlated with calcium and silt and the third axis of the 1988 INAI data was positively correlated with phosphorus and negatively correlated with calcium and clay. The direction of the correlations with soil texture and availability of Ca and P on the axes and the distribution of hill and sand prairies on the axes are in concordance. Similarly on the second axis CCA axis of the 1988 INAI data, sand and phosphorus had positive correlations and calcium was negatively correlated with this axis.

For some prairie-vegetation studies—particularly those conducted on smaller spatial scales—moisture gradients are closely correlated with nutrient gradients (Nelson and Anderson 1983, Anderson et al. 1984). Generally, these studies demonstrate that as moisture availability increases, nutrient availability also increases. However, these studies were conducted as a series of samples across a comparatively short topographic gradient at a single site, so that the soil parent material and development is similar within all samples. The major differences in the soils reflect movement of soil particles (silt and clay) and inorganic nutrients from upper to lower slope positions. In the current study, sites having soils that developed from a wide range of parent materials (sand, loess, or glacial till) occupied the same sector of the moisture gradient. This pattern is especially evident when comparisons are made among sites occurring on the extreme sectors of the moisture gradient where topography controls availability of soil moisture. Because parent material has a major influence on the potential nutrient availability of a soil (Brady and Weil 2002), we found few correlations between soil nutrient availability and soil moisture at a regional scale.

Which environmental factors exert the greatest influence on community composition depends on the spatial scale of the investigation. At the regional scale (this paper) as well as at the state scale in Illinois and Wisconsin (Curtis

1971, Umbanhowar 1992, Corbett 1999), soil moisture as affected by topography is the most important environmental factor affecting species composition. Most soil parameters (specifically, nutrient availability) have secondary importance at the regional scale, but for smaller-scale studies (e.g., Anderson et al. 1984), nutrients showed a stronger relationship with moisture availability. This likely reflects patterns of similarity and differences in parent material with spatial scale. Nevertheless, within specific sectors of the moisture gradient texture and availability of inorganic nutrients play an important role in determining species distributions on a regional scale.

The sites used in this study represent remnant sites that were sampled after most tallgrass prairie had been lost to agriculture or development. Some of the sites have been lost or degraded since their original sampling. However, sites that remain, in Illinois at least, represent a sample of the diversity of prairie—in terms of moisture availability, soil texture, topographic position and species composition—that originally existed within the state. Although these sites are valuable remnants and may represent genetic diversity for the species involved, they are still small and fragmented. Of the “high quality” prairies (grade A or B by the INAI), 83 % are less than 10 acres in size, and 30% are less than 1 acre in size (Robertson et al. 1997). These remnants will require high levels of maintenance in the future to have a chance of persisting into the next century.

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