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GRADIENTS IN GROUNDLAYER COMPOSITION,

STRUCTURE AND DIVERSITY IN

REMNANT AND EXPERIMENTALLY RESTORED

OAK SAVANNAS

by

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ABSTRACT

Surprisingly little is known about the composition, structure, and diversity of the groundlayers in Wisconsin oak (*Quercus* spp.) savannas. I initiated observations in 12 remnant savannas and experimental groundlayer restorations that relate the distribution and ecological characteristics of plant species to gradients in soil texture and light availability, which was determined by computer analysis of hemispherical canopy photographs. Comparisons of average composition along gradients showed that % sand had at least twice the effect on composition as did light availability. Forb cover increased on progressively finer-textured, nutrient-rich, moister soils, and, on average, was greater than graminoid cover in all but the sandiest, brightest environments. Physiologic (C_3 vs. C_4 photosynthesis, nitrogen fixation) and morphologic traits (leaf width, leaf inclination, leaf height) of herbaceous species had individualistic distributions in two-dimensional gradients of % sand and light availability that were consistent with expectations based on economic theory. Remnant groundlayers were species rich from fine to broad spatial scales and represent a previously overlooked opportunity for the conservation of biological diversity. Restoration experiments are shown to be useful compliments to field studies in remnant communities.

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Chapter 1

Soil and light gradients affect composition, structure,

and diversity in remnant oak savannas in southern Wisconsin

Abstract.

1)   Savannas with scattered oak canopies were once the most widespread communities in southern Wisconsin, but now are considered among the most endangered. Surprisingly little is known about the composition, structure, and horizontal patterning of their species-rich groundlayers. This study relates the distribution and ecological characteristics of 415 species to local and regional gradients in soil composition and light regime, based on an analysis of 722 1-m^2 quadrats in 12 remnant savannas.

(2)   Groundlayer composition was strongly related to among-site differences in soil texture and within-site differences in light availability, with variation in percent sand content accounting for twice as much turnover in species composition as direct PPFD (μmoles m^{-2} day^{-1}) estimated from hemispherical photographs. Most species reached their peak cover under sunny or partly shaded conditions; the distribution of flowering/fruiting within species was often skewed toward sunnier microsites.

(3)   Forb cover increased with percent silt content. Graminoid cover showed a curvilinear relationship to both light and soil texture, and was highest in well-lit and/or sandy microsites. Total groundlayer cover increased with percent silt content at a given level of irradiance; total cover increased with direct PPFD on

siltier sites, but decreased with direct PPFD on sandy sites.

(4)   Species richness of both forbs and graminoids increased linearly with cover by each group, when quadrats were stratified by percent sand content and direct PPFD; the number of forb species present for a given level of cover was, however, much greater.

(5)   Among graminoids, C_4 grasses were significantly more common in bright, sandy microsites; C_3 grasses and sedges had broader ecological distributions. Among forbs, leaf width increased and leaf inclination decreased toward shadier and siltier microsites; tall species were generally found in areas with dense groundlayer cover. Plants with N-fixing symbioses were found mostly in sandy, well-lit microsites, although vine-like species occurred on shadier and/or siltier microsites, where N-fixation might be expected to yield a lower energetic advantage. Most species were perennial (88%), with few being annual (6%) or biennial (6%).

(6)   Wisconsin savannas are unusually diverse. At small spatial scales, the mean number (± s. d.) of species was 16.1 ± 1.2 m^{-2}, compared with 11.4 ± 2.6 for prairies and 8.2 ± 2.2 m^{-2} for forests. At slightly larger scales, savannas showed a very high amount of internal turnover in species composition with distance, resulting in 89.3 ± 11.3 species per 20 m^2, compared with 42.8 ± 8.1 species for prairies and 41.5 ± 7.8 species for forests. Finally, a survey of 23 savanna remnants totaling 42 ha yielded 507 native species, about 27% of the indigenous vascular flora of Wisconsin (ca. 14×10^6 ha), suggesting that savannas show a

large amount of floristic differentiation at the largest spatial scales as well.

(7)   Common groundlayer species occupied a wide variety of soil/light microsites and occurred in a wide range of plant communities. Species in each of the two largest genera of forbs (Aster and Solidago) differed significantly in distribution, supporting habitat partitioning as a mechanism of coexistence.

(8)   Contrary to previous reports, savannas are forb-dominated (except on the sandiest or sunniest microsites). The release of forbs from competition with C_4 grasses under partly shaded conditions may help account for the high diversity of savanna groundlayers relative to prairies. The differential distribution of plants with different energy-capture adaptations - together with the large variation within sites in groundlayer light regime and among sites in soil texture - suggests that partitioning of light and soil gradients are also important for maintaining the high plant diversity of oak savannas at moderate to large spatial scales.

INTRODUCTION

Savannas with a scattered canopy of oaks (*Quercus* spp.) covered millions of hectares in the North American Midwest soon after settlement (Gleason 1913; Anderson 1983; Nuzzo 1986). Frequent fires (together with drought, soil poverty, and/or grazing) are thought to have maintained the open nature of oak savannas and created a mosaic of sunlit and shaded microsites in their groundlayers (Gleason 1923; Bray 1958, 1960; Curtis 1959; Grimm 1983, 1984; Anderson and Brown 1986; Packard 1988a, b, 1993; Tester 1989, 1995; Haney and Apfelbaum 1990; Pruka 1994). Following settlement and widespread fire suppression through overt means as well as landscape fragmentation (Leach and Givnish 1996), oak savannas disappeared or succeeded into woodlands or forests over much of their previous range; by the early 1980s, intact savanna remnants occupied only 0.02% of their pre-settlement extent (Nuzzo 1986).

In southern Wisconsin, oak savannas were the most extensive vegetation type soon after settlement, covering ca. 42% of the area below the Tension Zone (Curtis 1959; Hole 1976). Curtis (1959) recognized three primary kinds of oak savanna, based on canopy composition and substrate. Oak openings occupied mesic, loamy soils on upland sites and were dominated by large, single-stemmed bur oaks (*Quercus macrocarpa*), although white oak (*Q. alba*) and black oak (*Q. velutina*) were also sometimes common. Oak barrens occupied sandy or gravelly substrates on upland sites and were dominated by shrubby, multi-stemmed Hill's oaks (*Q. ellipsoidalis*) or black oaks. Lowland oak savannas (seen by Curtis as

related to oak openings) were an especially rare variation on floodplains and glacial lake beds, dominated by a combination of bur oak and swamp white oak (*Q. bicolor*). While there has been general agreement on the canopy composition of oak savannas, a lively debate has emerged regarding the nature of savanna groundlayers, which would have housed the vast majority of plant species in savannas communities. Based on field studies by Bray (1955, 1958, 1960), Curtis (1959) emphasized the close similarity of savanna groundlayers to prairies, noting the dearth of species that reached their peak abundance in savannas. Packard (1988b, 1993) argued that Bray and Curtis greatly underestimated the uniqueness of the savanna flora, and that their conclusions were an artifact of having studied savanna groundlayers after many decades of fire suppression. Based on a list of groundlayer species in central Illinois savannas soon after settlement (Mead 1846) and his own experience attempting to restore savannas, Packard (1988b, 1993) proposed that there had been many species that were savanna specialists, but that many had become marginalized or locally extirpated by fire suppression. In response, Mendelson et al. (1992) argued that Packard's work was speculative and based on sites more densely shaded than the savannas studied by Bray and Curtis. Largely overlooked in this controversy has been the question of whether the Bray-Curtis view of savannas as essentially "trees with a prairie groundlayer" was itself an artifact of having explicitly selected sites for study based on the abundance of prairie grasses there (Bray 1955, 1958, 1960).

To help resolve this controversy, in this paper I analyze patterns in

groundlayer composition, structure, and diversity of savannas along regional gradients of soil texture and local gradients of understory light regime. Twelve sites in southern Wisconsin were chosen for study based on their possession of (i) a scattered canopy of open-grown oaks; (ii) a groundlayer dominated by native species across the entire gradient from sunny to shady microsites; and (iii) a history of frequent fires during at least the past 10 years. These criteria were adopted to avoid the sampling biases inherent to the previous studies by Bray (1955, 1958, 1960), and to provide a more accurate picture of the nature of oak savannas, their horizontal patterning at local and regional scales, and their significance for the conservation of biological diversity.

METHODS

Site selection.--Remnant savannas in southern Wisconsin were screened using the criteria that each should have (i) a canopy of open-grown oaks; (ii) a groundlayer dominated by native species (woody or herbaceous, graminoid or forb) across the entire gradient from sunny to shady microsites; and (iii) a history of fire during at least the past 10 years. From the resulting pool of sites, several were eliminated because all or portions of their groundlayers contained very few species, most commonly a near-monoculture of *Carex pensylvanica.* The selected sites are being managed for their natural area quality, except for Range 32, Quarry Hill, Tarr 1 and Tarr 2, which have been subject to wildfire. None of the sites have been under continuous fire management since the time of settlement. Some sites had been previously grazed by cattle, but not within the previous 10 years. A few sites had some shrubs mechanically removed, but not within 5 years. The 12 sites chosen for intensive study happened to have low (< 9%) clay content; as a result, these sites are largely distributed along a uni-dimensional soil gradient ranging from 36 to 91% sand content (Table 1).

Canopy composition.--By their very nature, savannas are mosaic communities with a welter of open, closed, and partially shaded microsites mixed in patchy fashion at a variety of spatial scales. To characterize the canopy density and composition of this "froth" is inherently extremely difficult, with the values of traditional measures heavily dependent on where sample boundaries are drown around a stand of open-grown trees. The relative basal area of individual tree

species was quantified based on a stratified random sample along transects through each study site; no attempt was made to measure "average" canopy cover, a commonly used (Curtis 1959; White and Madany 1978; Haney and Apfelbaum 1994; Faber-Langendoen 1995) but flawed index.

Edaphic characteristics.--Cores for the upper 15 cm of soil were obtained from at least 10 locations within each site, pooled, and analyzed for % sand, silt, and clay, %organic matter, pH, concentrations of P, K, Ca, Mg, and % total N. All analyses were conducted by the University of Wisconsin Soil and Plant Analysis Laboratory using standard techniques.

Sampling of savanna groundlayers.--At each site, the composition, structure, and diversity of the groundlayer was quantified in 50 to 100 1-m^2 quadrats, stratified by light availability. Across sites, a total of 722 quadrats were inventoried. Groundlayer light regime was estimated via computer analysis of hemispherical photographs using SOLARCALC 5.41 (Chazdon and Field 1987). After full canopy leaf-out in the year of vegetation sampling, photographs were taken ca. 50 cm above the southern half of each quadrat, so as to exclude groundlayer foliage. The film plane was levelled and the top of the camera oriented to magnetic north; the orientation of the photographs was corrected for magnetic declination in SOLARCALC. Light availability during the growing season was estimated as the sum of direct potential photon flux density (PPFD, μmoles m^{-2} day^{-1}) for the summer solstice (June 22) and a point midway between the solstice and equinox (May 5 and August 4), expressed as a percentage of the maximum such sum for

an unobscured sky at the same latitude. For comparison, two other estimates of light availability were determined via SOLARCALC: total PPFD and %open sky. Percent sand content for each quadrat was taken to be the mean for the site. Total projected cover, maximum leaf height, and reproductive activity were visually estimated for each species occurring in a quadrat twice during a single growing season, in early and late summer. Cover classes were employed, with maximum values of 1%, 2%, 5%, 10%, 15%, ..., 100%. For analysis, the midpoint of each class was used. To distinguish the groundlayer from canopy, cover by woody plants > 2 m tall was ignored. Maximum leaf height was measured to the nearest 0.5 dm, and flowering/fruiting status was recorded. Species nomenclature followed Gleason and Cronquist (1991).

Species were classified into several kinds of guilds based on (i) maximum leaf width; (ii) leaf inclination: (iii) leaf height; (iv) growth form; (v) longevity; (vi) association with N-fixing symbionts; and (vii) possession of the C_3 vs. C_4 photosynthetic pathway. The morphological classifications were based on field measurements of mature, fully expanded foliage. Maximum leaf width (0 - 5 mm, 6 - 15 mm, 16 - 45 mm, > 45 mm) of forbs was based on the diameter of the largest circle that could be inscribed on a blade. Leaf inclination (o°, 30°, 60°, 90°) was taken to be the modal inclination from the horizontal as measured by clinometer; species with leaf inclinations that varied strongly with individuals or between microsites were excluded from analysis. Leaf height (0 - 10 cm, 11 - 20 cm, 21 - 40 cm, 41 - 80 cm, 81 - 160 cm, > 160 cm) was classified based on the tallest

individual observed. Growth forms included graminoids (Poaceae, Cyperaceae, Juncaceae, Hypoxidaceae) with grass-like foliage; forbs (herbs other than graminoids); woody vines; and shrubs. Species longevities (annual, biennial, or perennial) were taken from Gleason and Cronquist (1991). Species with N-fixing potential (all in Fabaceae, except *Ceanothus* [Rhamnaceae]) were as reported by Allen and Allen (1981). Grasses were classified as having the C_3 or C_4 photosynthetic pathway based on reports by Brown (1977), Heckathorn and Delucia (1991), and Kindscher (1992).

Data analysis.--Direct and indirect gradient analysis of groundlayer composition, structure, and diversity were conducted, using % sand content and % direct PPFD as the two primary gradients under study. To confirm that these two factors represented the most important environmental variables in the landscape of quadrats studied, I first conducted an ordination of quadrats in species space via non-metric multi-dimensional scaling (NMS; Minchin 1987), as implemented in PC-ORD (McCune and Mefford 1995). A "joint-plot" method was used to compare the direction and strength of relationships between various environmental variables and quadrat ordination scores in three dimensions. The "direction" of each relationship was the vector whose x, y, and z components were the Pearson correlations of the variable with each axis; the length of this vector represented the strength S (root-mean-square of the Pearson correlations) of the relationship. The current implementation of NMS in PC-ORD is limited to ca. 200 quadrats for the number of species involved, so 10 resampling trials were run using random subsets of

quadrats. Environmental variables included all soil parameters (see above) and % direct PPFD (see above), % open sky, and % total PPFD (Chazdon and Field 1987).

Two-dimensional Beta diversity. Beta diversity was analyzed simultaneously across sand and light gradients via multiple regression in a method similar to Hujik (1995). Both gradients were divided into five parts each containing as close to the same number of quadrats as was permitted by the data. Hence, each quadrat was sorted into one of 25 microhabitats. The Sorenson quantitative index of similarity (Magurran 1988) was calculated between the 300 unique pairs of microhabitats using mean cover for each species. For the multiple regression, the dependent variable was the natural logarithm of the Sørenson index values (Whittaker 1972) and the two independent variables were the differences in steps (0, 1, 2, 3, or 4) along each of the two gradients.

Correlation of gradients with ordination scores. Non-metric Multiple-Dimensional Scaling (NMS) ordinations of quadrats in species' space were produced using PCORD (McCune and Mefford 1995). A "joint plot" method was used to compare the strength of relationships between environmental variables and three-dimensional ordination scores. Strength $= (x^2 + y^2 + z^2)^{0.5}$, where x, y, and z are the squares of Pearson and Kendall correlations of the environmental variable (PPFD or sand) and the ordination's three axes. This version of NMS was limited to about 200 quadrats per trial, so 10 trials were run using random subsets of the quadrats. The differences between relative strength of %sand and %PPFD were

compared. In additions, a principal components analysis (Greig-Smith 1983; McCune and Mefford 1995) was conducted on the soil parameters to determine what fraction of the total variance in those parameters could be associated with a uni-dimensional gradient. Regression analysis was used to determine how well % direct PPFD could predict % open sky and % total PPFD.

To assess the relative importance of sand content vs. light availability in affecting groundlayer composition using direct gradient analysis, I calculated 2-dimensional β-diversity (slopes of species turnover) using the approach of Hujik (1995). Quadrats were grouped into quintiles along both the soil and light gradients, resulting in a classification of each quadrat into one of 25 microhabitats. The proportional species composition of each microhabitat was calculated, based on the average across quadrats of each species' maximum cover across sample dates. The quantitative Sørenson index of similarity (Magurran 1988) was then calculated between each of the 300 distinct, non-trivial pairs of microhabitats. Finally, the natural logarithm of the Sørenson index (see Whittaker 1972) was regressed simultaneously on the differences in the number of steps (0, 1, 2, 3, or 4) between microhabitats on each gradient (Hujik 1995). The slopes of this multiple regression represent the relative amounts of turnover in overall species composition along the soil and light gradients, respectively.

The mean ± standard deviation of a species' position along both soil and light gradients was calculated for the 87 "common" species that occurred in at least 5% of the quadrats. The mean position x_i of species i along each axis was

calculated as:

$$x_i = \Sigma C_{ij} z_j / \Sigma C_i, \tag{1}$$

where C_{ij} is the cover of species i in quadrat j, and z_j is the position of quadrat j along the gradient in question (% sand or % direct PPFD). The standard deviation s_i of species i's distribution along each axis was calculated as:

$$s_i = [(\Sigma \; C_{ij}(z_j - x_i)^2) / \Sigma \; C_{ij}]^{0.5}. \tag{2}$$

Standard Deviations of species' positions were used to compare their niche breadths along both soil and light gradients. To determine whether flowering individuals within a species tended to occur in more brightly lit microsites, the mean position of each common species was recalculated using only those quadrats in which flowering by that species had been noted. A signs test was then used to determine whether, across common species, flowering individuals occupied a significantly brighter position along the light gradient than all individuals of the same species.

The distribution and diversity of forbs and graminoids, the two dominant growth forms in the savanna groundlayers studied, were evaluated along both the soil and light gradients. As before, the light gradient was divided into quintiles based on % direct PPFD; the soil gradient, however, was divided into four steps, based on the standard soil-texture classes of sand, loamy sand, sandy loam, and silt loam (Brady 1974; Hole 1976). To assure that this method of analysis was not influenced by uneven distributions of light availability among the soil classes, the GLM procedure in SAS and the Student-Newman-Keuls test were used. Results

showed no significant relation between light availability and soil class (P > 0.53, d.f. = 718). The mean cover and species richness (# species m^{-2}) of forbs and graminoids was then calculated for each of the 20 resulting microhabitats. Mean cover and richness of each guild were related to each other using simple regression. Backwards-elimination multiple regression was used to relate cover and richness of each guild to position on the soil and light gradients, including as independent variables the step positions (S_s and S_L) of microhabitats on both gradients; the squares, natural logarithms, and squares of natural logarithms of step positions; products of step positions; and products of natural logarithms of step positions.

To illustrate the relative distributions of species or guilds of species, their mean coordinates were graphed. To test whether these distributions differed significantly along the % sand content and % direct PPFD gradients, I used a new non-parametric geostatistic utilizing the program GEODISTN (Syrjala 1996). The Syrjala test was originally used by its author to compare the geographic distribution of two populations in two dimensions. Here I use it, apparently for the first time, to evaluate the distribution of pairs of populations in a two-dimensional ecological space. The test requires that data on the abundance of the two populations being compared come from the same set of data points, with coordinates in a two-dimensional space. The null hypothesis is that the underlying distributions of the populations are identical; relative population size is immaterial. Each tests used at least 1000 replicate bootstrap resamplings. Syrjala tests were conducted to

evaluate the significance of observed differences in the soil x light distribution using cover data of (i) C_3 grasses, C_4 grasses, and sedges; (ii) different leaf width, inclination, and height guilds; (iii) potential N-fixing species; and (iv) species of *Aster* and *Solidago*.

Comparisons of species niche breadth within savannas with ecological breadth across habitats was analyzed based on comparisons with historical data compiled by Curtis (1959). First, indices of niche breadth were calculated for all species using 20 microhabitats (4 soil classes x 5 light classes - see above). Shannon and Simpson indices of diversity were calculated, using both qualitative (presence/absence) and quantitative (cover) data. The results obtained for each index were very similar in all cases (Spearman rank correlation > 0.96, P < 0.001), so only the results based on the qualitative Shannon index (potential range: 1-20) are presented. Based on studies of 1,232 sites in Wisconsin, Curtis (1959) presented a fidelity index for each of the common species in the flora, equal to the number of the 34 recognized native communities in which a species occurred. Relationships between niche breadth within savannas vs. between habitats were examined using rank correlation.

To compare levels of vascular plant richness in the three dominant native communities - savannas, prairies, and forests - in the uplands of southern Wisconsin, I compared my findings with data culled from unpublished field notes from the files of the Plant Ecology Laboratory (PEL) at the University of Wisconsin-Madison. Lowland stands were omitted. The PEL prairie and forest data were

collected in the 1940s and '50s by Curtis, his students and colleagues, and the PEL savanna data were collected by Bray. At least 10 of the 15 savanna sites were on sand, steep slopes, or thin soil. Typically the PEL field investigators recorded on pre-printed forms the presence of species in 20 1-m^2 quadrats per stand. Bray used the same form as used in the prairie studies, writing additional species in the margins. The species densities reported by these investigators were often under-reported, in part because alien species were often not tallied (G. Cottam, pers. comm.). To avoid spurious comparisons, I removed alien species from my savanna data before graphing and conducting statistical tests, but (for ease of collation and calculation) retained the few alien species in the PEL data base. This approach tended to bias the results in favor of greater diversity in the historical samples of prairies, savannas, and forests. For 16 upland prairies, 22 upland forests, 15 upland savannas from the PEL files and 8 upland savannas in the current study, I computed the mean number of species per quadrat (α diversity). For these same stands (omitting 4 PEL savanna stands in which the sample size was less than 20 quadrats) I also computed the total number of species found in 20 quadrats (γ diversity), and the amount of species turnover across 20 quadrats (β diversity = γ/α). Differences between each of the habitat means were compared using the SAS GLM procedure using the Student-Newman-Keuls test.

RESULTS

Community Characterizations. - Tree canopies at the 12 sites were dominated by open-grown oaks, which comprised 56 to 100% (mean = 82%) of total basal area (Table 1). Black oak tended to dominate on the sandiest sites, white and red oak on intermediate sites, and bur and swamp white oaks on the loamiest sites. The oaks tended to be aggregated in various configurations with open spaces near or between most trees. Non-oaks that contributed at least 10% to total basal included black cherry (*Prunus serotina*, 4 sites), basswood (*Tilia americana*, 2 sites), and jack pine (*Pinus banksiana*, 1 site). In most sites, trees that were commonly represented in smaller size-classes were generally fire-intolerant species (e.g., *Acer negundo, Prunus virginiana*) suggesting that these species had invaded during lapses in frequent fire.

Range 32 Barrens, which had the lowest percentage of oak basal area, would have been classified as Pine Barrens by Curtis (1959). Most of the remaining sites would have been classified as Oak Barrens or Oak Opening. However, a few sites could have been classified as savanna or forest, which Curtis (1959) distinguished with an arbitrary cut off average canopy of 50%. Because savannas are mosaic communities with a welter of open, closed, and partially shaded microsites mixed patchily at various spatial scales, it seems inappropriate to characterize the canopy density of such a froth with a single measure of "average" canopy density, given that the value of this measure would depend heavily on where the boundaries of a sample were drawn. All of the sites had,

however, a wide range of shaded, intermediate, and open microsites as determined by hemispheric photography.

Environmental gradients. - Percent sand content varied across sites from 36 to 91%; one locale (Tarr) was subdivided into two study sites based on an abrupt transition from sands to sandy loams (Table 1). A principal components analysis revealed that roughly 81% of the total variance in soil characteristics was explained by eigenvector 1, strongly associated with % sand content. All soil variables are significantly related to % sand content except pH ($P > 0.23$, 2-tailed t-test with 10 d.f.) and [P] ($P > 0.06$, 2-tailed t-test with 10 d.f.). Percent direct PPFD varied across quadrats from 0.0 to 100.0% (mean = 37.8 ± 29.5), was a significant predictor of both % open sky ($r^2 = 0.74$, $P < 0.0001$) and % total PPFD ($r^2 = 0.99$, $P < 0.0001$), and showed no significant correlation with % sand content ($r_s = 0.04$, $p > 0.33$, Spearman rank correlation with 722 observations). With three exceptions, the sites are situated on uplands. Marshall, Gratiot, and Tarr 2 lie within the flood plains of rivers or streams.

Gradients in species composition. - Ordination of quadrats in species space using non-metric multidimensional scaling showed that soil characteristics were all strongly correlated with axis 1, while aspects of light regime (% direct PPFD, % open sky, % total PPFD) were all strongly correlated with axis 2. These findings were obtained with 10 replicate resamplings of the quadrat data (see Methods). These results strongly suggest that there are two fundamental ecological gradients affecting the composition of savanna groundlayers in this study, corresponding to

soil texture and light availability. Percent sand was always more strongly related to ordination scores than was % direct PPFD (mean difference = 0.10 ± 0.03, P < 0.003, paired t-test).

A multiple regression of Sørenson similarity among pairs of 25 soil x light microhabitats showed that variation in soil texture had roughly twice the effect on average species composition as did light availability:

$$Ln(C) = 3.94 - 0.31G_{SAND} - 0.16G_{LIGHT}; \; r^2 = 0.56 , \qquad (3)$$

where C is the quantitative Sørenson index (Magurran 1988), and G_{SAND} and G_{LIGHT} are the number of steps separating a pair of microhabitats along the soil and light gradients, respectively. The coefficients (slopes) associated with G_{SAND} and G_{LIGHT} indicate the rate at which species composition changes with position on the soil and light gradients, and together are a 2-dimensional measure of β diversity (Hujik 1995).

A total of 417 native vascular plants were identified in 722 1-m^2 quadrats, representing roughly 22 percent of the native vascular flora of Wisconsin (T. Cochrane, pers. comm.). Forbs accounted for 64% of the total herbaceous cover, graminoids 34%, vascular cryptogams 2%. Perennials accounted for 88% of the species observed; annuals and biennials each accounted for 6%. In all, 83 families were represented. The most species-rich families were Asteraceae (74 spp.), Poaceae (46 spp.), Rosaceae (26 spp.), Fabaceae (20 spp.), Ranunculaceae (15 spp.), and Apiaceae (14 spp.). The mean positions along the soil and light gradients of the 83 most common species are given in Table 2. The average

standard deviation of common species' distributions along the light gradient was 3.2 times greater than that for the soil gradient (mean difference = 14.6, $P < 0.001$, paired t-test with 82 d.f.); 96% of the common species had broader amplitudes along the light gradient than along the soil gradient. Flowering individuals had mean distributions significantly skewed toward brighter microhabitats than the entire population of corresponding conspecifics ($P < 0.005$, 1-tailed signs test with 86 d.f.).

Gradients in community structure and diversity. - Average forb cover was greater than graminoid cover in all but the sandiest, brightest environments (Figure 1). Backward-elimination regression showed that average forb cover decreased in a significant, nonlinear fashion with increasing sand content of soil texture class S_c (silt loam = 1, sandy loam = 2, loamy sand = 3, sand = 4):

$$C_{FORB} = 386.3 - 415.2S_c - 380.6 \ln S_c + 53.4S^2_c \tag{4}$$

($r^2 = 0.88$, $P < 0.001$ for 16 d.f.). Graminoid cover varied non-linearly with both soil texture and light availability class (1 - 5 as above), and was greatest in well-lit, moderately sandy microhabitats (Figure 1):

$$C_{GRAM} = 71.2 - 23.2S_c + 37.3 \ln S_c - 18.9 \ln L_c \tag{5}$$

($r^2 = 0.85$, $P < 0.0001$ for 16 d.f.). Total cover by groundlayer plants increased non-linearly with % silt at a given level of irradiance; total cover increased with light availability on silty sites, but decrease at the highest PPFD levels on sandy sites.

Averaged across quadrats within each of 20 microhabitats (4 soil steps x 5 light quintiles), the mean numbers of species per quadrat of forbs and of

graminoids increased linearly with total cover by their respective groups (Figure 2). However, at a given level of cover by guild members, the mean richness of forbs was significantly greater than that of graminoids (P < 0.001, ANCOVA with 1, 18 d.f.). The trend for forbs to have greater total cover than graminoids in any given microhabitat, and to achieve much higher cover in some microhabitats than that for graminoids across microhabitats (Figure 2), reinforced the tendency toward higher species richness in forbs. Annuals and biennials contributed only 4.9% of total cover. Only four such species had a frequency > 5%: *Amphicarpaea bracteata* (19.8%), *Melilotus alba* (11.8%), *Rudbeckia hirta* (7.9 %), and *Ambrosia artemisiifolia* (5.1%).

Among graminoids, C_4 grasses were generally restricted to brightly lit microsites, except on sandier soils where *Schizachyrium scoparium* and *Andropogon gerardii* were also growing in semi-shade (Figure 3). C_3 grasses, and sedges were somewhat more widely distributed along the light gradient, but graminoids generally were most common on moderately sandy microsites (Figure 3). If cover by species in each of the three guilds of graminoids are pooled, the distributions of the three guilds differ significantly from one another (P < 0.0001, Syrjala test for all 3 pair-wise comparisons). C_4 grasses predominated in bright, sandy microsites; C_3 grasses, in shadier, siltier microsites; and sedges, in microsites that are somewhat intermediate on both the light and soil gradient.

Among forbs, the mean distributions of guilds based on different leaf widths, inclinations, or heights differed significantly by the Syrjala test from each other

(Figure 4A-C). On average, the distribution of forb species with progressively wider leaves shifted towards shadier, siltier microsites (Figure 4A), as expected based on between -habitat comparisons elsewhere and economic theory (Givnish 1987, 1988). The average distribution of herb species with progressively more steeply inclined leaves shifted toward more brightly lit microsites (Figure 4B); the expected tendency for steeply inclined leaves to be common in sand (and hence, drought and nutrient-poor) microsites as well (Givnish 1979, 1988) may be counteracted--in terms of the effect on the average distribution of species with vertical leaves--by the tendency for total cover to drop with % sand content on well-lit microsites (see Figure 2). As expected, taller leaf-height classes were associated with progressively siltier and brighter microsites (Figure 4C); such microsites favored greater amounts of total herb cover (Figure 2), which should in turn favor species with taller leaves (Givnish 1982, 1995; Tilman 1987).

Contrary to expectations (Givnish 1987; Leach and Givnish 1996), potential N-fixing plants were present across much of both the light and soil gradients (Figure 5). Most species, however, did grow on well-lit, sandy microsites, in accord with predictions that plants in such habitats should be strongly limited by N availability and thus likely to realize a net energetic and competitive advantage through investment in nitrogen fixation. Interestingly, 5 of the 6 species with N-fixing potential that grew in shadier or siltier microsites were climbing or scrambling vines; the shade specialist *Desmodium glutinosum*, a free-standing species, was exceptional in this regard.

The bivariate mean distributions of species in the two most diverse genera of forbs--17 species in *Aster* and 9 in *Solidago*--appeared staggered relative to each other (Figure 6A-B). Among species within each genus with a frequency > 2%, pairs of congeners differed significantly in their distributions along the 2-dimensional soil x light gradient ($P < 0.05$, Syrjala test) in 36 of 38 cases; the exceptions were *A. lanceolatus* and *A. puniceus* ($P > 0.10$, Syrjala test), and *S. juncea* and *S. nemoralis* ($P > 0.05$, Syrjala test).

Diversity in savanna vis-a-vis prairie and forest. -- Based on comparisons with earlier surveys of Wisconsin upland prairies, savannas, and forests by Curtis, Bray, and others, the upland savannas that I investigated had significantly higher levels of plant species richness on the α and γ scales (*sensu* Whittaker 1972). For the savannas in the current study, the mean number of species per quadrat (α diversity) was 16.1 ± 1.2 m^{-2}, significantly greater ($P < 0.0001$, Student-Newman-Keuls test, d.f. = 59) than that for prairies (11.4 ± 2.6 m^{-2}), Bray's savannas (9.3 ± 1.5), and forests (8.2 ± 2.2 m^{-2}) (Figure 7A). At slightly larger spatial scales, savannas in the current study showed a significantly higher amount of γ diversity ($P < 0.0001$, Student-Newman-Keuls test, d.f.= 56), averaging 89.3 ± 11.3 species per 20 m^2, more than twice that for forests (42.8 ± 8.1 spp. per 20 m^2) or prairies (41.5 ± 7.8 spp. per 20 m^2) (Figure 7B). Savannas in the current study thus showed a substantial amount of internal species turnover with distance (one measure of β diversity = γ/α), averaging 5.6 ± 0.9, significantly greater ($P < 0.0001$, Student-Newman-Keuls test, d.f. = 56) than that seen in prairies ($3.7 \pm$

0.5), but not significantly greater than in Bray's savannas (4.9 ± 1.5) nor in forests (5.4 ± 0.9) (Figure 7C).

An additional measure of the high level of plant diversity within and between savanna remnants is provided by comprehensive lists of vascular plants compiled by the author for the 12 study sites and an additional 10 chosen using the same sampling criteria in southern Wisconsin. In all, 507 native vascular plant species were tallied across 22 sites totalling 42 ha. This total comprises ca. 27% of the total native flora of Wisconsin (T. Cochrane, pers. comm.), which inhabits an area of roughly 14×10^6 ha. An additional 73 species of alien origin were noted. The 21 sites surveyed support 41 tree species, 42 shrubs species, 7 species of woody vines, 94 graminoids, 380 forbs, and 16 vascular cryptogams. A total of 9 species considered threatened or endangered in Wisconsin (Wisconsin DNR 1993) were encountered: *Agastache nepetoides, Asclepias purpurascens, Besseya bullii, Camassia scilloides, Cypripedium candidum, Gentiana alba, Hypericum sphaerocarpum, Parthenium integrifolium,* and *Polytaenia nuttallii.* In addition, seven species on the Wisconsin Natural Heritage Program's Watch List (Wisconsin 1990) were also found: *Botrychium simplex, Corallorhiza odontorhiza, Eupatorium sessilifolium, Napaea dioica, Talinum rugospermum, Thaspium trifoliatum,* and *Trillium recurvatum.*

Relationship of species niche breadth within savannas vs. ecological breadth across habitats. - There was a highly significant increase in the number of habitats a species occupied in Wisconsin (*fide* Curtis 1959) with increase in quantitative

Shannon Index based on average cover in 20 soil X light microhabitats within savanna remnants (Spearman rank correlation $r_s = 0.42$, $P < 0.0001$ for 353 d.f.). The 20 species that occupied the broadest range of microhabitats are listed in Table 3.

DISCUSSION

This study is the first since Bray's (1955, 1958, 1960) classic work to survey

patterns in the composition, structure, and diversity of oak savannas in Wisconsin

across a variety of edaphic conditions. Bray included only sites with a scattered

canopy and a groundlayer dominated by prairie grasses. This study differs

critically from Bray's work in its sampling criteria, including sites that have a

scattered oak canopy, a groundlayer dominated by native species across the entire

light gradient, and a recent history of fire. Bray's presupposition of groundlayers

dominated by prairie grasses may have lead, circularly, to the now-common

description of savannas as "prairies with trees" (e.g., see Tester 1995). It may

also explain why Bray could find no sites fitting his grass criterion on moister, siltier

soils, given that forbs dominated all but the sandiest microsites in the current study

(Figure 1). Because forb cover and richness exceeded those of graminoids in

most savanna microsites, it might be more appropriate to describe Midwestern oak

savannas as forblands rather than grasslands.

Including only sites burned during the previous 10 years meets one of the

key criticisms of Bray's research by Packard (1988b), who claimed that the

apparent dominance of savanna groundlayers by prairie grasses and apparent

rarity of savanna specialists were artifacts of studying heavily grazed, fire-

suppressed sites. The sites chosen for the current study were unusual in having

had a recent history of fire as well as a high diversity of native groundlayer species

with few invading aliens. While these sites collectively span a large range of

habitats, it must be recognized that several types of oak savanna (e.g., quartzite glades [Armstrong 1994], pygmy forests [Reich and Hinckley 1980], stands on clay soil) were not included in the current study.

The environmental gradients analyzed in this study--% sand and % direct PPFD--are complex gradients closely associated with other important gradients. Increasing sand content was associated with decreased organic matter, decreased nutrient, and water availability. Differences in light availability may be related to variations in soil temperature, soil moisture, ambient throughfall (Ko and Reich 1993) and in the disturbances caused by animals (e.g., Davis et al. 1995).

Turnover in groundlayer composition was roughly twice as great along the soil (% sand) gradient as along the light (% direct PPFD) gradient (e.g., 3). A potential criticism of this finding is that the soil gradient corresponds to a ranking of relatively few (12) sites based on their soil texture, while the light gradient corresponds to a ranking of many (722) quadrats along a range of light conditions replicated at each site. Consequently, it might be argued that turnover along the soil gradient reflects not only the response of species to % sand content, but also to site-specific factors confounded with soil texture, including site history, geographic location, and pool of species with access to that site. It is not possible, based on the data presented in this paper, to evaluate how important soil texture (and its regional correlates) is compared with such factors. However, the results of a savanna re-assembly experiment (Leach 1996) indicated that, when species pool, site history, and disturbance regime are carefully controlled across a range of

soil and light conditions comparable to those seen in the current study, species

turnover along the soil texture gradient is four times that along the light gradient.

This finding strongly suggests that the two-fold difference in species turnover along

soil vs. light gradients in savanna remnants is not an artifact of the soil gradient

being confounded with site history, location, and species pool. In any case, if sites

were significantly isolated by distance, we might expect the presence or absence

of individual species to be more substantially affected than gradients in the

ecological importance of entire guilds.

Trends in community structure. - Significant differences in the distributions of

graminoids vs. forbs, C_4 vs. C_3 grasses, potential N-fixers vs. non-fixers, and

species with different leaf widths, heights, and inclinations (see Figures 1, 3, 4, and

5) indicate that the competitive ability associated with different growth forms and

energy-capture strategies varies strongly across soil and light gradients. The

trends observed are generally consistent with those expected based on the

energetic and ecological impact of the traits involved. For example, in savanna

remnants C_4 grasses were dominant only in open, sandy microsites. C_4 grasses

generally transpire less water per unit of photosynthate than plants with the C_3

photosynthetic pathway, achieve higher photosynthetic rates under dry, sunny

conditions by suppressing photorespiration (Björkman and Berry 1973; Ehleringer

and Pearcy 1978), and achieve higher photosynthetic rates at a given leaf N

content (Field and Mooney 1986). Thus, C_4 species (mostly grasses in Wisconsin)

should have a competitive edge under the sunny, hot, dry, and nutrient-poor

conditions expected on open, sandy microsites. C_3 species should have an

advantage in shadier, moister, or more nutrient-rich microsites given the higher

quantum yield of the C_3 pathway under optimal conditions (Pearcy and Ehleringer

1984), and given that photosynthetic light capture in C_3 plant proceeds over the

entire leaf surface, not just the cells associated with the vascular bundles.

Potential N-fixers were generally concentrated in sandy, brightly lit

microsites, where N fixation would be expected to yield the greatest energetic

advantage (Leach and Givnish 1996). Under more nutrient-rich conditions,

perennial legumes generally have lower maximum growth rates than other

herbaceous plants (Grime and Hunt 1975), presumably because they divert

photosynthate toward maintaining symbiotic bacteria rather than to the production

of productive tissue (Tilman 1988). Under shady conditions, leaf N content (and

associated dark-reaction enzymes) does not limit photosynthesis as much as it

does under sunnier conditions (Björkman 1981), so it is less likely that N fixation

would yield a net advantage at low light levels. It is intriguing that 4 of the 6

legumes that peaked outside sunny, sandy microsites are vines (*Amphicarpaea,*

Lathyrus, Vicia, Apios) occurring on somewhat siltier soils (Figure 5). Such N-fixing

vines may be able to realize a greater growth rate on richer soils than free-

standing non-fixers, partly by allocating less to unproductive stem tissue. Given

the high specific conductance of many temperate vines (Teramura et al. 1991), and

their dependence on rapid rates of extension to out compete free-standing herbs,

N-fixing may be co-adapted to the vine habit, at least under moderately well-

illuminated conditions, N fixation would permit high rates of photosynthesis while requiring high rates of transpiration. It should be understood that, under the light levels typically inhabited by *Amphicarpaea*, *Apios*, *Lathyrus*, and *Vicia* (30 to 50 % direct PPFD), plants would spend a substantial fraction of each day (and conduct most of their photosynthesis) under high levels of irradiance, where leaf N content is limiting. More densely shaded sites would provide much shorter periods and amounts of net photosynthesis during sunflecks (see Chazdon 1990) to balance against the continual high cost of N fixation. Interestingly, all four N-fixing vines appear to avoid drought stress under hot, sunny conditions by folding their leaflets together and away from direct sunlight (pers. obs.). N-fixing vines may be restricted away from open sandy sites by the low moisture-holding capacity of sandy soils, and by the low density of free-standing forbs (their most likely structural host). The occurrence of *Desmodium glutinosum* under fairly dense shade (ca. 10% direct PPFD) is anomalous; it is reported to harbor N-fixing bacteria (Allen and Allen 1981) but should be investigated to determine whether it does so at low light levels.

The distribution of species differing in leaf width, leaf inclination, and leaf height varied in accord with predictions based on economic theory (see reviews by Givnish 1988, 1995). Forbs with narrow leaves tended to inhabit microsites that were sunnier (and hence, drier) and sandier (and hence, drier and more nutrient-poor) than those occupied by species with broader leaves. Narrow leaf surfaces reduce total water loss per unit area, at the cost of any increase to photosynthesis

caused by elevating leaf temperature over air temperature. Across herbs, leaf inclination increased toward sunnier sites, where steeply inclined foliage transpires less and suffers less heat loading while allowing photosynthesis to proceed under a saturating level of irradiance. Leaf inclination is expected to increase toward sandy sites as well, as supported by the distribution of 3 of the 4 inclination classes (see Figure 4B). The shift of the mean distribution of species with the steepest leaves toward siltier sites is partly an artifact of the reduction in total herb cover in the sunniest, sandiest microsites (see Figure 1). As expected, the mean distribution of herbs with progressively taller leaves shifts toward brighter, siltier sites that support a greater density of total herb cover. Denser cover favors taller herbs, but increasing the expected photosynthetic benefit of an increment in leaf height to be balanced against the energetic cost of building a taller stem (Givnish 1982, 1995).

Finally, the differential distribution of forbs vs. graminoids might be understood in terms of the characteristic differences between these growth forms and the advantage each might yield in different environments. Forbs cover increases toward siltier soils, while graminoids reach their peak in sunny, moderately sandy conditions (Figure 1). Forbs tend to have wider and more nearly horizontal leaves than graminoids, to have extensive rather than intensive root systems, and to have deeper root systems (Weaver 1954, Weaver and Albertson 1956). Consequently, we might expect forb cover to be greater on fine-grained soils, and graminoid cover to be greater on sunny, sandy microsites. The fall-off in forb cover toward the sunniest, sandiest microsites could be a result of differential

tolerance to drought stress between C_3 forbs and C_4 grasses (see Martin et al. 1991). Forbs might also gain an advantage on less frequently burnt microsites: their broad, often horizontal leaves should cast shade more effectively than grass blades, and confer greater shade tolerance. As a result, between fires the relative abundance of forbs might increase as they shade the grasses and sedges. However, because graminoids have basal meristems and so are pre-adapted to regenerate rapidly following fire, drought, or grazing (Gleason 1922, Tainton and Mentis 1984, Anderson 1990) their relative abundance might be expected to increase immediately following fire. To the extent that fine fuels are more likely to accumulate and have relatively low moisture content on sunny, nutrient-poor sites, the resulting increase in fire frequency would work to maintain dominance by graminoids on such sites.

The use of the Syrjala (1996) geostatistical test to evaluate the significance of differences between species or guilds along two ecological gradients simultaneously has been fruitful in the current study, and should prove extremely useful in other studies using direct gradient analysis.

Trends in plant species richness. - Upland savannas appear to have much higher levels of α- and β- diversity than Wisconsin upland prairies, savannas, and prairies surveyed during the 1940s and 1950s (Figure 7). Because the PEL data sets were collected using different methods - often involving a single census, which might lead to the exclusion of certain phenologically ephemeral groups - such comparisons should be viewed cautiously. However, the results of the

comparisons among the current savanna data and historic data for prairie and forest are consistent with the findings of Pruka (1994). He compared plant richness at the 1-m^2 scale in prairie, savanna, woodland, and forest along a single intact gradient in south-central Wisconsin, and found that richness peaked in savanna. Similar differences in α diversity can be found in richness m^{-2} between lowland savannas (this study: three sites, range = 16.8 to 19.7) and data from southern Wisconsin lowland forests (Menges [1983]: five sites, range = 2.8 to 10.1).

The higher levels of diversity I found in savannas compared to those recorded by Bray may be due to (i) differences is sampling visits (two visits vs. one), (ii) differences in effort to identify the species present, (iii) and actual differences in species richness. Bray's sites tended to be on sandy or shallow soil, often on steep slopes. Such sites are often very dry and may, as a result, support fewer species. Bray selected his study sites based on the abundance of prairies grasses (Bray 1955, 1958, 1960); abundant prairie grasses can lower local diversity (Glenn and Collins 1990).

The high levels of diversity found in Midwestern oak savannas at a variety of scales--from single square meters to large portions of southern Wisconsin--is a previously unrecognized property of such communities. But it is consistent with several hypotheses regarding diversity, based on environmental heterogeneity, release from dominance by C$_4$ grasses, disturbance, and dispersal. Environmental heterogeneity has long been recognized as important for maintaining diversity (see

Levin 1974; MacArthur 1975; Abrams 1988; Huston 1995). The broken canopy of an oak savanna creates internal mosaics involving spatial gradients of light, soil moisture, soil organic matter, soil temperature, and effective rainfall (Ko and Reich 1993; this study). As manifested by the differential distributions of individual species, pairs of congeners, and guilds based on different growth-forms and energy-capture strategies (Table 2; Figures 1, 3, 4, 5, 6), these gradients form resource spectrums that are exploited differently by each species or ecological groups. As manifested by the turnover in species composition with position on both the soil and light gradients (eq. 3), savannas that individually or collectively embrace broader portions of those gradients will encompass more species and guilds. Certain aspects of environmental heterogeneity within a savanna are temporal in nature. As in other, more closed communities dominated by deciduous woody plants, certain conditions vary seasonally in relation to tree canopies (e.g., light availability, soil temperature at various depths). Tree canopies themselves change over longer time periods with the birth and death of branches and boles. Compared with forests or prairies, individual savannas provide a more diverse array of microsites relative to canopy cover and associated ecological parameters, several of which may shift through seasonal or successional time. The greater patchiness of canopy cover and associated parameters in savannas should itself lead to higher levels of species diversity at the α-, β-, and γ-scales; the great diversity across savannas in substrate and disturbance regime should promote high diversity at the regional (δ) scale as well.

Release of forbs from competition with C_4 grasses may be another factor

promoting high diversity in savanna groundlayers relative to prairies. In the

Midwest, *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, and

other C_4 grasses often limit the growth of forbs in prairie (Glenn and Collins 1990).

Given that (i) forb richness is proportional to forb cover (Figure 2), and (ii) forb

richness at a given level of cover is greater than that for graminoids (Figure 2), any

substantial increase in forb cover based on a reduction in graminoids cover should

lead to an increase in overall groundlayer richness. Apparently, the partial shade

cast by savanna trees suppresses the growth of C_4 grasses somewhat, while

providing satisfactory conditions for a large number of C_3 forbs and to a lesser

extent, C_3 graminoids) adapted to a range of light levels.

Disturbance often plays a key role in maintaining biological diversity in

species-rich communities (Huston 1995). For examples, grazing helps maintain

high levels of local diversity (ca. 1-m^2 scale) in European chalk grasslands by

reducing coverage by tall competitive dominants (Grime 1977). Frequent fires help

promote high levels of plant diversity in pine-wiregrass savannas in North Carolina

(Walker and Peet 1980), oak savannas in Minnesota (White 1983), and prairies in

Wisconsin (Leach and Givnish 1996). Due to an internal mosaic within savannas

of physical and biological conditions (e.g., fuel density, composition, flammability,

and moisture content), savanna fires may be spatially and temporally patchy

(Anderson and Brown 1983); as a result , they may be less uniform in their extent

and intensity than the fires that frequently sweep through prairies or rarely (but

catastrophically) burn through forests. Disturbance (i.e., plant death) caused by drought may also be spatially more heterogenous in savannas than in prairies or closed forest, due to the mosaic of open and shaded microsites and the patchy distribution of tree roots. Certain forms of disturbance caused by animals might also be strongly patchy in savannas, given that many animals restrict their activity to open, closed or edge microsites, or behave differently under canopies than between canopies (e.g., Davis et al. 1995).

Dispersal may be another factor promoting high diversity in savannas. Given the large range of microsites within a savanna that favor different sets of species, and given the proximity of such microsites to each other, there should be a large pool of potential migrants for any given microsite. Repeated colonization of species into microsites might so "subsidize" populations that their time to local extinction is increased considerably, increasing diversity within microsites in an immigration-extinction balance. For example, at Marshall the few individuals of *Cypripedium candidum* found growing under open-grown bur oaks were apparently part of a much larger population in a nearby fen.

Biological distinctiveness of Midwestern oak savannas. - The positive correlation of within-savanna niche breadth and the range of habitats in which a species is found suggest that the processes limiting species distributions within savannas operate across communities as well. This finding does not support Packard's (1988a, 1988b, 1993) hypothesis that processes unique to savannas (*viz.*, frequent, locally catastrophic fires) select for a highly distinctive flora.

Nevertheless, within savannas a wealth of species do reach their peak average cover in microsites with intermediate illumination (Table 4), consistent with the idea that there are indeed species adapted to conditions that are especially prevalent in savannas. Most of Packard's (1988a) "oddball" species (listed as "distinctive savanna species" in Packard 1985), hypothesized by him to be savanna specialists, were found among the 722 quadrats, though they typically inhabited rather shaded microsites (mean % PPFD = 36.4 ± 20.3, n = 70). These findings are consistent with Pruka's (1994) hypothesis that Bray (1955, 1958, 1960) and Curtis (1959) greatly underestimated the distinctiveness of the savanna flora by tallying species that had persisted and reached their peak abundance in fire-suppressed former oak savannas (i.e., oak woodlands and forests) as forest specialists.

The finding that Midwestern oak savannas are especially rich in plant species, and show substantial turnover in composition along edaphic gradients, has several implications for conservation. First, any attempt to manage such savannas must maintain the ecological forces - frequent fires, internal patchiness, low competition from C_4 grasses, propinquity of sunny and shady microsites - that appear responsible for maintaining high levels of local species diversity and turnover in species composition. Second, a regional strategy for savanna conservation must encompass sites with a wide range of soil textures and (presumably) disturbance regimes. Third, conservation efforts aimed at savannas may pay rich dividends in terms of plant and insect conservation generally.

Twenty-two savanna remnants on less than a total of 50 ha can support more than a quarter of the entire native flora of Wisconsin, including 9 endangered and threatened plant species. Oak savannas and pine barrens often also support several globally rare insects, particularly Lepidoptera such as the Karner blue butterfly (*Lycaeides melissa samuelis*) or frosted elfin (Givnish et al. 1988; Bleser and Leach 1995). Fourth, the exceptional groundlayer of relatively intact savanna remnants - and its divergence from that seen in remnants which have been heavily grazed (pers. obs.) - reinforces the view that identification of communities as savannas must combine floristic data with physiognomic aspect if community classifications are to protect the biological diversity they are designed to reflect (e.g., Faber-Langendoen 1995). Finally, the recognition that many savannas are not "prairie with trees," but forblands with a paucity of prairie grasses in many microsites, should improve the ability of conservationists to identify sites worthy of conservation and management (see Pruka 1995). Conservation efforts (Leach and Ross 1995) may benefit by defining highly recoverable savanna remnants as areas with--or the potential for--(a) a canopy composed largely of open-grown oaks, (b) the scattered or broken canopy providing the groundlayer with considerable variation in light resources, and (c) a wide variety of native forbs, graminoids, and, possibly, woody plants in the groundlayer flora.

While savannas with intact, species-rich groundlayers are indeed extremely rare, several choked sites that might respond positively to fire-based management were seen during reconnaissance in southern Wisconsin and northern Illinois. The

exceptional potential diversity previously unrecognized in savanna remnants should

make the widespread implementation of prescribed burns and alien species control

on such sites a high priority.

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Table 2. Species showed individualistic patterns of frequency and mean position along gradients of % Direct PPFD and % Sand. Only species present in 5% or more of the quadrats are listed.

Species	%Freq	% Direct PPFD		% Sand	
		Mean	s.d.	Mean	s.d.
Acer rubrum	5.4	10.4	9.4	69.2	4.7
Achillea millefolium	14.4	50.8	24.7	81.3	12.0
Ambrosia artemisiifolia	5.4	42.3	27.8	78.1	0.0
Amorpha canescens	12.5	70.3	27.4	77.0	5.9
Amphicarpaea bracteata	21.2	33.2	26.0	72.0	2.7
Andropogon gerardii	18.1	56.9	24.2	84.2	0.6
Anemone cylindrica	8.0	49.0	27.4	73.9	21.1
Anemone quinquefolia	5.4	32.6	24.1	69.4	20.3
Anemone virginiana	6.8	24.6	23.8	66.2	7.4
Antennaria plantaginifolia	8.3	26.2	22.0	80.3	0.0
Asclepias syriaca	6.8	50.2	27.4	77.3	1.4
Aster oolentangiensis	10.0	39.1	30.7	82.5	0.0
Aster pilosus	10.9	56.1	28.3	78.9	13.7
Aster sagittifolius	26.7	39.2	25.9	70.5	0.0
Besseya bullii	5.3	46.1	19.7	73.8	0.0
Bouteloua curtipendula	6.4	66.7	19.4	74.7	21.5
Carex pensylvanica	46.4	24.7	23.1	76.0	0.0
Carya ovata	6.6	45.6	28.4	73.2	9.4
Circaea lutetiana	8.4	24.3	18.6	61.0	4.1
Comandra umbellata	10.9	66.4	23.0	75.0	5.9
Cornus racemosa	38.4	33.9	25.2	64.3	0.0

Corylus americana	13.0	40.3	31.1	73.5	8.3
Desmodium glutinosum	7.1	13.7	15.0	71.8	4.6
Elymus riparius	6.8	14.7	14.2	66.8	0.0
Elytrigia repens	11.5	35.1	27.3	75.7	15.3
Euphorbia corollata	32.4	56.3	25.5	80.0	4.1
Fragaria virginiana	15.5	44.0	23.8	64.2	1.5
Galium boreale	8.2	49.6	26.2	72.5	11.9
Galium concinnum	6.8	31.4	37.3	50.8	17.9
Galium trifidum	8.9	11.7	14.2	72.1	0.0
Geranium maculatum	9.4	25.7	29.3	59.3	8.4
Helianthus grosseserratus	5.3	53.0	25.6	46.3	17.9
Helianthus strumosus	23.4	50.7	25.8	65.9	2.9
Hepatica americana	6.5	10.6	10.9	73.3	2.7
Heracleum lanatum	6.5	26.0	26.2	34.2	14.2
Hydrophyllum virginianum	13.3	24.9	21.5	39.6	0.5
Lathyrus venosus	6.8	42.2	25.6	55.9	3.0
Liatris aspera	6.5	64.9	23.2	75.4	0.0
Lonicera X bella	5.7	27.4	24.4	77.5	4.8
Lysimachia lanceolata	5.5	37.6	27.6	85.4	18.6
Lysimachia quadrifolia	6.6	24.8	22.3	77.3	17.5
Melilotus alba	12.6	65.9	18.9	73.1	0.0
Monarda fistulosa	18.8	47.4	26.2	74.2	9.3
Oxalis stricta	13.6	32.2	28.0	57.7	17.9
Panicum ologisanthes X acuminatum	11.8	59.8	26.8	80.0	5.7

Panicum acuminatum	8.9	64.3	37.1	73.5	23.1
Phlox pilosa	10.7	56.0	28.8	80.3	0.0
Polemonium reptans	6.2	12.0	15.1	60.8	22.7
Polygonatum biflorum	10.4	47.5	33.6	56.8	3.0
Populus tremuloides	5.4	64.4	28.6	58.2	13.4
Potentilla simplex	7.9	25.9	23.7	69.1	5.5
Prunus serotina	30.1	25.0	22.2	67.9	11.5
Prunus virginiana	8.2	22.6	19.0	63.6	15.8
Quercus alba	5.8	35.8	24.6	73.9	0.4
Quercus macrocarpa	9.3	45.9	26.9	68.5	20.2
Quercus rubra	13.0	32.3	26.9	72.2	12.4
Quercus velutina	13.0	33.4	27.2	74.9	10.8
Rhamnus cathartica	11.8	47.1	20.5	73.9	1.9
Rhus glabra	21.7	56.3	28.4	69.8	4.4
Rosa carolina	9.8	57.8	28.6	78.8	6.9
Rubus allegheniensis	8.6	45.3	32.1	69.5	4.9
Rubus flagellaris	5.4	38.8	30.2	79.4	17.2
Rubus idaeus	6.4	37.0	21.3	50.1	9.4
Rubus occidentalis	10.9	46.4	24.6	68.2	23.2
Rudbeckia hirta	8.4	51.6	27.2	83.9	0.0
Rumex acetosella	8.6	37.4	30.7	77.4	5.0
Sanguinaria canadensis	5.3	24.7	19.1	45.6	7.2
Schizachyrium scoparium	22.4	74.6	23.7	78.3	11.6
Smilacina racemosa	21.5	26.0	23.5	63.2	5.0
Smilacina stellata	10.8	34.7	21.5	67.5	0.0

Smilax herbacea	7.5	36.8	31.8	58.8	0.0
Solidago canadensis	13.3	47.6	27.0	55.4	0.0
Solidago juncea	5.3	53.2	34.0	72.4	24.7
Solidago nemoralis	11.2	68.2	32.1	75.6	0.0
Solidago ulmifolia	8.3	44.3	19.3	74.2	24.9
Taraxacum officinale	27.6	29.8	24.8	75.5	0.0
Thalictrum dasycarpum	6.5	27.9	21.0	42.4	12.3
Tilia americana	5.3	14.9	14.5	60.9	4.3
Toxicodendron radicans	9.7	31.1	25.3	72.2	17.6
Tradescantia ohiensis	15.9	50.4	29.1	77.6	0.0
Viola cucullata	5.4	32.2	24.6	53.4	11.2
Viola sororia	5.4	19.8	19.4	75.0	1.3
Vitis riparia	23.0	35.2	25.4	68.9	0.9
Zanthoxylum americanum	7.2	20.9	21.8	72.0	7.5
Zizia aurea	5.4	58.2	25.9	45.3	19.5

Table 3. Niche breadth within savannas (the Shannon index [e^H] based on species presence in 1-m^2 quadrats in 20 light x sand microhabitats) was highly correlated with across-habitat ecological breadth as represented by the fidelity values of Curtis (1959). Fidelity value is the number of Wisconsin plant communities in which the species was known to occur. The species with the 20 highest values of e^H are listed.

Species	$e^{H'}$	Fidelity
Monarda fistulosa	15.2	17
Aster sagittifolius	13.1	12
Fragaria virginiana	12.7	25
Polygonatum biflorum	12.7	17
Corylus americana	12.6	21
Taraxacum officinale	12.2	no value
Oxalis stricta	12.1	4
Parthenocissus vitacea	11.0	26
Asclepias syriaca	10.9	15
Smilacina stellata	10.8	21
Prunus virginiana	10.1	13
Solidago canadensis	9.9	20
Smilax herbacea	9.9	15
Andropogon gerardii	9.7	19
Ranunculus abortivus	9.7	13
Aster oolentangiensis	9.6	14
Euphorbia corollata	9.6	15
Tradescantia ohiensis	9.4	15
Solidago speciosa	9.3	9
Carex pensylvanica	9.3	16

Table 4. The number of modal species, based on average cover, were well distributed among microhabitats, indicating that within each soil type many species achieve peak cover at intermediate light levels. Only species with frequencies > 2% were included. Microhabitats are based on four soil texture classes and % direct PPFD quintiles.

| | % Direct PPFD Quintiles | | | | | |
	1	2	3	4	5	Total
Sand	6	7	11	5	3	32
Loamy sand	8	3	1	4	21	37
Sandy loam	7	11	4	9	17	48
Silt loam	13	6	9	13	8	49
Total	34	27	25	31	49	166

Figure 1. Distribution of cover by (a) forbs and (b) graminoids as a function of light availability and soil texture. Contours reflect best-fit multiple regressions relating mean cover to five classes of % direct PPFD (set as 1 - 5) and four classes of soil texture (silt loam = 1, sandy loam = 2, loamy sand = 3, sand = 4). Absolute cover values are shown for each soil x light microhabitat.

Figure 2. Plot of mean quadrat richness vs. mean cover by forbs and graminoids in 20 microhabitats based on 4 soil texture x 5 %direct PPFD classes. Fitted lines are from linear regressions (Forbs: $S_F = 7.7 + 0.051\ C_F$, $r^2 = 0.73$, $P < 0.0001$, d.f. = 19; Graminoids: $S_G = 1.1 + 0.074\ C_G$, $r^2 = 0.69$, $P < 0.0001$, d.f. = 19).

Figure 3. Two-dimensional mean position of graminoid species along % sand and % direct PPFD gradients. Only species with frequency greater than five percent are shown.

Figure 4. Mean two-dimensional position along % sand and % direct PPFD gradients for guilds of (a) forb leaf width, (b) herb leaf inclination, and (c) herb leaf height. In all cases, the bivariate distributions of adjacent guilds were significantly different (Syrjala [1996] test, p < 0.05).

Figure 5. Mean two-dimensional position along %sand and %direct PPFD gradients of potential nitrogen-fixing species (Allen and Allen 1981). Error bars represent one standard deviation. Only species with frequency greater than five percent are shown. Vine-like species included *Amphicarpaea bracteata*, *Apios americana*, *Lathyrus venosus*, and *Vicia americana*.

Figure 6. Mean distribution along gradients of % sand and % direct PPFD are

shown for members of (a) *Aster* and (b) *Solidago*. Error bars represent one standard deviation.

Figure 7. Comparisons among southern Wisconsin upland savanna, prairie, and forest for (a) α diversity, (b) γ diversity, and (c) β diversity. The prairie, oak opening, forest data sets are from unpublished field notes gathered in the 1940s and 1950s by the Plant Ecology Laboratory (PEL).

Figure 1 56

Figure 1

Figure 2

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Figure 3

Figure 4   59

Remnant Savannas

Figure 5

Figure 6

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Figure 7

A — α diversity (Native species m^{-2})

B — γ diversity (Species per 20 m^2)

C — β diversity ($\beta = \gamma/\alpha$)

1 Savanna (This study)   2 Prairie (PEL)   3 Oak Opening (PEL)   4 Forest (PEL)
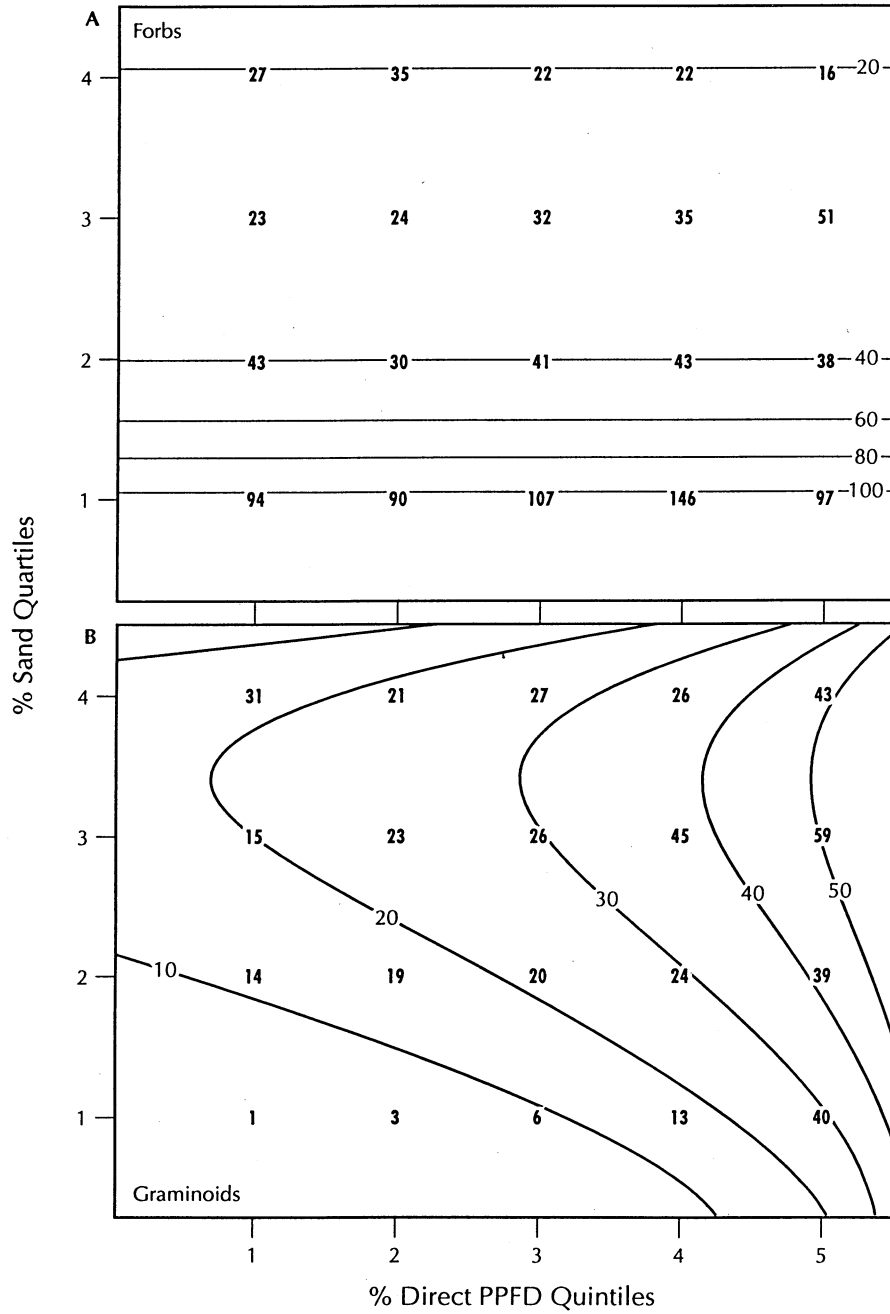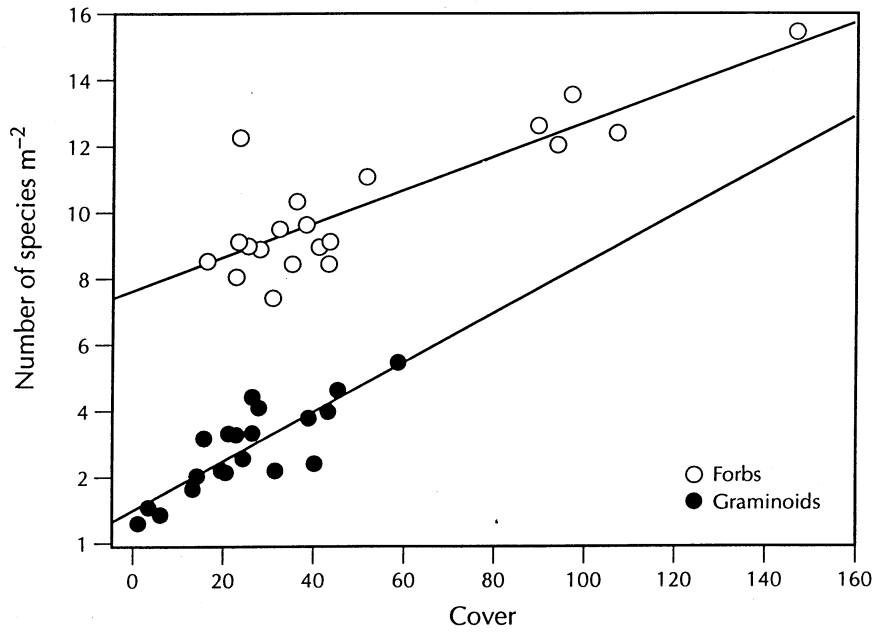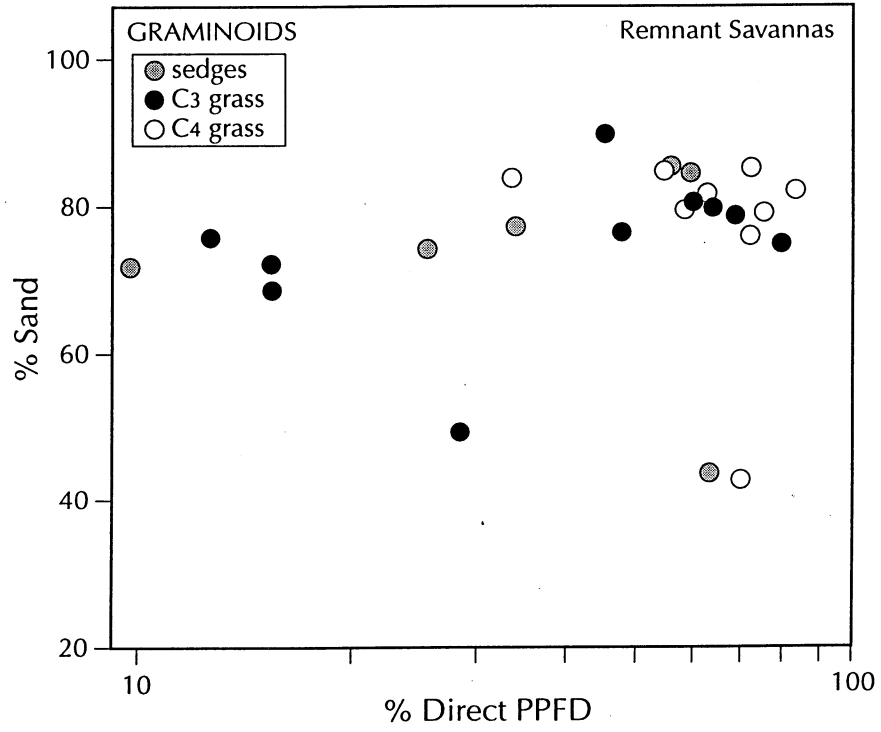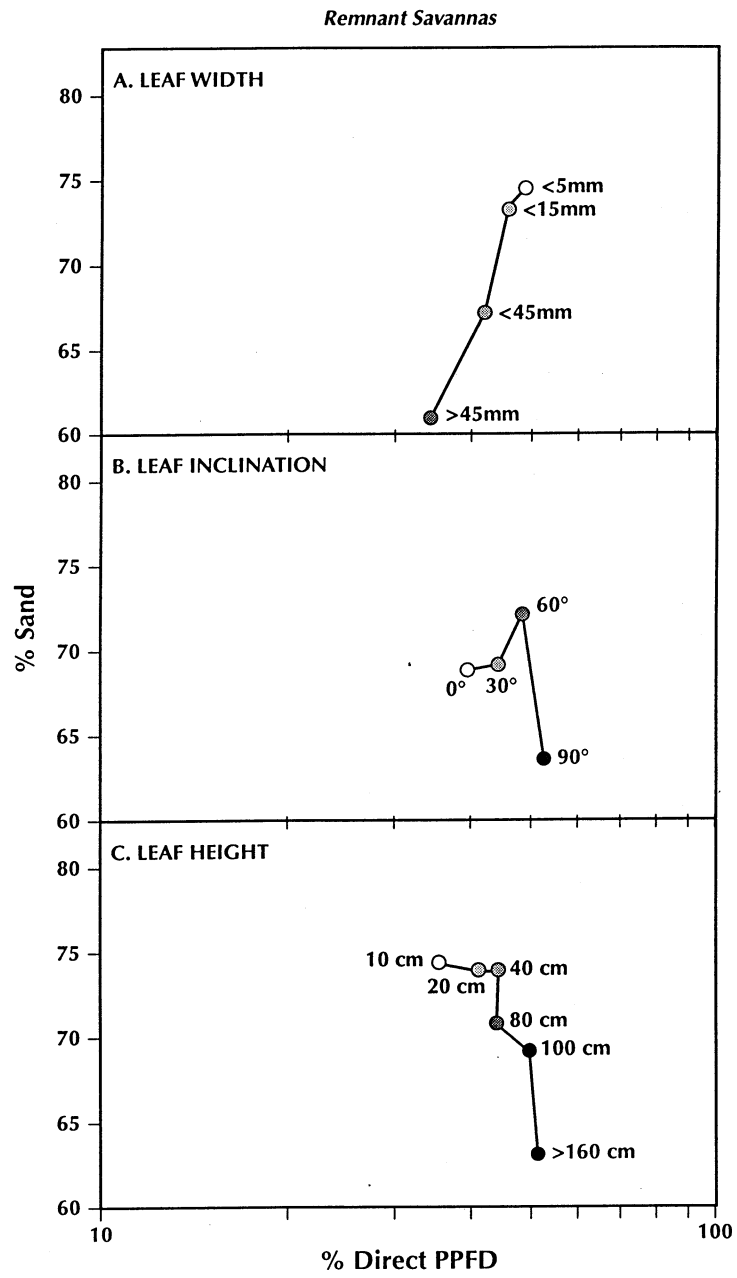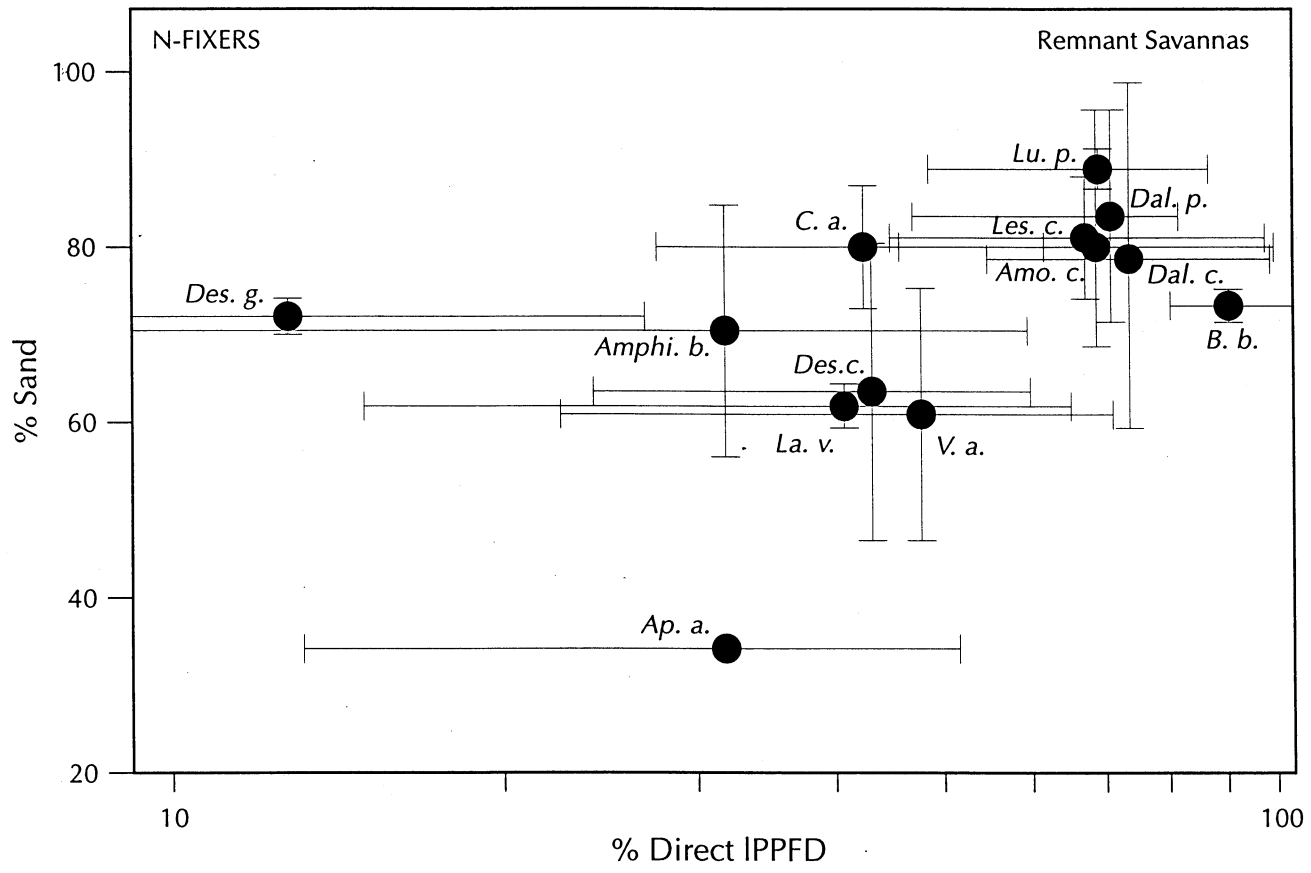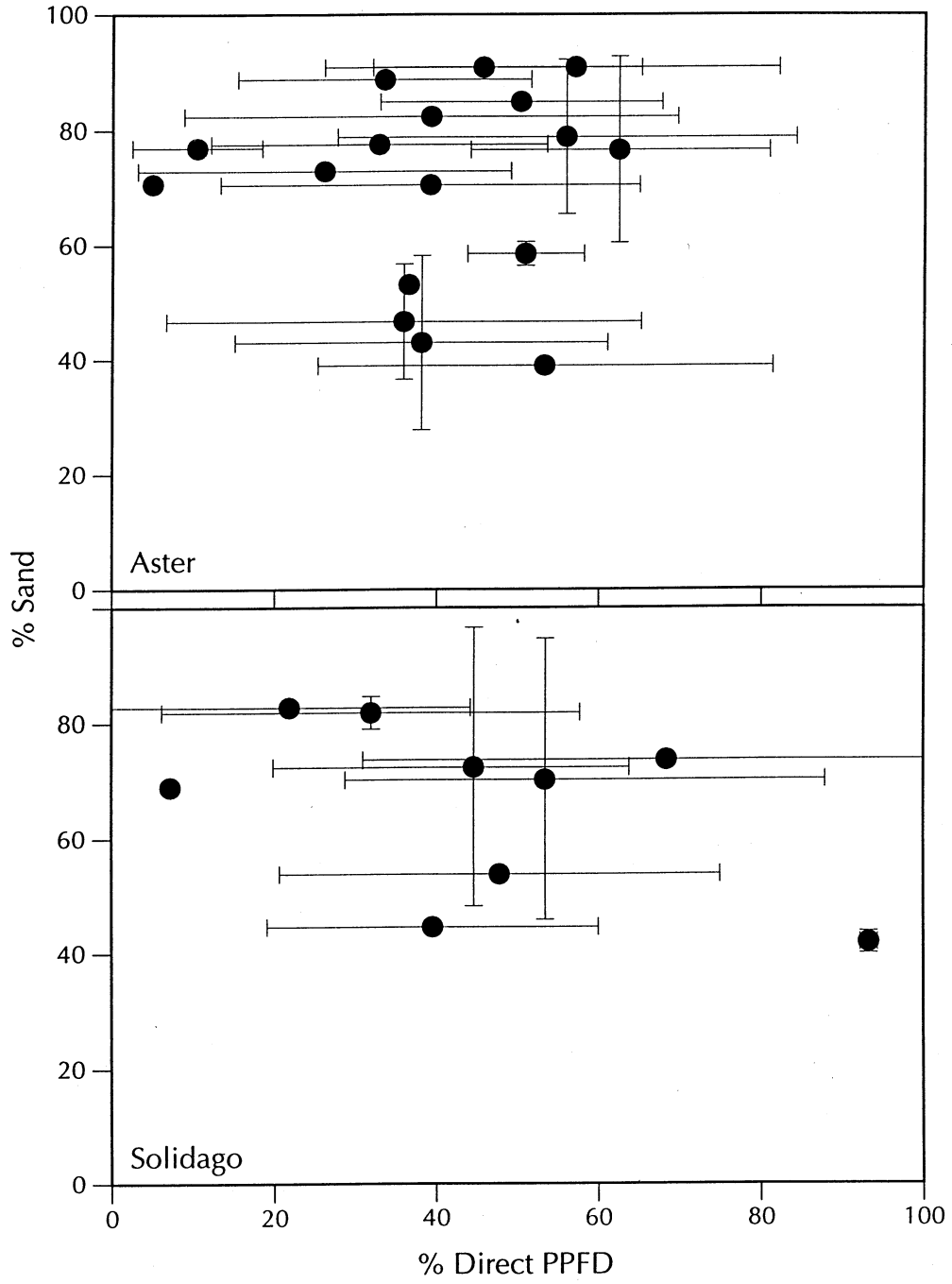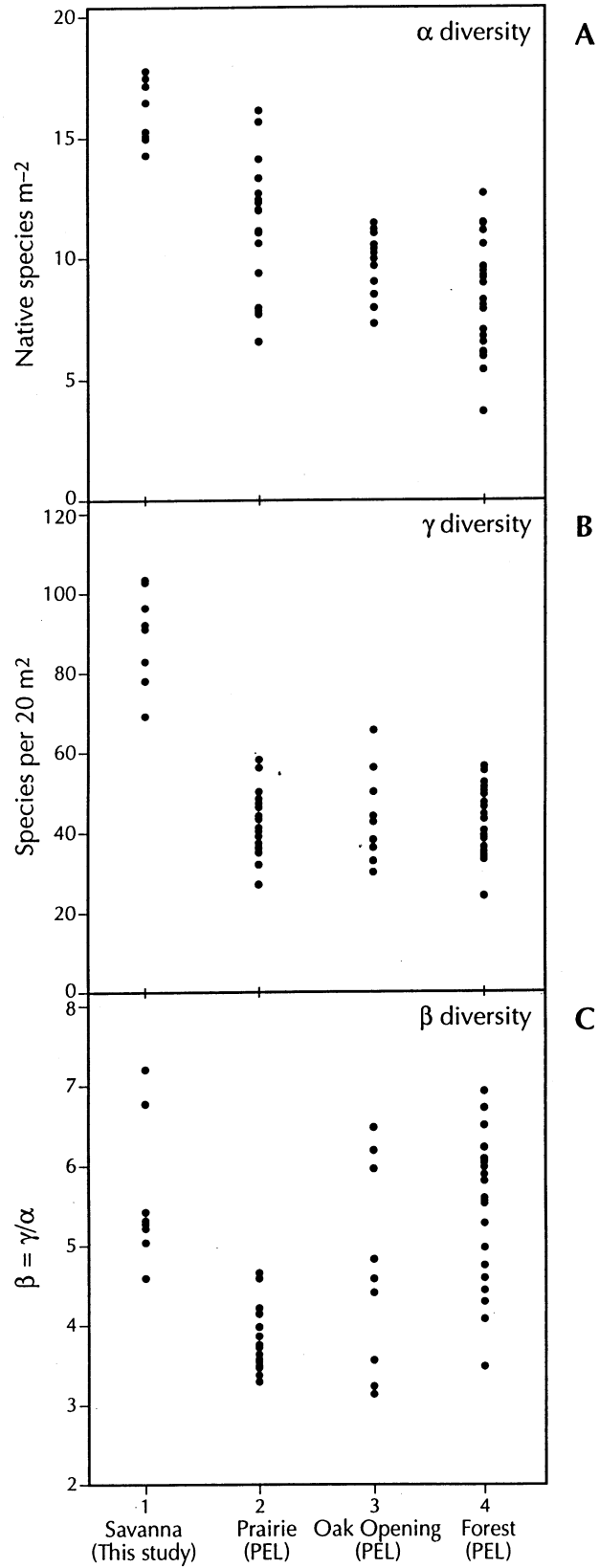
CHAPTER 2

EXPERIMENTAL RE-ASSEMBLY OF COMMUNITY

COMPOSITION, DIVERSITY, AND STRUCTURE ALONG SOIL

AND LIGHT GRADIENTS IN

WISCONSIN'S OAK SAVANNA

ABSTRACT

Oak savannas with scattered canopies were once the most widespread natural communities in southern Wisconsin, but those with intact groundlayers are considered to be extremely rare, and the composition and nature of this species-rich and horizontally structured synusium has been the subject of considerable debate. To help resolve this debate, I initiated a long-term field experiment on the reassembly of savanna groundlayers under and between existing oaks at the University of Wisconsin Arboretum. On silts to loamy sands, a mesic seed mix of 84 species was planted in 275 1-m^2 quadrats in 24 de-vegetated strips running from sunny to shady microsites. On sandier soils, a xeric mix of 83 species was planted in 136 quadrats in 14 strips. Thus, the quadrats represented a large proportion of the soil x light microsites expected in Wisconsin's oak savannas. The species were carefully selected to represent the diversity of physiologic and morphologic traits represented in the local herbaceous flora, with the goal of observing how these traits affect species sorting along soil and light gradients. Data on the composition, structure, and diversity of the groundlayer during the third growing season are presented here, and compared with results of a recent

survey of intact savanna remnants.

Analysis of results revealed significant variation in composition along soil and light gradients, with soil having over four times the influence on species composition than did irradiance. This confirms a similar finding among remnant savannas. Comparisons of bivariate distributions between 21 pairs of congeneric species revealed high degrees of niche differentiation. The relative distribution of forbs and graminoids was in concordance with their distribution in savanna remnants, with forb cover increasing with percent silt content and grass cover increasing toward sunnier or sandier microsites, with C4 grasses reaching their highest cover on sandier or brighter microsites. Collectively, C3 grasses were distributed more widely along both soil and light gradients than were C4 grasses, as also seen in a survey of savanna remnants. Potential N-fixing species tended to be more common in sunnier, sandier microsites, also reflecting their distribution in savanna remnants. Guilds based on differences in leaf width, inclination, and height showed complex distribution along light and soil gradients that differed from those seen in remnants. The distributions of guilds based on physiological differences (C3 vs. C4, N-fixing vs. non-fixing) tended to be more similar to each other under experimental and remnant conditions than did the distributions of guilds based on certain morphological differences (leaf width, height), perhaps because the latter are more plastic and can differ dramatically between juveniles and adults, slowing the process of species sorting and community assembly along gradients.

Species richness tended to decrease with total herb cover. Richness was especially low on nutrient-rich silts and silt loams, where a groups of tall, morphologically similar forbs (especially *Heliopsis helianthoides*) had dense cover. Both richness and total cover were low in the shadiest, sandiest microsites.

The frequency of individual species varied among mesic mix species from 0 to 92.4 percent. Mean frequencies of 33 common species in their modal microhabitats (3 soil x 3 light) equaled 75.2 ± 23.7 %, providing strong evidence for the operation of local stochastic effects on early establishment. Experimental re-assembly can provide independent tests of questions regarding community ecology in nearly vanished ecosystem and as well a basis for savanna restoration by identifying the importance of environmental gradients affecting composition, structure, and diversity.

INTRODUCTION

In the Midwestern United States and Canada efforts are underway to restore large areas to oak savanna ecosystems (see Packard 1993, Henderson 1995, Bleser and Leach 1995, Leach and Ross 1995). The identification, restoration, and conservation of savannas have suffered from the lack of published documentation regarding the composition and horizontal patterning of their groundlayer communities. As a result, there has been a lively debate regarding approaches to savanna restoration and management (see Packard 1998a, 1998b, 1993, Anderson 1991, Mendelson, et al. 1992, Pruka 1994).

Until recently, the most comprehensive studies of Wisconsin's oak savannas were by Bray (1955, 1958, 1960) and discussed by Curtis (1959). Bray and Curtis characterized savanna groundlayers as being closely allied with true prairies, hence the common description of savanna as "prairie with trees" (e.g., Tester 1995). However, Bray's observations were made on a limited range of sites, and, as a site selection criterion, only those supporting prairie grasses and forbs (Bray 1955). No additional survey was made of Wisconsin savanna remnants until Leach (1996a), who avoided possible circularity in the findings, by selecting sites with abundant native species regardless of their kind. In that study Leach (1996a) sampled 1-m^2 quadrats that were stratified along light gradients within sites and %sand gradients among sites. Leach (1996a) found that, except on the sandier or brighter microsites, savanna differed considerably from prairie by lacking dominance by C_4 grasses and other graminoids and by supporting

comparably high levels of diversity at local scales. Leach (1996a) also reported that savannas have species-rich groundlayers with soil (i.e., % sand) gradients having about twice the effect of light gradients on groundlayer composition. Nitrogen-fixing species and C_4 grasses tended to be most common on bright and/or sandier microsites, although certain legumes, e.g. *Amphicarpaea bracteata* and *Desmodium glutinosum*, were shade specialists. The remnant study also found that species richness at the 1-m^2 level tended to increase toward siltier sites and with total herbaceous cover. Because steps along the soil gradient represented separate sites, those findings could have been the result of correlations of % sand with other site factors, including site histories and the composition of local species pools.

To address the issues of patterns in savanna groundlayer composition, structure, and diversity along soil texture and light gradients, I established experimental restorations at the University of Wisconsin Arboretum in Madison. The positions along % sand and % PPFD gradients were determined for 411 1-m^2 quadrats that were arranged in strips running from shaded microsites under open-grown oaks to sunnier areas between trees on soils ranging from silty to sandy. I planted all 1-m^2 quadrats in November, 1992 with either of two carefully selected and quantified seed mixes: a mesic seed mixture with 84 species and a xeric seed mixture with 83 species. Here I report results from data collected in the third growing season (i.e., 1995) on species cover and the influence of sand and light gradients on groundlayer composition, richness, and structure. I then compared

these trends with results from the previous study in savanna remnants (Leach 1996a).

METHODS

Site Descriptions. -- Re-assembly experiments were initiated at the University of Wisconsin-Madison Arboretum on two sites with open-grown oaks and a range of soils. The Wingra site can be characterized as grove of large (> 16 m tall, 63 - 95 cm dbh) bur oak trees (*Quercus macrocarpa*) on never-plowed silt and silt loam soil. For the previous 50 years the area has been maintained as a lawn, dominated by grasses, including *Poa pratensis* and *Muhlenbergia screberii*, and low forbs, such as *Viola sororia*, *Glechoma hederacea*, and *Taraxacum officinale*. The Southwest Grady site was farmed in the past, but the fields were abandoned ca. 50 yr ago. The site spans a wide range of soils from sand to silt loam. Many of the existing oak trees were planted as acorns in the 1950s and include bur oak, white oak (*Q. alba*), red oak (*Q. rubra*), and hybrids of black (*Q. velutina*) and Hill's (*Q. ellipsoidalis*) oak. These trees are smaller than those at Wingra (mostly 7 to 12 m tall, 24 to 51 cm dbh). Prior to this experiment the groundlayer was a blend of native and alien grasses, forbs, and shrubs: *Bromus inermis*, *Agrostis gigantea*, *Phleum pratense, Solidago canadensis, Lonicera X bella* and *Pastinaca sativa* on the siltier soils; and *Panicum oligosanthes* var. *scribnerianum, Poa pratensis,* and *Elytrigia repens* on the sandier soils.

Experimental plantings.-- Percent sand and %direct PPFD were chosen *a priori* as gradients for analysis and as a means of comparison with observations made in

remnant savannas (Leach 1996a). To assure wide representation along both gradient, 38 strips on a wide range of soils were laid out from beneath tree canopies to open areas between trees. Within those strips 411 1-m^2 quadrats were established. Thirteen strips containing 181 quadrats were located at Wingra and 25 strips containing 230 quadrats were located at Southwest Grady. I placed a large number of quadrats on the narrow range of soils at Wingra due to a greater need for restoration information on siltier soils.

The strips were denuded of existing vegetation by removing woody plants and twice treating herbaceous plants with foliar applications of Roundup®, a glyphosphate herbicide. Treatment was effective on most species except *Viola soraria*, *Rumex obtusifolia*, and *R. acetosella*. These and invasive species were later controlled by hand by the author.

Seed Mix Preparation and Planting.-- Two seed mixtures were prepared: the mesic mix for areas with sand content < 70 % and the xeric mix for areas with a higher sand content (Table 1). The one variable held constant in this experiment was the identity and number of seeds sown into each quadrat. To assure uniformity, several volunteers spent over 200 hrs carefully weighing or counting, in cases where seeds were especially large, seeds into separate units for each of 411 quadrats. The word "seed" is used here in its general sense of mature embryo with associated parts (Harper, et al 1970). Based on prior experience, the weight or number of seed per species was designed to promote establishment of all species without dominance by large, overly aggressive species. However, for

several rare species the number of seeds planted was severely limited by availability (e.g. *Camassia scilloides*). Fleshy-fruited seeds (e.g., *Arisaema triphyllum, Smilacina stellata*) and *Amphicarpaea bracteata*, which were handled separately, were kept moist and cool (4°C.) until planting. Total dry weight of seeds planted was approximately 8 g m^{-2} for the mesic mix and 9 g m^{-2} for the xeric mix. The total number of seeds planted per m^2 was estimated to be 9,000 for both mixes.

To provide adequate contrast for analysis, the species were chosen for each mix to provide a) a large degree of intra-specific variation in leaf width, leaf inclination, leaf weight, longevity, and seed weight; b) large numbers of both "sun" and "shade" species, as listed by Bray (1958) and Packard (1988a); c) ample representation of the lists of "savanna" species given by Curtis (1959) and Packard (1988a, 1988b); d) adequate numbers of shade-tolerant grasses to help carry fire; and e) several species with nitrogen-fixing ability. The mixes include 110 species in 75 genera and 30 families. The families with the most species are Asteraceae (mesic mix, 19; xeric mix 21), Poaceae (mesic mix, 9; xeric mix, 7), Fabaceae (mesic mix, 8; xeric mix 10) and Ranunculaceae (mesic mix, 6; xeric mix, 4). All species were native to Dane County. Except for two low shrubs, *Amorpha canescens* and *Ceanothus americanus,* all seeds were from herbaceous species.

To the extent practicable, seeds were wild gathered in southern Wisconsin from habitats similar to those at the Arboretum. Additional seeds were purchased

from nurseries (i.e., Genesis Nursery, Walnut, Illinois; Prairie Moon Nursery, Winona, Minnesota; Prairie Nursery, Westfield, Wisconsin; Prairie Ridge Nursery, Mount Horeb, Wisconsin; Taylor Creek Restoration Nurseries, Brodhead, Wisconsin) from stock of local or regional origin. Most species of the wild-gathered seeds came from a single location. Although I know little about the genetic variation present within the seeds of any species, certainly the genetic variation between species was greater than the variation within species.

In the first two weeks of November 1992 the seeds were evenly scattered by hand on the soil surface of each quadrat including about a 25 cm strip on either side. In the days immediately after planting the nightly freezing and daily thawing readily incorporated the seeds into the soil surface. To assure the presence of nitrogen fixing bacteria, appropriate inocula of *Rhizobium* spp. were mixed with the seeds immediately prior to planting.

Environmental Data. -- Values for % sand were determined for each quadrat. First, soil cores of the top 15 cm were collected from approximately every third quadrat in the linear strips. The cores were analyzed at the University of Wisconsin Extension Soil and Plant Analysis Laboratory for percent sand, silt, clay, and organic matter. Finely the results were linearly interpolated to assign % sand values to each quadrat.

A position along a light gradient was determined for each quadrat via computer analysis of hemispherical canopy photographs. During the summer of 1993, a hemispheric photograph was taken by placing the camera 40 cm above

the southern portion of each quadrat with the plain of the film level and the top of the camera directed toward magnetic north. The resulting photographs were scanned, corrected for true north, and analyzed for seasonal direct photosynthetic photon flux density (PPFD) in the computer program SOLARCALC 5.41 (Chazdon and Field 1987).

Vegetation data. -- To quantify the composition of the experimental quadrats, I visually estimated the aerial cover of each species over every quadrat during spring (May to June) and summer (July to August) of 1995. I also estimated cover again in October for species that reach peak cover in fall (e.g., *Eupatorium rugosum*). For each species, the largest of the three seasonal cover estimates was used in analysis.

To aid in field identification of young plants, in early spring of 1993 I raised seedlings of most of the planted species. The seedlings were photographed and specimens were pressed and dried. For most field observations my level of certainty of correct identification was high, especially by 1995. However, not all plants could be identified to species with total confidence and certain pairs of species were hopelessly confusing as juvenile plants. The latter included *Anemone cylindrica* and *A. virginicus*, *Gentiana flavida* and *G. puberula*, *Asclepias exaltata* and *A purpurescens*. In addition very few individuals in the Lilliaceae (e.g., *Smilacina racemosa*, Polygonatum biflorum) were determined to species. For purposes of analysis, only data for individuals identified to species were used. Nomenclature follows Gleason and Cronquist (1991).

Species were classified into overlapping guilds based on (i) leaf width, (ii) leaf height, (iii) longevity, (iv) N-fixing potential, and (v) possession of the C_3 vs. C_4 photosynthetic pathway. The leaf guilds were based on measurements of fully expanded foliage on mature plants in remnant savannas (Leach 1996a). Four guilds of maximum leaf width (0 - f mm, 6 - 15 mm, 16 - 45 mm, > 45 mm) of forbs was based on the diameter of the largest circle that could be inscribed on a blade. The classification of leaf height (0 - 40 cm, 41 - 80 cm, > 80 cm) was based on the tallest individuals observed in savanna remnants. Two growth forms were considered: graminoids (Poaceae, Cyperaceae) with grass-like foliage and forbs with generally broader foliage. Longevity (annual, biennial, or perennial) was based on species descriptions in Gleason and Cronquist (1991). Species with N-fixing potential were describe by Allen and Allen (1981). The photosynthetic pathway of grasses were as described by Brown (1977) and Kindscher (1992).

Data Analysis. -- Direct gradient analysis of groundlayer composition, structure, and diversity were conducted with methods similar to those used to study remnant savannas (Leach 1996a). In both studies, quadrats were stratified along gradients of % sand and % direct PPFD, although in the current study the distribution of quadrats along the % sand gradient was skewed toward siltier soils, while the remnant quadrats were most abundant on sandy loams. The experimental soils also differed somewhat from the remnants soils by having, on average, a slightly higher clay component.

Quadrats were first into 4 soil texture classes and 3 light-availability classes, defining a total of 12 soil x light microhabitats. For the quadrats planted with the mesic mix, the % sand gradient was divided into 3 parts ($\leq$ 11%, 12 - 24%, 25 - 82%) each containing as close to the same number of quadrats as numerically possible. The quadrats planted with the xeric mix (all on the sandiest soils) were all placed in a fourth soil texture class. For convenience, these soil classes are referred to by familiar soil class names--"silt," "silt loam," "loam," "loamy sand"--but quotation marks are used because these classes are not precisely congruent with the standard soil-texture classes. All quadrats were classified into one of three light-availability classes based on % direct PPFD (< 25%, < 50%, > 50%). The distribution of quadrats along the light gradient did not vary significantly among the soil classes (General Linear Models Procedure and Student-Newman-Keuls test, P > 0.22, d.f. = 407).

To compare the relative influence of soil texture vs. light availability in affecting groundlayer composition, beta diversity was analyzed simultaneously across sand and light gradients via multiple regression (Hujik 1995, Leach 1996a). Using only the data from the mesic-mix plantings, quadrats were grouped into nine microhabitats by placing each into terciles along the sand and light gradients. The proportional representation of each species in each microhabitat was determined. The Sorenson quantitative index of similarity (Magurran 1988) was calculated between the 36 unique pairs of microhabitats. Finally, the natural logarithm of the Sorenson index (see Whittaker 1972) was regressed simultaneously on the

differences in steps (0, 1, or 2) between microhabitats along each gradient (Hujik 1995, Leach 1996a). The slopes of this multiple regression represent the relative amounts of turnover in overall species composition along the soil and light gradients, respectively.

To test for differential distributions along gradients of sand and light of closely related species, 21 pairs of congeneric species, each having at least two percent frequency, were examined via GEODISTN (Syrjala 1996). This program compares the geographic distribution of two populations in two dimensions and was first applied to the distributions of species along two-dimensional ecological gradients by Leach (1996a). The null hypothesis is that the underlying distributions of the two populations being compared are identical. The comparisons used data only from the seed mix or mixes from which both species were planted. For each species pair, at least 1000 permutations were calculated to determine the boot-strapped p-value. The species tested were *Anemone virginiana* and *A. cylindrica*; *Aster prenanthoides*[M], *A. oolentangiensis*[M], and *A. leavis*; *Dalea candida* and *D. purpurea*; *Desmodium canadense, D. illinoense*, and *D. glutinosum*; *Eupatorium purpureum*[M], *E. rugosum*, and *E. sessilifolium*: *Elymus canadensis, E. hystrix, E. villosus*[M], and *E. virginicus*[M]; *Helianthus occidentalis*[X] and *H. strumosus*[X]; *Hieracium longipilum*[X] and *H. scabrum*[X]; *Monarda fistulosa* and *M. punctata*[X]; and *Penstemum gracilus*[X] and *P. grandiflorum*[X] (superscripts indicate inclusion in a single seed mix: "m" in the mesic mix, "x" in the xeric mix).

The distribution of total cover by forbs and graminoids, the two dominant

herbaceous growth forms found in savanna remnants (Leach 1996a), were evaluated along soil and light gradients. For each of 12 %sand x %direct PPFD microhabitats (as above), the mean cover of forbs and graminoids was determined. Similarly, the distribution of cover was determined for C4 grasses and nitrogen fixing species.

To determine if certain morphologic traits important for energy capture were distributed similarly in the experimental restoration as determined for savanna remnants (Leach 1996a), the bivariate mean positions were calculated as

$$x_i = \sum C_{ij} z_j \ / \ \sum C_{ij}, \tag{1}$$

where C_{ij} is the cover of species i in quadrat j, and z_j is the position of quadrat j along the gradient in question (either % sand or % direct PPFD). The null mean position represents the hypothetical mean assuming that soil texture and light availability had no influence on plant growth; it was calculated by setting $C_{ij} = 1$ for all quadrats, and equalled the mean % sand and mean % direct PPFD across all quadrats.

The mean ± standard deviation of a species positions along both soil and light gradients was calculated for all species present, with

$$s.d. = [(\ \sum C_{ij}(z_j - x_i)^2\ )\ /\ \sum C_{ij}]^{0.5}\ . \tag{2}$$

Separate values were calculated for quadrats planted with each species mix. Mean positions were used for comparing niche differentiation and the standard deviations of species' positions were used for comparison of their niche breadth along both soil and light gradients. Mean bivariate positions were calculated for

classes of species in three morphological guilds and compared with results from remnant savannas.

The relationship of total plant cover, richness and diversity was compared at both the quadrat and the microhabitat level. For each quadrat total plant cover, species richness (S), and diversity ($e^{H'}$) were calculated; these indices were compared via Spearman rank correlation, with separate tests for quadrats planted with the mesic and xeric mixes.

To detect stochastic effects on species distribution, I examined the presence of common species in their most favored (i.e., modal) microhabitats . For this purpose species with an overall frequency > 10% in the quadrats planted with the mesic mix were considered common. The frequency of each species within its modal microhabitat was determined. The average of these frequencies was determined across species.

RESULTS

Quadrat Environments. -- The areas used for this re-assembly experiment were on a range of soil textures from silt loam to sand and featured open grown trees that provided a light continuum from nearly full sun to heavy shade. The use of percent sand as a single useful soil variable was supported by its significant rank correlation with silt (-0.99 ***), pH (-0.89 ***), %organic matter (-0.74 **), K (-0.87 ***), Ca (-0.95 ***), Mg (-0.96 ***), and N (-0.68 *).

As intended, quadrats were widely scattered along sand and PPFD gradients (Figure 1). The mesic mix was planted in quadrats on soils ranging from

7% sand (silty) to 82 percent sand (loamy sand); mean = 21.2 ± 16.8%. The xeric

mix quadrats were on loamy sand to sandy soils containing 72 to 91 percent sand;

mean = 83.4 ± 5.5. Percent organic matter was higher and had a wider range at

Wingra than Grady. At Wingra percent organic matter was greatest in shade,

suggesting that in the absence of plowing organic matter accumulated under oak

canopies. Relatively fewer quadrats at Wingra were found at the low end of the

light gradient (Figure 1) due to the larger trees having higher canopies.

Species. -- Of the species planted, 64 (76%) in the mesic mix and 61 (74%) in the

xeric mix were growing in the plots in 1995. These observations underestimate

the number of species actually present, due to the presence of unidentifiable

juvenile plants. Species differed considerably in frequency, mean cover, mean

bivariate position, and standard deviation of the mean (Table 2).

Turnover along light and soil gradients. -- The coefficients of the dependent

variables indicate the relative influence of the two gradients of spatial turnover

(Hujik 1995):

$$\text{Ln } C = 4.34 - 0.26\ G_{SAND} - 0.06\ G_{light} \qquad\qquad (3)$$

For the regression $r^2 = 0.37$; for G_{SAND} $P = 0.0001$ and for G_{LIGHT} $P = 0.33$. Soil

texture had 4.3 times the influence on species turnover as did light.

Habitat Partitioning.-- The cover of forbs increased with silt content, while

graminoid cover increased toward sun and sand (Table 3). In all microhabitats,

the total cover of forbs was several times higher than the total cover of grasses.

On the three siltiest microsites, forbs contributed over 90 percent of the total

cover. C3 grasses were more widely distributed than C4 grasses, which where most abundant in the brightest or more sandy microsites.

Nitrogen-fixing species in aggregate were distributed similarly to C4 grasses, with cover increasing toward bright or sandier microsites. Individual species varied in their distributions, with two N-fixers not following this pattern. *Amphicarpaea bracteata* was nearly excluded from the sandiest soils, and, along with *Desmodium glutinosum*, tended to be in shadier habitats. These two species had similar distributions in remnant savannas (Leach 1996a).

The distribution of largest leaf-width guild was skewed toward the shade, but the pattern of the narrower guilds was not clearly skewed toward brighter habitats as expected (Figure 3 (a)). Contrary to expectations, leaf-height classes showed little consistent relation to sand and light gradients (Figure 3 (b)).

In 12 out 21 comparisons between pairs of congeneric species, the species had significantly different bivariate distributions ($P < 0.05$, often $P < 0.01$). However, there was an exception in most genera: *Anemone virginiana* and *A. cylindrica* ($P > 0.4$), *Aster laevis* and both *A. prenanthoides* ($P > 0.3$) and *A. oolentangiensis* ($P > 0.06$), *Elymus hystrix* and *E. virginicus* ($P > 0.056$), *Eupatorium rugosum* and *E. sessilifolium* ($P > 0.1$), *Desmodium illinoense* and *D. canadense* ($P = 0.3$; Figure 2), *Helianthus occidentalis* and *H. strumosus* ($P > 0.2$), and *Hieracium scabrum* and *H. longipilum* ($P > 0.7$).

Total Cover, Diversity, and Richness. -- Total cover was significantly and negatively correlated (Spearman rank) with diversity (mesic mix: r_s = -0.314, p = 0.0001, for 275 observations; xeric mix: r_s = -0.224, p = 0.009, for 136 observations). Cover was negatively correlated with richness in the mesic mix (r_s = -0.127, p = 0.035, for 275 observations) and positively correlated in the xeric mix (r_s = 0.249, p = 0.004, for 136 observations). Calculations of means of total cover, diversity, and richness for the 12 microhabitats (Table 4), reveals that total cover tended to decline toward sandier, shadier microsites; diversity and richness tended to increase, among the mesic mix, with percent sand.

A survey of plants dominating microhabitats with low diversity and high total cover reveals a set of apparent competitive dominants. The herbaceous canopy of the quadrats at Wingra were shared by a group of mostly morphologically similar species (Figure 4) including *Heliopsis helianthoides, Monarda fistulosa, Eupatorium purpureum, E. rugosum,* and *Helianthus strumosus.*

Stochastic variation. -- Thirty-three species had frequencies > 10% among the mesic-mix quadrats. Their %frequencies in their modal habitats indicate the level of stochastic variation affecting their presence, with 100% frequency indicating no stochastic variation. Their mean modal frequencies = 75.2 ± 23.7%. Nine species had modal frequency of 100%.

DISCUSSION

The data used in this study are from the third year of a long-term

restoration experiment. Although I do not wish to imply that three years is sufficient for species to complete their self-sorting, in that time the species have developed a considerable degree of spatial patterning.

Reassembly experiments provide an independent test of new generalizations regarding oak savanna groundlayers, their composition, structure, and horizontal patterning (Leach 1996a). Previous studies on Wisconsin savannas have emphasized the individualistic distribution of groundlayer species along the community gradient from prairie through savanna to forest, and, hence, the transitional nature of savanna (e.g., Bray 1955, 1958, 1960, Curtis 1959, Pruka 1994). Such studies, by the nature of the community gradient considered, emphasize the role of the light gradient in spatial turnover between sites. However, Leach (1996a) showed that among savannas arrayed across a range of soil textures, that species turnover along the soil gradient was twice that found along the light gradient. That finding was reported as preliminary because soil texture was correlated with the sites themselves; due to geographic isolation sites did not share a common species pool, so the effects of soil could not be clearly separated from effects of species pool variation. The reassembly experiment eliminates the problem of soil-species pool correlation by the sowing of identical species mixes into a wide range of soil and light microsites. Even starting with identical seed mixtures, the results of three years of community development show soil having four times the influence on composition than did light (Eq. 3). This ratio between sand and light gradients is roughly twice that found among remnant

savannas (Leach 1996a). Species sorting along the experimental gradients is faster for % sand than % direct PPFD (Leach 1996b), indicating that plant growth is constrained more by edaphic conditions than by levels of light availability. These findings strongly support the generalization by Hujik (1995) that edaphic factors within savannas (in his case factors related to elevation in lowland sites) can influence species composition more than does light availability.

Habitat partitioning along soil and light gradients, although not at the levels observed in savanna remnants (Figure 4), was evident among species. The bivariate distributions along soil and light gradients were significantly different for 12 out of 21 congeneric pairs. These observations are consistent with the idea that habitat partitioning is partly responsible for the high diversity found in savanna remnants and provide further evidence of the individualistic distribution of species within savanna landscapes (Bray 1955, 1958, 1960; Curtis 1959; Gilbert and Curtis 1953; Pruka 1994; Hujik 1995; Leach 1996a).

Oak savanna remnants on shadier or siltier microsites tend to be forb, rather than grass, dominated (Leach 1996a). Comparisons in the restoration experiment show that forb cover was greater than graminoids in all microhabitats, but the difference was least in sandier-sunny microsites (Table 3). The experimental distributions of two C4 grasses, *Andropogon gerardii* and *Schizachyrium scoparium*, which typically dominate Wisconsin prairies (Curtis 1959), were highly skewed toward sandy or bright microsites. These findings are consistent with the view expressed by Leach (1996a) that natural savannas were

dominated by C_4 prairie grasses only in nutrient- poor or sunny microsites and that more generally savannas are forb, rather than grass dominated.

Morphological traits of leaf width and leaf height, which had shown strong distribution patterns along gradients of soil and light in remnant savannas (Leach 1996a), did not show clear relationships with gradients in the experimental restoration. The failure of among-class mean distributions of morphologic classes to parallel their distributions among savanna remnants, may be more the result of problems with classification than with bivariate analysis. Species were classified by measurements of traits on mature individuals, but morphologic traits often differ between juvenile and adult individuals (Keddy 1990). Future observations are needed to learn if and when remnant-like patterns emerge in the experiment.

The relationship of total cover and species richness were negative in experiments and positive in remnants (Leach 1996a). The negative relation in the experiment was apparently the result of competitive exclusion on resource-rich microsites by a morphologically similar group of perennial forbs that formed nearly a continuous canopy over the plots (Figure 5). These species attained much lower cover on sand x light microsites in remnants.

On more nutrient-poor microsites there was less total cover and no continuous canopy of tall herbs. Several species were more common on these microsites. Presumably such species are adapted for nutrient-poor habitats by allocating more resources below ground.

One of the more distinctive challenges of ecological restoration is the establishment of the high levels of species diversity and richness typical of natural communities (Gross 1987). Competitive exclusion on nutrient rich sites may be a common problem in savanna and prairie restorations. On the finer-texture, nutrient-rich soils a group of tall, mostly clonal forbs gained high total cover (Figure 5), presumably at the expense of many shorter, or more slowly growing species. One such recent restoration experiment in mixed-grass prairie suggests that artificial reduction of N availability may aid establishment of native species (Wilson and Gerry 1995). Similar experiments should be conducted for savanna restorations on nutrient rich sites.

The role of stochasticity has been rarely documented in restoration projects, yet may have a considerable influence on resulting communities. Overall, the wide range in frequencies in modal habitats, provides strong evidence for the operation of local stochastic effects on germination and early establishment. These high levels of stochasticity suggest that at the species level, restorationists may have limited control over establishing species-defined associations. In savanna restoration, it may be easier to establish a prescribed range of functional groups, then to establish particular species from those groups.

There are several clear implications of this study for savanna restoration. The groundlayers of oak savannas, which contain the bulk of plant biodiversity, vary considerably with soil texture; to preserve that variation will require the restoration and conservation of savannas on a wide range of soil conditions. With

savanna preserves, the heterogeneity of soil and light environments should be maintained to provide suitable microhabitats for a diverse flora. When choosing species to re-assemble as herbaceous communities, traits important for energy capture should be matched with microhabitats and thereby increase the speed of re-assembly and decrease seed costs.

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Table 1. Two mixtures of seeds were planted. The mesic seed mix was planted on "silty" to "loamy" microsites, and the xeric seed mix was planted on "sandy loam" microsites. Weight (g) and number (n) of seeds planted per quadrat are given. Weight were not determined for fleshy fruited seeds.

	Mesic Mix		Xeric Mix	
	g	n	g	n
Allium cernuum	0.06	20	0.06	20
Amorpha canescens	0.06	50	0.06	50
Amphicarpaea bracteata		1		1
Andropogon gerardii	0.25	74	0.25	74
Anemone cylindrica	0.06	90	0.06	90
Anemone virginiana	0.08	50	0.08	50
Apocynum androsaemifolium	0.01	90	0.01	90
Apocynum cannabinum			0.06	90
Aquilegia canadensis	0.04	45	0.04	45
Arisaema triphyllum		3		
Asclepia purpurascens	0.01	2		
Asclepias amplexicaulus			0.03	5
Asclepias exaltata	0.10	14		
Asclepias tuberosa			0.10	12
Asclepias verticillata			0.03	12
Asclepias viridiflora			0.05	6
Aster laevis	0.06	130	0.06	130
Aster oolentangiensis	0.02	12	0.02	12
Aster prenanthoides	0.01	30	0.01	30
Aster sagittifolias	0.14	350	0.14	350
Aster sericeus			0.09	300

Aster shortii	0.09	210	0.09	210
Aster umbellatus	0.02	45		
Baptisia bracteata			0.80	50
Baptisia lactea var lactea	0.40	24		
Besseya bullii	0.03	110	0.03	110
Blephilia hirsuta	0.06	250		
Bromus kalmii	0.38	190	0.38	190
Cacalia atriplicifolia	0.02	50		
Camassia scilloides		3		
Campanula americana	0.03	170		
Carex bicknellii			0.02	11
Carex gravida			0.03	50
Ceanothus americana			0.85	210
Cinna arundinacea	0.18	450		
Circaea lutetiana	0.07	14	0.07	14
Conyza canadensis	0.02	120	0.02	120
Coreopsis palmata	0.03	25	0.03	25
Cyprepedium calceolus	trace	200	trace	200
Dalea candida	0.02	16	0.02	16
Dalea purpurea	0.03	25	0.03	25
Desmodium canadense	0.18	30	0.18	30
Desmodium glutinosum	0.08	4	0.08	4
Desmodium illinoense	0.09	15	0.09	15
Dodecatheon meadia	0.02	100	0.02	100
Elymus canadensis	0.54	110	0.54	110
Elymus hystrix	0.22	40	0.22	40

Elymus villosus	0.34	85		
Elymus virginicus	0.23	23		
Eupatorium purpureum	0.10	240		
Eupatorium rugosum	0.01	35	0.01	35
Eupatorium sessilifolium	0.02	45	0.02	45
Euphorbia corollata	0.12	70	0.12	70
Gaura biennis	0.08	25		
Gentiana flavida	0.04	350	0.04	350
Gentiana puberulenta	0.01	240	0.01	240
Gentianella quinquefolia	0.01	120		
Geranium maculatum	0.02	3	0.02	3
Gerardia grandiflora			0.12	160
Geum canadense	0.06	110	0.06	110
Helianthemum canadense			0.00	2
Helianthus occidentalis			0.02	15
Helianthus strumosus	0.03	6	0.03	6
Heliopsis helianthoides	0.18	45	0.18	45
Heuchera richardsonii			0.05	140
Hieracium longipilum			0.01	40
Hieracium scabrum			0.00	1
Liatris aspera	0.14	70	0.14	70
Lilium michiganiense	0.05	20		
Lilium philadelphicum			0.00	2
Lobelia spicata			0.01	200
Lupinus perennis			0.40	14

Lysimachia ciliata	trace	100	0.00	100
Monarda fisulosa	0.03	90	0.03	90
Monarda punctata			0.05	200
Napaea dioica	0.54	135		
Oenothera biennis	0.03	70	0.03	70
Oenothera clelandii			0.20	1050
Penstemon gracilis			0.02	320
Penstemon grandiflorus			0.02	12
Phlox pilosa			0.19	220
Phryma leptostachya	0.06	9		
Physalis virginiana			0.03	11
Polemonium reptans	0.22	145		
Polygonatum biflorum	0.02	9		
Polytaenia nuttallii	0.05	6	0.05	6
Ranunculus fascicularis	0.03	12	0.03	12
Ratibida pinnata	0.12	120	0.12	120
Rudbeckia hirta			0.08	290
Sanicula marilandica	0.18	32		
Schizachyrium scoparium	0.30	100	0.30	100
Scrophularia lanceolata			0.01	60
Senecio pauperculus			0.04	170
Silene stellata	0.13	210	0.13	210
Smilacena racemosa	0.19	6	0.19	6
Smilacena stellata			0.08	4
Solidago flexicaulus	0.04	125		

Solidago rigida	0.06	100	0.06	100
Solidago speciosa	0.12	530	0.12	530
Sporobolus heterolepis	0.36	180	0.36	180
Stipa spartea			0.17	9
Taenidia integerrima	0.06	16	0.06	16
Tephrosia virginiana			0.34	30
Thalictrum dasycarpum	0.05	14		
Thalictrum dioicum	0.10	35		
Triosteum perfoliatum		3		
Veronicastrum virginicum	0.05	1500		
Viola sagittata			0.00	4
Zizia aptera	0.06	20	0.06	20
Zizia aurea	0.06	34		

Table 2. Species showed individualistic patterns of percent frequency (% f), mean cover (C), and mean position and s.d. along gradients of % direct PPFD and % sand. These are shown for quadrats planted with the (a) mesic seed mix and the (b) xeric seed mix.

a. Mesic-mix data

Species	% f	C	% Direct PPFD		% Sand	
			Mean	s.d.	Mean	s.d.
Allium cernuum	0.4	0.00	11.4	0.0	37.0	0.0
Amorpha canescens	0.4	0.00	98.3	0.0	36.0	0.0
Amphicarpaea bracteata	37.8	3.16	35.8	26.6	39.4	20.3
Andropogon gerardii	42.9	6.72	62.6	25.6	35.7	16.8
Anemone cylindrica	2.2	0.04	35.5	18.6	22.6	10.7
Anemone virginiana	4.4	0.22	48.0	16.5	19.2	15.1
Aquilegia canadensis	23.6	0.32	40.1	29.2	40.9	18.6
Arisaema triphyllum	21.8	0.12	30.7	20.7	33.1	21.6
Aster laevis	48.0	1.16	51.4	25.4	23.3	19.3
Aster oolentangiensis	2.2	0.03	59.0	25.3	33.6	8.4
Aster prenanthoides	55.3	2.51	50.1	25.3	20.6	17.2
Aster umbellatus	8.0	0.09	43.4	22.5	23.5	18.0
Baptisia lactea var lactea	17.1	0.87	56.2	32.5	49.5	16.0
Besseya bullii	1.5	0.01	20.2	7.9	56.0	13.6
Bromus kalmii	26.5	0.66	63.8	26.4	37.4	17.7
Cacalia atriplicifolia	16.0	0.51	63.3	31.7	27.0	21.3
Campanula americana	2.5	0.01	21.6	9.8	29.7	24.0
Cinna arundinacea	26.9	0.61	30.9	21.7	29.4	23.4
Circaea lutetiana	65.1	1.96	35.2	21.3	14.4	10.5
Conyza canadensis	3.6	0.03	60.3	22.2	45.4	25.6

Coreopsis palmata	7.6	0.11	58.6	37.8	32.9	20.6
Dalea candida	0.4	0.00	87.2	0.0	70.0	0.0
Dalea purpurea	0.7	0.01	71.1	27.8	62.5	13.0
Desmodium canadense	14.2	1.12	66.5	28.0	46.2	17.6
Desmodium glutinosum	5.1	0.15	28.8	20.6	51.3	13.0
Desmodium illinoense	0.7	0.03	58.3	6.0	55.0	7.0
Dodecatheon meadia	4.0	0.02	42.3	27.1	35.1	11.7
Elymus canadensis	70.5	2.92	48.4	26.5	20.6	14.7
Elymus hystrix	66.9	1.82	29.7	19.0	20.9	15.9
Elymus villosus	80.4	2.78	33.9	22.2	18.7	14.5
Elymus virginicus	36.7	0.88	26.7	18.2	21.9	16.9
Eupatorium purpureum	86.5	12.54	36.5	21.0	13.4	9.4
Eupatorium rugosum	76.0	15.53	33.8	19.1	12.8	6.5
Eupatorium sessilifolium	1.5	0.01	28.2	24.3	29.5	8.3
Euphorbia corollata	8.0	0.09	46.7	27.0	48.5	14.3
Gaura biennis	12.7	0.47	61.1	27.0	30.7	20.2
Gentiana flavida	2.5	0.22	56.5	25.4	49.9	13.2
Geranium maculatum	16.0	0.25	30.7	17.8	19.2	13.8
Geum canadense	90.9	6.05	34.8	20.6	16.3	13.3
Helianthus strumosus	5.8	0.25	50.0	33.7	17.8	15.7
Heliopsis helianthoides	88.7	32.02	44.0	25.3	15.6	12.1
Lysimachia ciliata	22.5	0.30	45.5	25.6	23.3	16.5
Monarda fisulosa	92.4	11.78	50.1	24.6	20.4	17.0
Napaea dioica	45.1	2.31	28.0	17.3	12.4	6.1
Oenothera biennis	22.9	0.45	44.0	27.1	37.8	21.0
Phryma leptostachya	0.7	0.01	48.3	8.1	16.0	13.2

Polemonium reptans	92.0	8.55	36.0	23.0	15.9	12.7
Polytaenia nuttallii	3.6	0.02	43.1	31.7	35.4	24.3
Ranunculus fascicularis	1.1	0.01	49.6	18.1	61.7	10.4
Ratibida pinnata	14.2	0.60	54.3	29.6	30.3	17.4
Sanicula marilandica	1.5	0.01	13.4	1.7	60.8	12.5
Schizachyrium scoparium	26.2	1.91	62.0	26.2	41.5	18.1
Silene stellata	23.3	0.37	54.2	28.9	29.3	24.8
Solidago rigida	1.8	0.02	48.8	31.0	52.8	10.4
Solidago speciosa	0.4	0.00	11.4	0.0	37.0	0.0
Sporobolus heterolepis	6.5	0.14	65.5	23.0	35.1	12.2
Thalictrum dasycarpum	0.4	0.00	35.3	0.0	11.0	0.0
Thalictrum dioicum	0.4	0.00	19.6	0.0	14.0	0.0
Triosteum perfoliatum	0.4	0.00	29.3	0.0	12.0	0.0
Veronicastrum virginicum	58.2	1.57	56.8	26.0	34.0	21.8
Zizia aptera	0.4	0.00	87.2	0.0	70.0	0.0
Zizia aurea	64.7	3.75	44.6	25.8	20.9	14.9

Table 3. The total cover of (a) forbs , (b) graminoids, (c) C_4 grasses, and (d) N-fixers varied along gradients of soil texture and light availability. The "loamy sand" quadrats received the xeric seed mix, while the other soils receive the mesic seed mix.

| | % Direct PPFD | | |
	< 25%	< 50%	> 50%
A. Forbs			
"Loamy sand"	43.2	64.4	67.2
"Loam"	59.0	62.4	91.8
"Silt loam"	123.3	109.5	105.1
"Silt"	125.9	134.5	135.0
B. Graminoids			
"Loamy sand"	6.3	12.2	34.3
"Loam"	18.8	31.9	53.5
"Silt loam"	16.4	15.7	17.1
"Silt"	5.5	8.5	11.9
C. C_4 grasses			
"Loamy sand"	1.8	9.7	32.2
"Loam"	8.1	23.5	42.1
"Silt loam"	0.1	3.8	10.5
"Silt"	0.0	0.7	4.3
D. N_fixers			
"Loamy sand"	3.7	10.4	12.8
"Loam"	11.6	11.6	13.4
"Silt loam"	1.4	4.4	2.8
"Silt"	0.0	0.7	0.3

Table 4. Community attributes of (a) total groundlayer cover,
(b)species richness and (c) diversity (e$^{H'}$) varied along
gradients of soil texture and light availability. The "loamy
sand" quadrats received the xeric seed mix, while the other
soils receive the mesic seed mix.

| | % Direct PPFD | | |
	< 25%	< 50%	> 50%
A. Cover			
"Loamy sand"	49.8	76.7	101.6
"Loam"	77.8	94.2	145.4
"Silt loam"	140.0	125.1	122.2
"Silt"	131.4	143.0	146.9
B. Richness			
"Loamy sand"	13.6	15.5	15.7
"Loam"	20.8	21.1	20.5
"Silt loam"	12.3	13.9	14.5
"Silt"	11.8	13.2	15.8
C. Diversity			
"Loamy sand"	9.0	7.9	7.4
"Loam"	12.8	12.3	10.9
"Silt loam"	6.2	6.6	6.9
"Silt"	5.7	7.0	8.1

Table 5. For each of 12 microhabitats (4 % sand X 3 % direct PPFD) % frequency and average cover are listed for species with the 20 highest frequencies in a given microhabitat. Microhabitats are listed in order of decreasing sand content, and, within each soil class, by increasing light availability.

1. "Sandy loam"
    a. < 25% direct PPFD

SPP	FREQUENCY	COVER
Geum canadense	100	4
Monarda fistulosa	95	7
Aquilegia canadensis	88	2
Elymus hystrix	76	3
Heuchera richardsonii	71	1
Eupatorium rugosum	69	7
Aster laevis	64	1
Heliopsis helianthoides	60	2
Circaea lutetiana	57	1
Scrophularia lanceolata	55	9
Silene stellata	55	1
Elymus canadensis	52	1
Andropogon gerardii	38	1
Desmodium glutinosum	36	1
Hieracium scabrum	33	1
Oenothera biennis	33	0
Desmodium canadense	31	2
Schizachyrium scoparium	31	1
Besseya bullii	31	0
Geranium maculatum	26	1
Bromus kalmii	26	0

2. "Sandy loam"
    a. 25 - 50% direct PPFD

SPP	FREQUENCY	COVER
Monarda fistulosa	100	11
Geum canadense	85	3
Aquilegia canadensis	82	3
Schizachyrium scoparium	69	4
Heuchera richardsonii	69	1
Eupatorium rugosum	67	10
Aster laevis	64	1
Heliopsis helianthoides	62	4
Silene stellata	62	2
Elymus hystrix	56	1
Andropogon gerardii	54	6

SPP	FREQUENCY	COVER
Scrophularia lanceolata	51	9
Lupinus perennis	51	6
Rudbeckia hirta	44	4
Bromus kalmii	44	0
Circaea lutetiana	41	1
Penstemon gracilis	38	1
Lobelia spicata	36	0
Helianthus occidenta	33	1
Conyza canadensis	33	0
Besseya bullii	33	0

3. "Sandy loam"
    a. > 50% direct PPFD

SPP	FREQUENCY	COVER
Andropogon gerardii	98	21
Monarda fistulosa	98	20
Schizachyrium scoparium	91	11
Heliopsis helianthoides	84	8
Lupinus perennis	73	7
Penstemon gracilis	73	2
Helianthus occidentalis	67	2
Geum canadense	64	1
Rudbeckia hirta	56	4
Aquilegia canadensis	56	1
Bromus kalmii	55	1
Aster laevis	55	1
Conyza canadensis	44	1
Scrophularia lanceolata	40	5
Desmodium canadense	40	5
Heuchera richardsonii	40	1
Elymus canadensis	38	1
Besseya bullii	38	0
Lobelia spicata	36	0
Euphorbia corollata	35	0

4. "Loam"
    a. < 25% direct PPFD

SPP	FREQUENCY	COVER
Veronicastrum virginicum	94	2
Geum canadense	91	4
Polemonium reptans	89	5
Amphicarpaea bracteata	86	9
Monarda fistulosa	86	7
Eupatorium purpureum	86	3
Heliopsis helianthoides	80	6
Elymus hystrix	80	2

Elymus villosus	74	2
Zizia aurea	69	4
Aquilegia canadensis	66	1
Andropogon gerardii	60	6
Circaea lutetiana	60	1
Elymus canadensis	57	3
Aster laevis	57	1
Arisaema triphyllum	57	0
Aster prenanthoides	54	2
Eupatorium rugosum	51	2
Schizachyrium scoparium	46	2
Elymus virginicus	46	1
Bromus kalmii	46	1

5. "Loam"
   a. 25 - 50% direct PPFD

SPP	FREQUENCY	COVER
Andropogon gerardii	100	18
Heliopsis helianthoides	100	9
Amphicarpaea bracteata	100	9
Monarda fistulosa	100	8
Zizia aurea	93	6
Eupatorium purpureum	93	3
Elymus canadensis	87	3
Veronicastrum virginicum	87	3
Geum canadense	87	2
Polemonium reptans	80	1
Baptisia lactea	67	4
Aster prenanthoides	67	3
Elymus villosus	67	2
Elymus hystrix	67	1
Bromus kalmii	67	1
Aster laevis	67	1
Schizachyrium scoparium	60	5
Eupatorium rugosum	60	1
Lysimachia ciliata	60	1
Aquilegia canadensis	60	1
Oenothera biennis	53	1

6. "Loam"
   a. > 50% direct PPFD

SPP	FREQUENCY	COVER
Andropogon gerardii	100	31
Heliopsis helianthoides	100	25
Monarda fistulosa	97	16
Elymus canadensis	97	5

Veronicastrum virginicum	97	5
Schizachyrium scoparium	93	10
Bromus kalmii	93	3
Polemonium reptans	86	3
Desmodium canadense	72	7
Eupatorium purpureum	72	3
Amphicarpaea bracteata	66	5
Baptisia lactea	66	4
Aster laevis	66	2
Zizia aurea	62	4
Elymus villosus	59	1
Geum canadense	59	1
Aquilegia canadensis	59	1
Aster prenanthoides	55	2
Elymus hystrix	52	1
Ratibida pinnata	48	2
Gaura biennis	45	2
Sporobolus heterolepis	45	1
Oenothera biennis	45	1

7. "Silt loam"
   a. < 25% direct PPFD

SPP	FREQUENCY	COVER
Elymus hystrix	100	5
Elymus villosus	97	6
Geum canadense	94	9
Eupatorium rugosum	91	27
Polemonium reptans	91	14
Monarda fistulosa	91	5
Eupatorium purpureum	71	10
Elymus virginicus	71	3
Circaea lutetiana	71	2
Heliopsis helianthoides	69	43
Napaea dioica	63	6
Zizia aurea	51	3
Elymus canadensis	49	2
Cinna arundinacea	31	1
Aster prenanthoides	26	1
Amphicarpaea bracteata	26	1
Aster laevis	20	0
Silene stellata	20	0
Veronicastrum virginicum	14	0
Arisaema triphyllum	11	0
Geranium maculatum	11	0
Lysimachia ciliata	11	0

8. "Silt loam"
   a. 25 - 50% direct PPFD

SPP	FREQUENCY	COVER
Geum canadense	100	8
Elymus villosus	100	5
Polemonium reptans	84	5
Circaea lutetiana	84	3
Eupatorium rugosum	80	34
Eupatorium purpureum	80	21
Monarda fistulosa	76	6
Elymus hystrix	76	3
Heliopsis helianthoides	72	20
Elymus virginicus	72	2
Zizia aurea	56	2
Napaea dioica	52	2
Amphicarpaea bracteata	44	4
Aster prenanthoides	44	1
Elymus canadensis	40	2
Veronicastrum virginicum	32	1
Bromus kalmii	32	0
Arisaema triphyllum	32	0
Cinna arundinacea	28	1
Silene stellata	28	0
Andropogon gerardii	24	3
Lysimachia ciliata	24	1

9. "Silt loam"
   a. > 50% direct PPFD

SPP	FREQUENCY	COVER
Monarda fistulosa	100	16
Heliopsis helianthoides	93	39
Geum canadense	93	4
Eupatorium purpureum	85	9
Polemonium reptans	85	4
Elymus canadensis	85	3
Elymus villosus	74	2
Zizia aurea	70	3
Eupatorium rugosum	67	11
Andropogon gerardii	67	8
Veronicastrum virginicum	67	2
Circaea lutetiana	63	1
Aster prenanthoides	48	3
Elymus hystrix	44	1
Aster laevis	44	1
Amphicarpaea bracteata	41	3
Schizachyrium scoparium	30	2
Bromus kalmii	30	1
Napaea dioica	30	1

Ratibida pinnata	22	1
Aquilegia canadensis	22	0

10. "Silt"
    a. < 25% direct PPFD

SPP	FREQUENCY	COVER
Eupatorium purpureum	100	26
Polemonium reptans	100	14
Geum canadense	100	8
Heliopsis helianthoides	96	37
Elymus villosus	92	24
Circaea lutetiana	88	2
Monarda fisulosa	75	4
Elymus hystrix	71	5
Napaea dioica	67	1
Elymus canadensis	50	5
Zizia aurea	50	1
Aster prenanthoides	46	2
Aster laevis	42	1
Elymus virginicus	29	1
Cinna arundinacea	12	0
Arisaema triphyllum	12	0
Silene stellata	12	0
Cacalia atriplicifol	8	0
Veronicastrum virgin	8	0
Oenothera biennis	8	0
Amphicarpaea bractea	8	0

11. "Silt"
    a. 25 - 50% direct PPFD

SPP	FREQUENCY	COVER
Monarda fistulosa	96	18
Polemonium reptans	96	10
Geum canadense	96	9
Heliopsis helianthoides	90	41
Eupatorium purpureum	90	20
Eupatorium rugosum	86	20
Elymus canadensis	86	3
Circaea lutetiana	75	3
Elymus villosus	75	2
Zizia aurea	73	4
Aster prenanthoides	73	3
Elymus hystrix	61	1
Napaea dioica	53	3
Veronicastrum virginicum	49	1
Aster laevis	35	1

Cinna arundinacea	25	0
Elymus virginicus	22	0
Silene stellata	18	0
Andropogon gerardii	16	1
Cacalia atriplicifolia	16	1
Amphicarpaea bracteata	12	1
Arisaema triphyllum	12	0

12. "Silt"
    a. > 50% direct PPFD

SPP	FREQUENCY	COVER
Heliopsis helianthoides	100	48
Monarda fistulosa	100	18
Polemonium reptans	100	11
Eupatorium purpureum	97	13
Eupatorium rugosum	94	14
Geum canadense	89	5
Elymus canadensis	86	4
Aster laevis	86	3
Elymus villosus	83	2
Veronicastrum virginicum	78	2
Aster prenanthoides	72	5
Zizia aurea	69	6
Circaea lutetiana	69	3
Napaea dioica	61	1
Andropogon gerardii	53	4
Elymus hystrix	47	1
Silene stellata	33	1
Oenothera biennis	28	0
Elymus virginicus	25	0
Cinna arundinacea	25	0

Figure 1. Quadrats were widely distributed along gradients of % direct PPFD and % sand. The mesic seed mix was planted in the quadrats at Wingra and Grady-Mesic and the xeric seed mix was planted at Grady -Xeric.

Figure 2. The bivarient distributions of three species of *Desmodium* were compared along % direct PPFD and % sand gradients by the Syrjala (1996) test. Pair-wise comparisons were significantly different, except between *D. illinoense* and *D. canadense*. See text for details.

Figure 3. Mean position along gradients of % direct PPFD and % sand were plotted for (a) leaf-width guilds and (b) leaf-height guilds.

Figure 4. Plots of the mean position along gradients of % direct PPFD and % sand for 10 common species in the (a) remnants savannas (Leach 1996a) and the (b) experimental restorations reveal greater habitat differentiation in the former.

Figure 5. The total cover across the light gradient of four tall perennial forbs was considerably higher on the fine-textured, nutrient-rich soil at (a) Wingra than on the coarser-textured, nutrient-poor soil at (b) Grady.
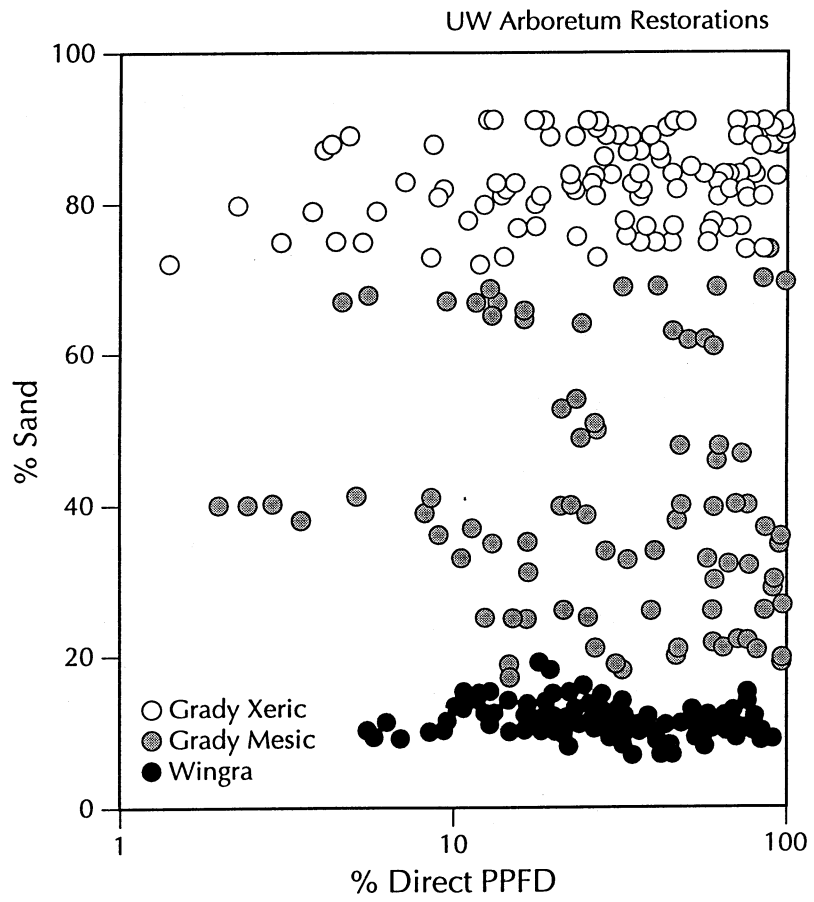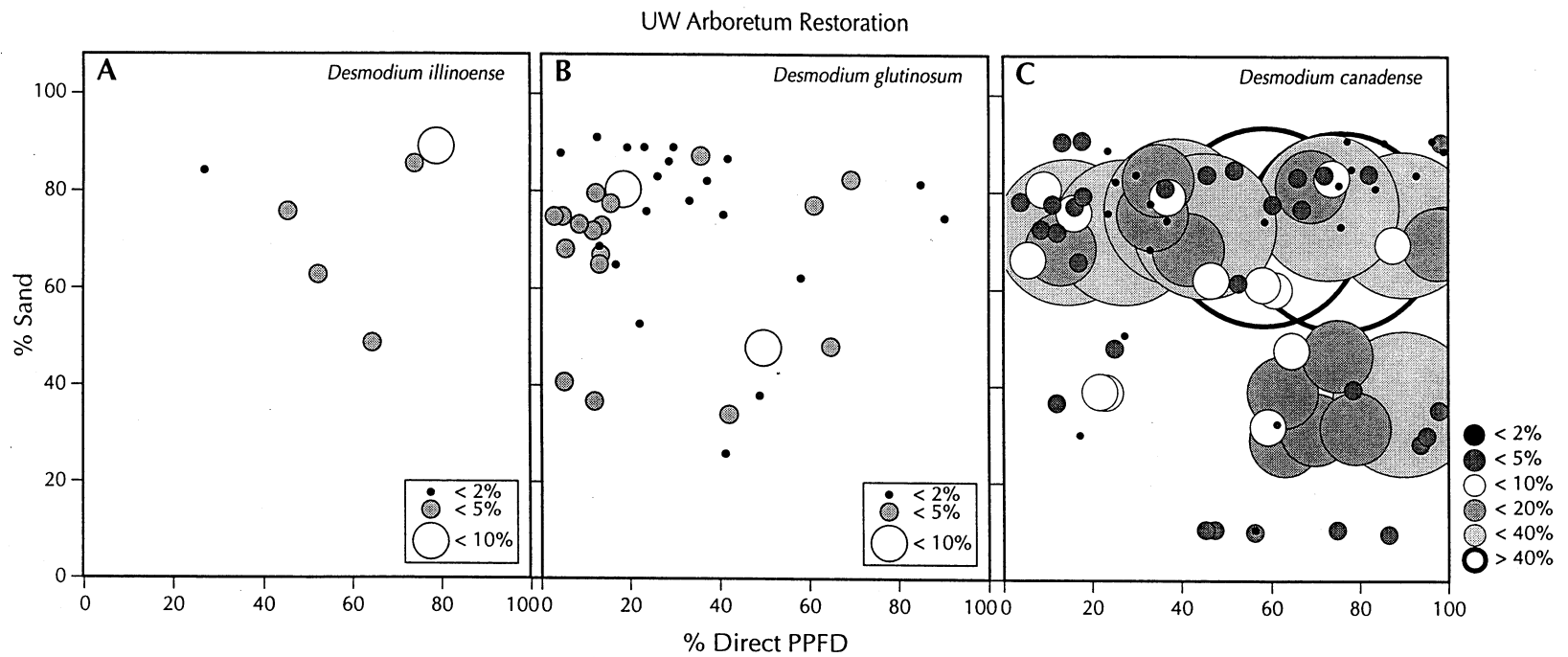
Figure 1

UW Arboretum Restorations

% Sand (y-axis)

% Direct PPFD (x-axis)

○ Grady Xeric
◉ Grady Mesic
● Wingra

UW Arboretum Restoration

Figure 2
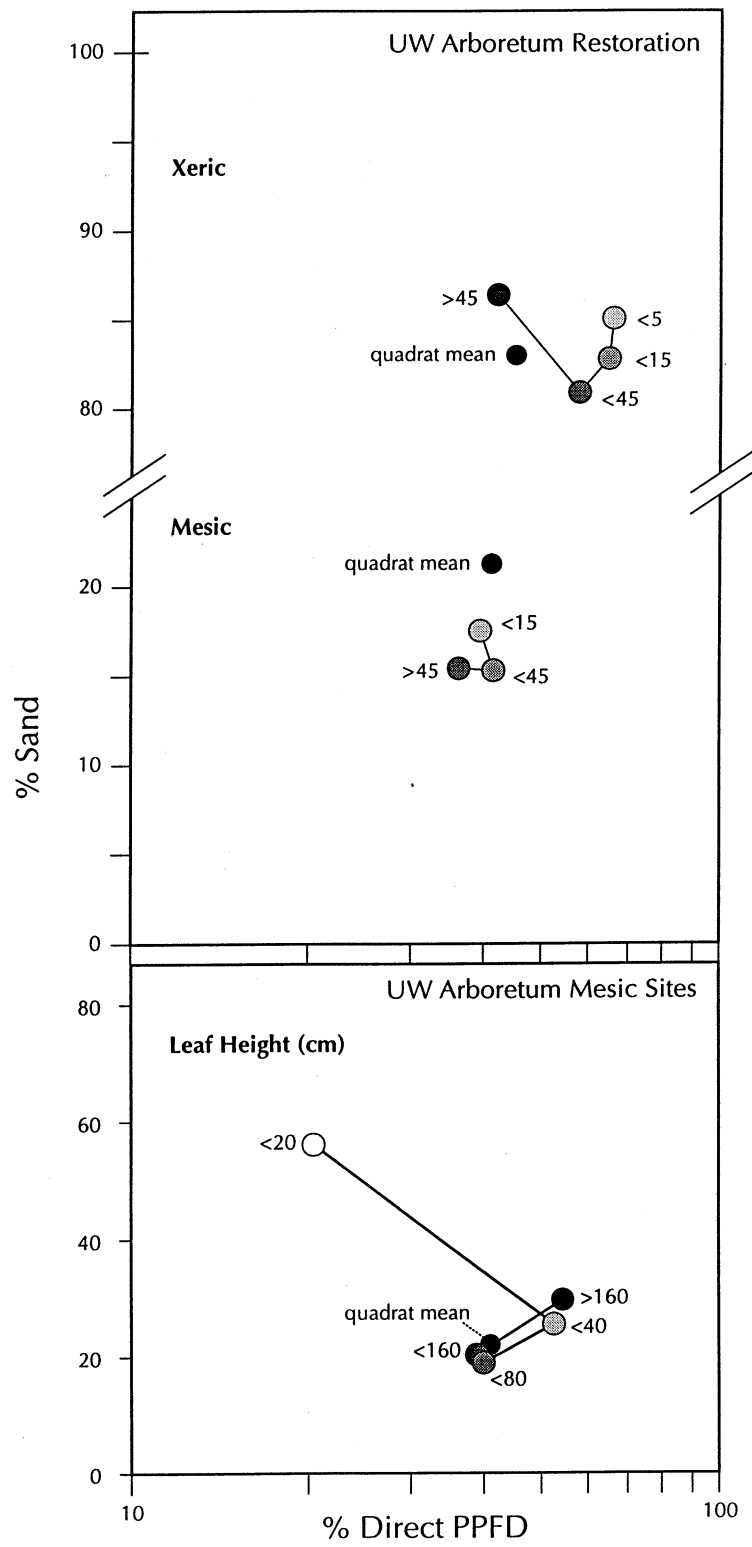
108
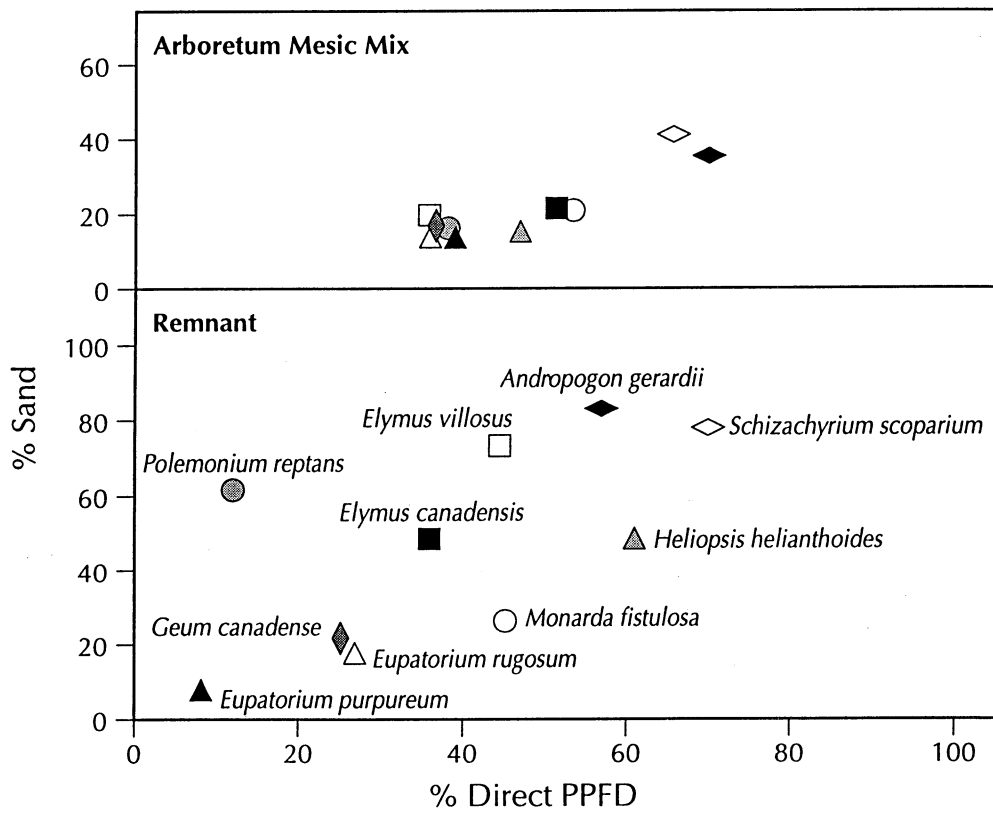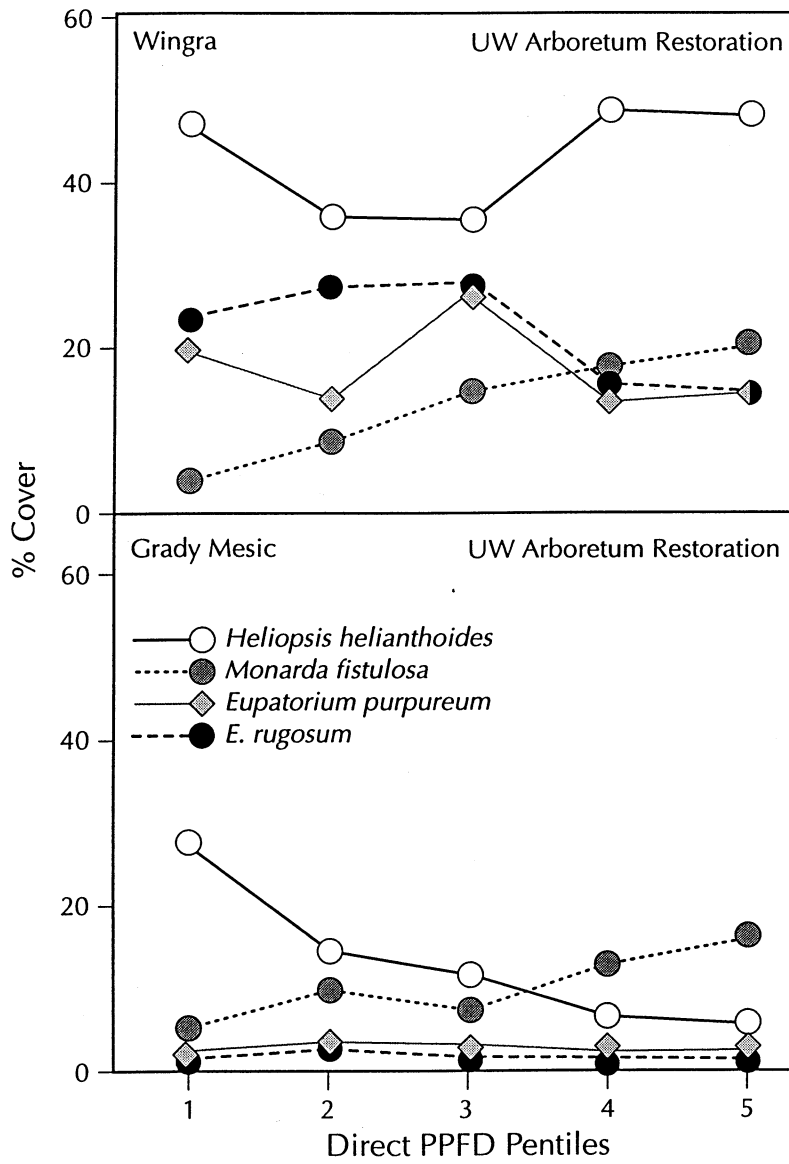
Figure 3 109

Figure 3

Figure 4

Figure 5

CHAPTER 3

COMMUNITY DYNAMICS IN AN EXPERIMENTAL
RESTORATION OF OAK SAVANNA GROUNDLAYERS

Abstract

Experimental restorations of the groundlayers of Midwestern oak savannas were initiated to test hypotheses on the nature of these now rare communities and to examine the influence of soil texture and light availability on community re-assembly. These long-term experiments involved planting uniform mixes of species into 411 1-m^2 quadrats arranged under and among open grown oak trees across a range of soil textures, assuring that broad environmental gradients of soil texture and light availability were available along which communities and community gradients could re-assemble. Replicated seed mixtures were planted on silty to loamy soils (84 spp) and on sandier soils (83 spp). Species coverage was quantified during each of three years following planting. Total forb cover was greater than that of graminoids in all habitats; the relative dominance of forbs increased through time except on the sandiest habitats. Cover by annuals peaked during Year 1; cover by biennials peaked during Year 2. Cover by plants with different traits important for energy capture (i.e., photosynthetic pathway, leaf width, leaf height) varied along soil and light gradients in ways consistent with economic theory. Total groundlayer cover increased each year, while species richness and diversity peaked in the second year. Species turnover (sum of the average numbers of species lost and recruited) was higher between Years 1 and 2

(9.9 ± 1.9 spp. m^2) than between Years 2 and 3 (7.7 ± 1.2 spp. m^2), largely due to decreased recruitment. Over time, groundlayer composition became increasingly influenced by soil texture relative to light availability, with roughly 4 times as much change in species composition associated with the soil gradient vs. the light gradient by Year 3. Over time, dominant species tended to increasingly diverge in their mean position along the soil and light gradients. Contrary to expectations, each year the average niche breadths of these species along the soil and light gradients increased. The experimental re-assembly of savanna groundlayers provide a basis for savanna restoration by identifying which species are competitively successive in such groundlayers and where they should be planted. Experimental re-assemblies are also useful for testing our understanding of the composition and functioning of a nearly vanished community.

Introduction

In North America, oak savannas were once the dominant vegetation in a broad transition zone between the prairies of the Great Plains and the deciduous forests of the East (Gleason 1913; Anderson 1983; Nuzzo 1986). Frequent fire, occasional severe drought, and other factors created conditions suited for a low density of trees, creating a great diversity of sunny and shaded microsites for species-rich groundlayers. Subsequent to settlement, most savannas were cleared for agriculture, or, as a result of fire suppression, succeeded to woodland or forest (Curtis 1959; Nuzzo 1986). By the early 1980s, savanna with intact groundlayers occupied 0.02% of their presettlement extent, and were especially uncommon on nutrient-rich, fine-grained soils (Nuzzo 1986). In recent years public and private conservation agencies have shown increased recognition of the importance of restoring and managing large tracts of oak savanna landscapes (Botts et al. 1994; Bleser and Leach 1994; Henderson 1995; Martin et al 1995; Leach and Ross 1995).

To date, efforts to replant savanna groundlayers have invoked a considerable controversy as to what constitutes a natural savanna and which species should be planted (see Packard 1988a, 1988b, 1993; Anderson 1991; Mendelson et al. 1992; Pruka 1994; Packard and Balaban 1995; Stevens 1995). In the upper Midwest, much of this debate pivots on the epistemology of ecological knowledge. Many professional ecologists and restorationists often rely upon Curtis (1959) for

descriptions of plant community composition and structure. His treatment of savanna relied heavily, in turn, on studies by Bray (1955, 1958, 1960). Both Curtis and Bray emphasized the close similarity of savanna groundlayers to prairies, noting that very few species were found in savannas that were not also found in prairies; they described savannas as essentially a scattered canopy of open-grown trees with a prairie groundlayer.

Four sets of findings throw doubt on this generalization. First, attempts to restore savanna groundlayers by planting mixtures of prairies species under open-grown oak trees have often resulted in low diversity, weed-filled vegetation (Packard 1988a, b; 1993; pers. obs.). Second, Packard (1988a, b) unearthed an account of plant species found in oak barrens (a kind of savanna) in central Illinois in the 1840s. This account included many "oddball" species that today are nowhere dominant, and typically occur in partially shaded microsites. Third, Pruka (1994) found that many of the species occurring in partly shaded, savanna-like conditions along a prairie-savanna-woodland gradient in southern Wisconsin were not those typical of prairies, and had instead been considered typical of dry oak forests by Curtis (1959). Finally, Leach (1996a) suggested that Bray's site criteria may have directly biased his findings in favor of a "prairie with trees" conclusion. To avoid sites damaged by grazing, Bray (1955, 1958, 1960) studied only those sites with abundant prairie grasses and forbs. Leach (1996a), attempting to avoid any circularity based on site selection criteria, chose to study remnant savannas based on the presence of native species throughout the mosaic of groundlayer

microsites, regardless of whether those species were typically found in prairie or not. Leach (1996a) found that the groundlayers of savanna in his sample were unusually species-rich and dominated by forbs, several of which are not frequently found in prairies; C_4 prairie grasses dominated only the most sunlit, sandiest microsites. Soil texture appeared to have a more profound effect on groundlayer composition and structure than variation in light differences among sites, while each site had microsites exposed to a wide range of light regimes. As a consequence, the stronger influence of soil texture on savanna groundlayers may or may not be an artifact of geographic differences in other environmental factors or in the species pool available for colonization.

To explore the determinants of groundlayer composition, structure, and dynamics and to test which species and species groups would be most successful in different savanna microsites, I initiated a savanna re-assembly experiment at the University of Wisconsin-Madison Arboretum (Leach 1996b). This long-term experiment involved the planting of uniform seed mixes along devegetated strips running from tree boles into openings on sites with a scattered tree canopy and a wide variety of soil textures. An analysis of the distribution and abundance of species and guilds during the third growing season following establishment showed that soil texture had roughly four times the effect of light availability on groundlayer composition (Leach 1996b), supporting a similar finding in savanna remnants (Leach 1996a).

This study examines the influence of soil and light gradients on the dynamics of

groundlayer re-assembly during the first three years of a long-term field experiment, focusing on trends in species composition, community structure, species richness and species diversity. Its aim is to provide insights into temporal trends in the importance of different species and species groups in savanna groundlayers following establishment, testing ideas regarding the competitive advantages of forbs vs. graminoids, of N-fixers vs. non-fixers, and of tall vs. short plants. Insights into these issues may enhance our understanding of a nearly vanished, mosaic ecosystem and aid attempts to restore these highly diverse and heterogeneous communities.

Methods

Site Descriptions

Reassembly experiments were initiated at the University of Wisconsin-Madison Arboretum to study the ecological sorting of savanna groundlayer species along gradients in soil-texture and light availability. The U. W. Arboretum is located within Madison and Fitchburg in Dane County in southern Wisconsin (43°4'N 89°24'W). Two areas were selected for experimental treatment--Wingra Savanna and Southwest Grady Tract--each with open-grown oaks, and together spanning a range of soil textures from silty to sandy.

The Wingra Savanna features an old grove of bur oaks (*Quercus macrocarpa*) on silt and silt loam. The scattered, open-grown oaks are 63 to 95 cm dbh, greater than 16 m tall, and more than 120 years in age. This area has apparently

never been plowed and has been maintained in a park-like condition with a mowed turf for 50 years (Kline 1992). Prior to this experiment, the groundlayer was characterized by lawn grasses (e.g., *Poa pratensis, Muhlenbergia screberii*) and short-stature herbs of disturbed, mesic sites (e.g., *Viola sororia, Prunella vulgarus, Glechoma hederacea,* and *Taraxacum officinale*).

Southwest Grady comprises a set of partially closed old fields roughly 50 years after abandonment, and includes soils ranging from silt loam to sand. Many of the oaks present were planted as acorns in the 1950s as part of a plan to restore the area to oak savanna (Kline and Cottam 1989, Kline 1992)); they include bur oak, white oak (*Q. alba*), red oak (*Q. rubra*), and hybrids of black oak (*Q. velutina*) and Hill's oak (*Q. ellipsoidalis*). These trees are now mostly 7 to 12 m tall, with 25 to 50 cm dbh. Since the planting of acorns, this area of the Arboretum has received little management attention other than weed species control and occasional prescribed fires (Kline 1992). Prior to the re-assembly experiments, the groundlayer on this site was a blend of native and alien grasses, forbs, and shrubs. On the siltier soils, these included *Agrostis gigantea, Bromus inermis, Lonicera X bella, Pastinaca sativa, Phleum pratense,* and *Solidago canadensis*. On sandier soils, common species included *Elytrigia repens, Panicum oligosnathes* var. *scribnerianum,* and *Poa pratensis*.

Gradients in soil texture (% sand) and light availability (% potential direct PPFD [photosynthetic photon flux density]) were chosen *a priori* as the basis for studies of the re-assembly of savanna groundlayer composition, structure, and diversity.

Research on remnant upland savannas in Wisconsin (Leach 1996a) had indicated

that these two environmental factors were important correlates of groundlayer

composition, and that each was strongly correlated with a variety of other factors

(e.g., concentrations of various soil nutrients, % open sky and total PPFD) likely to

affect savanna groundlayers. Prior to establishing the locations of the

experimental plantings, a reconnaissance revealed that a substantial range in soil

textures was available. The intentional placement of quadrats along broad

portions of gradients of soil texture and light availability helped ensure

comparability of data gathered from remnant and restored savannas, and provided

a mesocosm in which to conduct experiments on the effects of two important

factors affecting savanna groundlayers.

Site Preparation. During 1992, 38 strips 3 m in width were marked, running

from beneath tree canopies to open sunlit areas. Down the center of each strip,

the corners of a contiguous linear series of 1-m^2 quadrats were permanently

marked with steel rods. The number of quadrats per strip varied with tree size

and strip orientation, ranging from 5 to 19; longer strips were associated with the

taller trees at the Wingra site. A total of 411 1-m^2 quadrats were located to

represent broad portions of the gradients in soil texture and light availability.

During summer and early fall 1992, the strips were denuded of existing

vegetation by removing woody plants (using saws and weed wrenches) and twice

treating herbaceous plants with foliar applications of a glyphosphate herbicide.

The later was effective on most species except *Viola sororia, Rumex acetosella,*

and *R. obtusifolia*. These and invading species were later carefully hand weeded by the author. During the first two weeks of November 1992, the seed mixture prepared for each quadrat (see below) was evenly distributed on the soil surface of that quadrat and the adjoining 25 cm on either side of the strip of quadrats. An additional buffer ca. 75 cm in width on either side of the strip was planted with a mixture of *Elymus virginianus* and *Liatris aspera*. In the days immediately following planting, the nightly freezing and daily thawing readily incorporated the seeds into the soil surface. To assure the presence of nitrogen-fixing bacteria, appropriate inocula of *Rhizobium* spp. was mixed with the seeds immediately prior to planting.

Seed Mixtures. Two seed mixes were prepared and used for planting: a mesic mix for areas with sand content less than ca. 70%, and a xeric mix for areas with higher sand content (Table 1). The species chosen provided ample representation of the contrasting lists of "savanna" species given by Curtis (1959) and Packard (1988a, 1988b). In addition, they provided large numbers of "sun" and "shade" species (as listed by Bray [1958] and Packard [1988a]), extensive variation among species in leaf height, leaf width, plant longevity, and nitrogen-fixing ability, and adequate numbers of sun- and shade-adapted graminoids to help carry the fires planned for later stages of the experiment.

The mixes represent 110 species in 75 genera and 30 families. Families with the most species represented are Asteraceae (19 mesic, 21 xeric), Poaceae (9 mesic, 7 xeric), Fabaceae (8 mesic, 10 xeric) and Ranunculaceae (6 mesic, 4

xeric). All species are native to the Madison area. Except for two low shrubs (*Amorpha canescens* and *Ceanothus americanus*), all species included are herbaceous. Most seeds were collected from wild populations in Dane County and others parts of southern Wisconsin; some seeds were purchased from nurseries from stock of local or regional origin.

To ensure their even distribution among quadrats, seeds for each species were carefully weighed (or for large seeds, counted) into 411 separate planting units. The word "seed" is used here in its general sense of mature embryo with associated parts (Harper, et al 1970). The weight or number of seeds per species was chosen, based on prior experience, to promote the establishment of all species and to avoid problems with overly aggressive species. However, for several species the number of seeds planted was limited by availability. Fleshy-fruited seeds (e.g., *Arisaema triphyllum, Smilacina stellata*) and the massive below ground seeds of *Amphicarpaea bracteata* were kept moist and cool ($4°C$) until planting. The total dry weight of seeds planted per quadrat (1 m^2 plus 0.5 m^2 adjoining strip) was approximately 8 g for the mesic mix and 9 g for the xeric mix. The total number of seeds planted per quadrat (including the adjoining strips) was ca. 9,000 for both mixes, or ca. 6,000 seed m^{-2}.

Characterization of Soil and Light Gradients. In 1993, soil cores of the top 15 cm were collected from 128 quadrats in each of the experimental strips; roughly every third quadrat was sampled in this way. Soil samples were analyzed at the University of Wisconsin Extension Soil and Plant Analysis Laboratory for % sand,

% silt, % clay, and % organic matter. These data were linearly interpolated to assign values to each quadrat. Because clay content of all samples was relatively low, the quadrats formed an approximately linear series from sand to silt, characterized by % sand content.

The light regime of each quadrat was quantified via computer analysis of hemispherical photographs using SOLARCALC 5.41 (Chazdon and Field 1987). After canopy leaf-out in 1993, photographs were taken ca. 50 cm above the southern half of each quadrat, with all groundlayer vegetation excluded from the viewing field. The film plane was levelled and the top of the camera oriented to magnetic north; the orientation of the photographs was later corrected for magnetic declination in SOLARCALC. The amount of available light, integrated over the growing season, was estimated as the sum of direct photosynthetic photon flux density (PPFD, μmoles m^{-2} day^{-1}) for the summer solstice (June 22) and dates midway between the solstice and equinox (May 5 and August 4), expressed as a percentage of the maximum such sum for an unobscured sky at the same latitude.

Characterization of vegetation. Leaf cover of each species was estimated in every quadrat during spring (May/June) and summer (July/August) in 1993, 1994, and 1995. For species that reached maximum cover in the fall (e.g., *Eupatorium rugosum*), cover was also estimated in October. Cover classes were employed, with maximum values of 1%, 2%, 5%, 10%, 15%, ..., 100%. For each year and for each species, the midpoint of the largest of the three cover estimates was used to characterize the abundance of that species in a given quadrat.

To aid in the difficult task of identifying young individual of 110 species, I raised seedlings of almost all the planted species in early spring 1993. The seedlings were photographed and herbarium specimens were prepared. For most field observations my level of certainty of correct identification was high. However, not all individuals could be identified with total confidence. Certain pairs of species were hopelessly confusing as juveniles; these included *Anemone cylindrica* and *A. virginicus*, *Gentiana flavida* and *G. puberula*, *Asclepias exaltata* and *A purpurescens*. Very few individuals in the Lilliaceae could be determined to species. For purposes of analysis, I used only the data from individuals identified to species. Nomenclature follows Gleason and Cronquist (1991).

Species were classified into guilds based on (i) leaf width; (ii) leaf height; (iii) growth form, (iv) longevity, (v) association with N-fixing symbionts; and (vi) possession of the C_3 vs. C_4 photosynthetic pathway. The morphological classifications were based on measurements of fully expanded foliage on mature plants in remnant savannas (Leach 1996a). Maximum leaf width (0 - 5 mm, 6 - 15 mm, 16 - 45 mm, > 45 mm) of forbs was based on the diameter of the largest circle that could be inscribed on a blade. Leaf height (0 - 40 cm, 41- 80 cm, > 81 cm) was classified based on the tallest individual observed. Growth forms included graminoids (Poaceae, Cyperaceae) with grass-like foliage and forbs with broader foliage. Longevity (annual, biennial, or perennial) was based on species descriptions in Gleason and Cronquist (1991). Species with N-fixing potential (all Fabaceae, except *Ceanothus americana* [Rhamnacea]) were as described by Allen

and Allen (1981).   Possession of the C_3 or C_4 pathway by grasses based on reports by Brown (1977) and Kindscher (1992).

Data analysis

To determine how gradients of % sand and % direct PPFD affected the year-to-year trends in structure and composition of restoration plantings, quadrats were first sorted into 4 soil texture classes and 3 light-availability classes, defining a total of 12 soil x light microhabitats. For the quadrats planted with the mesic mix, the % sand gradient was divided into 3 parts ($\leq$ 11%, 12 - 24%, 25 - 82%) each containing as close to the same number of quadrats as numerically possible. The quadrats planted with the xeric mix (all on the sandiest soils) were all placed in a fourth soil texture class. For convenience, .these soil classes are referred to by familiar soil class names--"silt," "silt loam," "loam," "loamy sand"--but quotation marks are used because these classes are not precisely congruent with the standard soil-texture classes. All quadrats were classified into one of three light-availability classes based on % direct PPFD (< 25%, < 50%, > 50%). The distribution of quadrats along the light gradient did not vary significantly among the soil classes (General Linear Models Procedure and Student-Newman-Keuls test, P > 0.22, d.f. = 407).

For each microhabitat in a given year, the mean total cover of the groundlayer was calculated as the average of the total cover in each of the quadrats falling into that microhabitat. Because microhabitats contained different numbers of quadrats, and because light availability within a quadrat can affect total coverage (see Leach

1996a), the mean total cover for each soil class was calculated as the average of the mean total covers for each of the constituent microhabitats. A similar procedure was used to calculate the mean cover each year in each microhabitat of (i) forbs vs. graminoids, (ii) C_3 vs. C_4 graminoids, (iii) N-fixing species, (iv) annuals vs. biennials, (v) the four leaf-width classes, and (vi) the three leaf height classes. I used these data to test a series of predictions regarding the distribution of species in these guilds; these predictions are based on economic theory (Givnish 1982, 1987, 1988; Leach and Givnish 1996) and observations on community structure in remnant savannas (Pruka 1994, Leach 1996a).

The number of species reported in a 1-m^2 quadrat is its species richness. A quadrat's diversity was calculated as the exponential Shannon index ($e^{H'}$; Whittaker 1972, Magurran 1988) based on % cover of all the species present. For each microhabitat and soil class, mean species richness and diversity were calculated for each year of the study.

A species present one year in a quadrat but absent the next represents a loss. If a species is absent one year but present the next, it represents a recruitment. The sum of losses and recruitments equals species turnover for that quadrat. Mean levels of loss, recruitment, and turnover were determined for each microhabitat, soil class, and light class. Means for light classes were determined as the mean of microhabitats sharing the same light classes and planting mixes.

Because the quadrats planted with the mesic mix span most of the % sand gradient while sharing an identical planting list, these quadrats were in some ways

better suited for certain kinds of analysis than the entire set of quadrats. The effects of soil texture, light availability, and year on species richness, diversity, recruitment, loss, and turnover in the mesic-mix quadrats were therefore explored using ANOVA via the SAS GLM routine; contrasts among treatment means were tested using the Student-Newman-Keuls test (Tilman 1993). Results were considered significant if $P \le 0.05$.

To test for the possible effect of total cover in year i on species losses between years i and i + 1, all quadrats were sorted into one of 7 classes (< 50%, 51- 75%, 76 - 100%, 101-125%, 126 - 150%, 151 - 175% > 175%) based on total cover during year i. The relation of species loss to cover class was explored via rank correlation, using separate tests for each year and for quadrats receiving the mesic and the xeric mixes. To determine the contribution of short-lived species to turnover, for each year turnover was determined for annuals and biennials and compared with that for all species.

To assess the relative importance of sand content, light availability, and years since planting in influencing quadrat composition using direct gradient analysis, I calculated 3-dimensional indices of species turnover. This approach is an extension to 3 dimensions of the 2-dimensional beta-diversity calculations of Hujik (1995; Leach 1996a, 1996b). Mesic-mix quadrats were sorted as above into 9 microhabitats based on a three-step soil gradient and three-step light availability gradient. The temporal dimension of three years of data collection in the 9 microhabitats yields 27 data classes. The proportional species composition for

each data class was calculated, based on each species' mean cover across quadrats within the data class. The quantitative Sørenson index of similarity (Magurran 1988) was then calculated between each of the 351 distinct, non-trivial pairs of data classes. Finally, the natural logarithm of the Sørenson index (see Whittaker 1972) was regressed simultaneously on the differences in the number of steps (0, 1, 2) between data classes on each of the three gradients. The slopes of this multiple regression represent the relative amounts of turnover in overall species composition along the three gradients (Hujik 1995).

An alternate approach to comparing the relative influence of sand, light, and time gradients on average composition is by comparing the strength of relationships of these three gradients with data class ordination scores in three dimensions. The 27 data classes were ordinated in species space via non-metric multiple-dimensional scaling (NMS, Minchen 1987), as implemented in PC-ORD 2.02 (McCune and Mefford 1995). The strength S of each gradient's relation with ordination scores was calculated as the root-mean-square of Pearson correlations with the three ordination axes. The relative magnitudes of S for % sand, % direct PPFD, and year indicate the relative influence of soil, light, and time gradients on average species composition.

To detect changes with time in the relative influence of soil and light on groundlayer composition, for each of the three years I calculated a separate index of 2-dimensional beta-diversity (Hujik 1995) for mesic-mix microhabitats based on % sand and % direct PPFD. Quantitative Sørenson index values were determined

for the 36 within-year pairs of microhabitats and regressed simultaneously on step differences on the soil and light gradients. Changes through time in r^2 and the slopes of these multiple regressions were taken to represent the relative influence of the combined and individual influence of soil and light on groundlayer composition (Hujik 1995).

To evaluate hypotheses regarding the temporal change in species patterning along environmental gradients following uniform seeding, each species' mean position along both soil and light gradients relative to the null mean were compared between years. The mean position x_i of species i along each gradient was calculated as:

$$x_i = \sum C_{iJ}z_J / \sum C_{iJ}, \qquad (1)$$

where C_{iJ} is the cover of species I in quadrat J, and z_J is the position of quadrat J along the gradient in question (either % sand or % direct PPFD). The null mean position represents the hypothetical mean assuming that soil texture and light availability had no influence on plant growth; it was calculated by setting $C_{iJ} = 1$ for all quadrats, and equalled the mean % sand and mean % direct PPFD across all quadrats. Increased dispersion of a species' mean away from the null mean indicates an increased differentiation of that species distribution from the average of environments across quadrats. Using 42 common species, which were observed in all years with frequency > 10% in at least one year-- present from the mesic mix, the sign test was used to compare centrifugal movement (+) with no or centripetal movement (-) for each species along each gradient, including

comparisons between Year 1 and Year 2, and between Year 2 and Year 3. Similarly, habitat shifts were calculated as the difference between first- and third-year positions of a species along both environmental gradients; levels of significance of such shifts were determined by t-tests. Results were termed significant only if $P \leq 0.05$.

The general expectation in successional communities is for niche breadths to narrow with time, as competition and other biological interactions narrow the distribution of a species from the range over which it could survive in the absence of such interactions (Werner and Platt 1976). The niche breadth of species i was calculated as the standard deviation of its distribution along the % sand or % direct PPFD gradients:

$$s_i = [(\sum C_{ij}(z_j - x_i)^2) / \sum C_{ij}]^{0.5} . \tag{2}$$

For 42 common species, the overall expansion or contraction of niche breadths along soil and light gradients was assessed using the sign test for each pair of successive years.

Results

Temporal Trends in Total Cover and Guild Dominance. Each year, most of the planted species were detected in at least one of the quadrats planted with the mesic mix (74% for Year 1; 76.2% for Years 2 and 3) or the xeric mix (74% for Year 1; 77% for Year 2; 78% for Year 3). Many of the species that were not found, or found in low numbers, such as many of the Liliaceae, require two or

more seasons to break dormancy (Baskin and Baskin 1988). Other species (e.g.,
Liatris aspera) have been noted by restorationists for their inconsistent
establishment in restoration plantings (B. Bader, pers. com.).

Average total cover generally increased each year in each of four soil classes,
with total cover decreasing within years with increasing sand content (Figure 1a).
In every year and for each soil class, the total cover of forbs was greater than the
total cover of graminoids (Figure 1b). Furthermore, forb cover increased relative
to graminoid cover each year, except on the sandiest sites (Figure 1b).

Among graminoids, cover by C_3 species peaked in Year 2 on sites receiving the
mesic mix; C_3 cover peaked in Year 1 on sites receiving the xeric mix (Figure 1c).
The total cover of C_4 grasses increased each year on all soil types, with the
steepest rise occurring on soils with higher sand content; on such soils, total cover
of C_4 exceeded that by C_3 graminoids by Year 3 (Figure 1c).

Cover by annuals peaked sharply in Year 1 except in "loamy" microsites, where
their cover fluctuated relatively little between years (Figure 1d). As expected,
cover by biennials peaked during Year 2 in all soil classes (Figure 1d), but had
nearly disappeared by Year 3, when their highest cover (3.4%) was on "loamy
sand." Perennials consistently had higher total cover than annuals and biennials
combined; as shown by the mean contribution by perennials to total cover of all
species averaged across soil classes (70 ± 7% in Year 1, 81 ± 5% in Year 2, 96 ±
4% in Year 3).

Cover by potential N-fixing species did not differ significantly across the four soil

classes during Year 1 (mean = 2.3 ± 0.7%, P > 0.29, ANOVA with 3 d.f.).

However during Years 2 and 3, cover by potential N-fixers increased sharply on the two soil classes with high sand content, while declining on siltier sites (Figure 1e).

On fine-textured soils, forbs with wide leaves increased their share of total cover from Year 1 to Year 3 (Figure 1f). On the sandiest soils, cover by forbs with narrow leaves increased the most over time (Figure 1f).

Temporal and Spatial Trends in Species Richness and Diversity. For each year, an ANOVA was performed to determine the effect on average species richness of membership in % sand classes and % direct PPFD classes. For Year 1, % sand had significant ($F_{2, 266}$ = 23.3, P < 0.0001) effect on species richness; neither light ($F_{2, 266}$ = 2.13, P > 0.12) nor the soil x light interaction ($F_{4, 266}$ = 0.71, P > 0.58) had a significant effect. For Year 2, % sand had a stronger effect on species richness ($F_{2, 266}$ = 30.7, P < 0.0001). In addition, there was a significant effect of % direct PPFD on species richness ($F_{2, 266}$ = 3.46, P < 0.033), but no significant of the soil x light interaction ($F_{4, 266}$ = 1.15, P > 0.33). Finally, for Year 3, species richness was affected even more strongly by both % sand ($F_{2, 266}$ = 134.8, P < 0.0001) and % direct PPFD ($F_{2, 266}$ = 9.3, P < 0.0001), and the effect of the soil x light interaction became significant ($F_{4, 266}$ = 4.02, P < 0.004).

Similarly, analysis of variance revealed a significant and increasing effect of soil on diversity in Year 1 ($F_{2, 266}$ = 5.68, P < 0.004), Year 2 ($F_{2, 266}$ = 31.6, P < 0.0001), and Year 3 ($F_{2, 266}$ = 125.5, P < 0.0001). In contrast, the effect of light upon

diversity was not significant in any year (maximum F value over three yr = 0.82, P > 0.4), however the soil x light interactions increased their effect on diversity from Year 1 ($F_{4, 266}$ = 0.73, P > 0.56), to Year 2 ($F_{4, 266}$ = 2.88, P < 0.024), to Year 3 ($F_{4, 266}$ = 6.05, P < 0.0001).

A 3-way ANOVA relating species richness to soil texture, light availability, and year showed that soil and year had the greatest significant direct effects with light alos highly significant. All two-way effects (except light x year) were also significant, but at a lower level (Table 2a). Similarly, species diversity varied greatly in response to soil and year, but not light level (Table 2b). Again, the two-way effects except light X year were significant at a reduced level. In addition, there was a significant three-way effect. ANOVAs for species turnover, recruitment, and loss (Table 3) also showed that soil texture and year had greater effects than light.

Among the mesic mix quadrats, each year species richness tended to be higher on coarser-grained "loam" than on finer-grained "silt" and "silt loam" soils (Figure 2, 3). Within soil classes species richness varied more among years than among light classes and was increasingly influenced by both years and light on increasingly fine-textured soils (Table 4). For each soil class, species richness generally increased with light availability, but not always during Year 1 (Figure 2). Species richness and diversity peaked during Year 1 on "silt" and "silt loam" soils. On "loam" and "sandy loam" soils, species richness peaked during Year 2 while diversity varied comparably little between years (Figure2, 3). As species richness

and diversity declined from the initial seeding level of ca. 80 species m^{-2} (far above levels seen in savanna remnants [Leach 1996a]), the relationship of diversity to richness became tighter (r^2 = 0.36 for Year 1; r^2 = 0.60 for Year 2; r^2 = 0.71 for Year 3; P < 0.0001 for 274 d.f. for all comparisons). The average amount of species turnover was greater on coarse-grained soils and always decreased over time (Figure 4). As expected, species losses contributed more to turnover than recruitments (5.1 ± 0.6 species lost m^{-2} vs. 4.8 ± 2.1 species recruited m^{-2} between Years 1 and 2; 5.1 ± 0.8 lost m^{-2} vs. 2.6 ± 0.8 species recruited m^{-2} between Years 2 and 3; values are averages of means for 12 microhabitats) as species richness "relaxed" from its artificially high starting point.

Total herbaceous cover was a poor predictor of species losses between years. Species losses between Year 1 and Year 2 showed no significant correlation with 7 classes of total cover during Year 1 (r_s = 0.04, P > 0.41, for 411 observations), nor was there a significant correlation between Year 2 to 3 losses and total cover in Year 2 (r_s = 0.08, P > 0.10, for 411 observations). No significant relationships between proportional species losses and cover were detected.

Although annuals and biennials species underwent rapid turnover, they contributed little to between-year turnover (12.5% between Years 1 and 2; 5.28% between Years 2 and 3). The richness of these short-lived species was highest Year 1 and declined rapidly thereafter, peaking in Year 1 in quadrats seeded with the mesic mix while peaking in Year 2 in xeric-mix quadrats.

Temporal and Spatial Trends in Overall Species Composition. A multiple

regression of Sørenson similarity on gradient distances between distinct pairs of the 27 year x soil x light data classes revealed that composition changed more among years and soil texture classes, and less among light availability classes:

$$\ln C = 4.34 - 0.15\ G_{YEAR} - 0.15\ G_{SAND} - 0.06\ G_{LIGHT}; \qquad (3)$$

($r^2 = 0.43$, $P < 0.0001$ for 447 d.f.), where C is the quantitative Sørenson index (Magurran 1988), and G_{YEAR}, G_{SAND}, and G_{LIGHT} are the number of steps separating a pair of microhabitats along the time, soil, and light gradients, respectively. The relative strengths (S) of the correlations between NMS ordination scores and positions of quadrats along the time, soil, and light gradients confirm these conclusions. Average species composition changed most among years (S = 0.95), somewhat less with % sand (S = 0.82), and least with % direct PPFD (S=0.56).

Two-dimensional multiple regressions of Sørenson similarity on differences between microhabitats in a given year show that variations in soil texture had more influence on average composition than did light availability, that the influence of sand increased to roughly four times that of light over time, and that the influence of light remained at low levels :

$$\text{Year 1:} \quad \ln C = 4.30 - 0.11\ G_{SAND} - 0.05\ G_{LIGHT}; \ r^2 = 0.31; \qquad (4)$$

$$\text{Year 2:} \quad \ln C = 4.36 - 0.14\ G_{SAND} - 0.09\ G_{LIGHT}; \ r^2 = 0.31; \qquad (5)$$

$$\text{Year 3:} \quad \ln C = 4.34 - 0.26\ G_{SAND} - 0.06\ G_{LIGHT}; \ r^2 = 0.37 \qquad (6)$$

($P \leq 0.003$ for 33 d.f. in each case)

Temporal shifts in mean gradient position

The year-to-year change in a species' mean position along gradients of % sand and % direct PPFD were determined for 42 common species. On average, the distance D between a species' mean position on the % sand gradient and the null mean (average of all quadrats) increased each year ($D_{SAND,YR1} = 0.078$, $D_{SAND,YR2} = 0.108$, $D_{SAND,YR3} = 0.117$). Similarly, the distance between a species mean position on the % direct PPFD gradient and the null mean also increased each year ($D_{LIGHT,YR1} = 0.074$, $D_{LIGHT,YR2} = 0.091$, $D_{LIGHT,YR3} = 0.119$). The mean of species distances to the null mean increased significantly between Year 1 and Year 3 for both the % sand gradient ($p < 0.001$; paired t-test with 81 d.f.) and the % direct PPFD gradient: ($P < 0.02$; paired t-test with 81 d.f.). This net movement of species average positions form their initial distribution in % sand x % direct PPFD space can perhaps best be described as centrifugal species sorting.

Shifts in a species' distribution were examined by comparing its distributions along the % sand and % direct PPFD gradients during Years 1 and #. Such shifts were statistically analyzed using 2-tailed paired t-test, and considered significant if $P < 0.05$. Shifts may result from differential patterns of loss, recruitment, and growth along a gradient. Overall, 27 species shifted toward sandier and sunnier microsites (Table 5), 15 toward sandier and shadier microsites. Only 8 species shifted toward less sandy microsites: 4 toward sunnier microsites and 4 toward deeper shade. This disparity in shift direction is even greater if we consider only significant shifts. Thirty of 33 significant shifts were toward sandier microsites, while 19 of 24 significant shifts were toward sunnier microsites. No species

showed simultaneous, significant shifts toward both shadier and siltier microsites.

Between Year 1 and Year 3, the annual and biennial species all had highly significant shifts toward sandier soils, perhaps reflecting a rapid closure of vegetation and loss of seedling establishment sites on richer soils. Most perennial forbs shifted toward increased sand and light.

Two C_4 grasses typical of Wisconsin's prairies--*Andropogon gerardii* and *Schizachyrium scoparium*--had highly significant shifts toward sand, but, somewhat surprisingly, their shifts toward light were not significant. Remarkably, a third C_4 grass, *Sporobolus heterolepis* had no significant shift along either gradient. Individual C_3 grasses shifted in 3 of the 4 possible directions (Table 5).

Most potential N-fixing species shifted toward sandier and sunnier microsites (Table 5). The exceptions were two relatively wide-leaved species *(Desmodium glutinosum* and *D. canadense*) that showed a non-significant shift toward shadier microsites and a small shrub (*Amorpha canascens*) that shifted toward sunnier, siltier microsites.

Dynamics of niche breadth

The mean niche breadth (s.d. of position) for 42 common species along both the % sand and % direct PPFD gradients increased each year (Figure 6). The means of the standard deviations of position were significantly different between Year 1 and Year 3 for both % sand ($P < 0.001$, 2-tailed paired t-test with 84 d.f.) and % direct PPFD ($P < 0.014$, 2-tailed paired t-test with 84 d.f.).

Discussion

Gradients in soil texture and light availability are strongly related to local and regional variation in the composition, structure, and diversity of the groundlayer in remnant Midwestern oak savannas (Leach 1996a). Variation in light availability among microsites appears to have a substantially smaller effect on the groundlayer, however. The current study shows that soil texture and light availability also have strong effects on the rate and direction of groundlayer re-assembly during savanna restoration, with soil texture again playing a leading role.

Following the uniform planting of species across % sand and % direct PPFD gradients, species and guilds showed individualistic patterns of development through time along both gradients (Figures 1, 5). Differences in the dynamics of graminoids vs. forbs, C_3 vs C_4 graminoids, potential N-fixers, and species with different leaf widths and heights (Figure 1) suggest that the competitive ability associated with different growth forms and energy-capture strategies varies strongly across soil and light gradients. The observed trends appear to be generally consistent with expectations based upon the energetic and ecological impact of the traits involved.

Total forb cover increased each year relative to that by graminoids in all but the sandiest microsites (Figure 1b). Many forbs have wider and more nearly horizontal leaves than graminoids, have extensive rather than intensive root systems, and have deeper root systems (Weaver 1954, Weaver and Albertson 1956). The broad, nearly horizontal leaves of forbs may give them an edge over graminoids in the abilities to both cast and tolerate dense shade. Graminoids may

gain an advantage on drier, more open microsites given their narrow, more nearly erect foliage, their heavier allocation to roots, and their possession (at least in several dominant grasses) of the C_4 photosynthetic pathway. The last is thought to contribute strongly to drought tolerance, given that C_4 species can achieve higher rates of photosynthesis at a given rate of water loss under sunny conditions, and effectively avoid photorespiration (Björkman and Berry 1973; Martin et al. 1991). Finally, the basal meristems of graminoids should allow them to suffer less damage and resprout more quickly following damage by fire or herbivores. As a consequence of these considerations, we might expect (i) graminoids to dominate on coarse-grained, droughty soils; and (ii) forbs to dominate on finer-grained soils with a substantial water- and nutrient-holding capacity.

Spatial and temporal trends in the relative abundance of graminoids and forbs lend partial support to each of these predictions. Forbs dominated graminoids on all soil textures, but to a much smaller degree on more coarsely grained soils (Figure 1b). If C_4 grasses continue the trend of rapidly increasing their cover on these sandier soils (Figure 1c), graminoids will likely soon dominate forbs in sandier microsites. Forbs dominate finer-grained soils and graminoids dominate sunlit, coarse-grained soils in remnant savannas as well (Leach 1996a).

During Year 1, C_3 graminoids had a higher total cover than did C_4 grasses across the soil gradient; subsequently, the total cover of C_4 grasses increased rapidly relative to C_3 graminoids, especially on sandier soils (Figure 1c, Table 5).

This pattern is consistent with the greater supply of moisture presumably available to individual plants during Year 1 (when total cover - and hence, transpiration - was relatively low), and the fact that the seedlings of C_4 grasses tend to allocate more to below-ground growth than do C_3 grasses (Weaver 1954). C_4 grasses should thus be at a competitive disadvantage where soil resources are not limiting the above ground growth of competitors for light. The rapid growth of C_4 grasses in sandier and sunnier microsites is consistent with their dominance in savanna remnants only on similar microsites (Leach 1996a).

In savanna groundlayers, N-fixation should yield the greatest energetic advantage on sandy, brightly lit microsites (Leach and Givnish 1996). Where greater supplies of soil nitrogen are available, perennial legumes (which comprise almost all the potential N-fixers in savanna groundlayers) generally have lower maximum growth rates than their herbaceous competitors (Grime and Hunt 1975). Presumably, this is because they divert resources toward maintaining symbiotic bacteria rather than to the production of more photosynthetic tissue (Tilman 1988). In Year 1, N-fixing species were more or less uniformly distributed across soil classes (Figure 1e), perhaps due partly to their large seed that might allow establishment over a wide range of conditions. As expected, however, during Years 2 and 3 N-fixers rapidly expanded their total cover on sandier soils, but declined on finer-textured soils, and were generally (with the notable exception of *Desmodium glutinosum*) much less abundant in shade (Table 5).

Narrow leaves or leaf divisions suffer less water loss per unit area then wider

leaves or leaf divisions, but at the cost of lower leaf temperature and reduced rates of photosynthesis; as a consequence, narrow leaves are favored in dry, infertile, and sunny microsites, while broader leaves are favored in moist, fertile, and shady microsites (Givnish 1979, 1988). These predictions are consistent with the spatial trends observed in the groundlayers of remnant oak savannas (Pruka 1994, Leach 1996a), but not with the spatial trends seen in this study (Leach 1996b). However, the dynamics of cover by narrow- and broad-leaved forbs in this study are concordant with expectations: Forbs with leaves < 5 mm wide decreased in cover and were nearly lost from fine-grained soils, but increased in relative cover on the sandiest soils (Figure 1f). Forbs with > 45 mm wide came to dominate "silt" and "silt-loam" soils.

Herbs that hold their leaves high above the ground must allocate substantial amounts of fixed carbon to relatively unproductive support tissue but gain an advantage in competition for light, which is likely to more be more intense on densely covered sites; as a consequence, optimal leaf height should increase with the density of herbaceous cover (Givnish 1982, 1995). Because tall herbs must allocate so much to support tissue and require substantial photosynthate in order to achieve maximum height, cover by such herbs should increase through time soon after seeing on moist, fertile sites. The denser total cover found on moister, more nutrient-rich, finer-grained soils in this study (Figure 1g) did in fact favor taller species, and cover by such species increased through time.

Gradients of soil texture and light availability strongly influenced species

temporal trends in species richness and diversity (Figure 1, 2, 3, 4, Table 2).

Analysis of variance indicated that the influence of soil texture on richness was

larger then that of light availability and grew in relative influence each year. This

conclusion is buttressed by similar findings for ANOVAs involving diversity and by

ordination analysis of the dominant ecological factors correlated with compositional

variation (Eqs. 3-6).

Quadrats were initially seeded with ca. 80 species, far more than coexist in the

groundlayers of remnant savannas (Leach 1996a). Consequently, one would

expect species richness and diversity to "relax" toward equilibrium levels, at a rate

determined partly by the intensity of competition. In fact, species richness and

diversity within individual quadrats peaked during Year 1 on finer-grained, more

productive soils, and peaked during Year 2 on coarser-grained, less productive

soils (Figure 3). Species turnover was always higher between the Years 1 and 2

than between years 2 and 3 (Figure 4). When the seedlings emerged initially,

there were manifestly sufficient resources for their establishment. As plant cover,

height, and (presumably) above-ground competition increased, many individuals

died. However, the ensuing loss of species from quadrats seems less consistent

with competitive exclusion of adult than with competitive exclusion of seedlings

and consequent depression of recruitment. Species losses were relatively

constant across light classes and years, with decreases in recruitment accounting

for most of the decrease in species richness on silty soils (Figure 4). Fine-

grained, nutrient-rich soils appear to become "closed" to new recruits very quickly;

subsequent losses, however, might be expected to vary with environmental conditions in accord with the tempo and intensity of developing plant-plant interactions. These findings suggest that, at least in restorations begun from seed on devegetated sites, the "closing" of communities to seedling recruits precedes competitive exclusion of species represented by adults. These research plantings were not burned during the first three years, so it not known if fire would have increased diversity (perhaps by limiting growth of competitive dominants) or lowered diversity (by increasing mortality).

Dominant species appear to be undergoing a process of centrifugal species sorting along the soil texture and light availability gradients, showing a pattern of dispersion that appears headed roughly toward their mean distribution in remnant savannas

The differential loss, recruitment, and yearly variations in total cover for individual species along gradients of soil and light availability indicate species' competitive sorting and was revealed by their centrifugal diffusion along % sand and % direct PPFD gradients (Figure 5). Species appear to be individualistically dispersing along environmental gradients in a way consistent with the high levels of habitat partitioning observed in savanna remnants (Hujik 1995, Pruka 1994, Leach 1996a).

The finding that niche breadths along soil and light gradients increased each year (Figure 6) was unexpected and rather perplexing. During succession, niche breadths tend to narrow as plant-plant interactions intensify and remove species

from sub-optimal habitats (Werner and Platt 1976). In this study, the apparent increase in niche breadth along the % sand gradient may be an artifact, related to the high proportion of quadrats on fine-textured soils. As many species shifted their mean position along the % sand gradient became distanced from the concentration of quadrats and increased the standard deviation of their position along the soil gradient relative to the null expectation.

While this explanation may account for the observed increase in niche breadth along the % sand gradient, it can not account for a similar increase in niche breadth along the light gradient, along which the quadrats were more evenly distributed. It may take several years for above- and below-ground interactions to narrow species distributions along the soil and light gradients.

This study has shown that experimental restoration can aid in the testing of our understanding of now-rare ecosystems (Bradshaw 1987, Jordan et al. 1987). For example, the observed dynamics of C_4 grasses vs. forbs lends support to the view of Leach (1996a, 1996b) that the groundlayers of Midwestern oak savanna were species rich because the diverse assemblage of forbs were released from competition by C_4 grasses, except in sunny, sandy microsites where the C_4 photosynthetic pathway yields a substantial advantage. This experimental restoration has lent further support to the conclusion that savanna groundlayers were forb-dominated, and that edaphic conditions had a stronger effect than light availability on groundlayer composition, structure, and diversity. Finally, the dynamics of the experimental restoration implied a pattern of species sorting--

perhaps driven in part by interspecific competition--that suggest a self-assembly of groundlayer communities and gradients approaching (but not yet reaching) those seen in remnant savannas.

The implications of this study for savanna restoration and conservation are clear. To represent the great diversity of oak savannas once common in the Midwest, sites involving a wide range of soil conditions must be represented. Heterogeneity of soil and light environments within preserves should be maintained to provide suitable habitats for a rich groundlayer flora--which is far more diverse at a variety of spatial scales than forest or prairie ecosystems (Leach 1996a). Savanna managers should give much greater consideration to the heterogeneity of light availability within sites than to the commonly used measure of "average" canopy cover (e.g., Curtis 1959; White and Madany 1978; Faber-Langendoen 1995; Packard and Balaban 1995). When choosing species to plant in the various microsites, traits important for energy capture should be used to screen taxa and thereby increase economic efficiency and perhaps decrease the amount of time required for restoration. Even with an intact tree layer, restorations of savanna groundlayers will take far longer than three years.

The most effective use of this restoration experiment is probably to test ideas regarding the nature and function of a nearly vanished ecosystem. By helping to identify which species are competitively successful in a savanna environment and where along soil and light gradients they are successful, the study may provide an important basis for savanna restoration in the Upper Midwest. Other kinds of

experimental restoration--in which, for example, the mechanism of restoration (e.g., different seeding densities, different fire or grazing regimes, different canopy treatments) is varied--might be more useful in determining specific strategies of savanna restoration. Taken together, both kinds of restorations should help make large-scale ecological restoration more cost effective and the product more realistic in composition, structure, and diversity. Restorationsists who test predictions on the assembly of communities and gradients may make important contributions to community ecology and help transform restoration from a craft to a predictive science.

Prior to full-scale restorations, small-scale restoration experiments will be very useful to identify problems, such as high-levels of competitive exclusion on fine-textured soil, and to evaluate strategies for establishing high-levels of diversity in heterogeneous habitats. Thus the use of restoration experiments should help make restorations more cost effective and the product more accurate in composition and structure. Restorationists who test predictions on the assembly of communities as part of their restoration may make important contributions to community ecology by transforming restoration from a craft to a predictive science.

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Table 1. Two mixtures of seeds were planted. The mesic seed mix was planted on "silty" to "loamy" soils, and the xeric seed mix was planted on "sandy loam" and "sandy" soils. Weight (g) and number (n) of seed planted per quadrat are given. Weight were not determined for fleshy fruited seeds.

	Mesic Mix		Xeric Mix	
	g	n	g	n
A. C3 Graminoids				
Bromus kalmii	0.38	190	0.38	190
Carex bicknellii			0.02	11
Carex gravida			0.03	50
Cinna arundinacea	0.18	450		
Elymus canadensis	0.54	110	0.54	110
Elymus hystrix	0.22	40	0.22	40
Elymus villosus	0.34	85		
Elymus virginicus	0.23	23		
Stipa spartea			0.17	9
B. C4 Graminoids				
Andropo gon gerardii	0.25	74	0.25	74
Schizachyrium scoparium	0.30	100	0.30	100
Sporobolus heterolepis	0.36	180	0.36	180
C. Nitrogen-fixers				
Amo rpha canescens	0.06	50	0.06	50
Amphicarpaea bracteata		1		1
Baptisia bracteata			0.80	50
Baptisia lactea var lactea	0.40	24		
Ceanothus americana			0.85	210

Species				
Dalea candida	0.02	16	0.02	16
Dalea purpurea	0.03	25	0.03	25
Desmodium canadense	0.18	30	0.18	30
Desmodium glutinosum	0.08	4	0.08	4
Desmodium illinoense	0.09	15	0.09	15
Lupinus perennis			0.40	14
Tephrosia virginiana			0.34	30
D. Annuals				
Amphicarpa ea bracteata		1		1
Conyza canadensis	0.02	120	0.02	120
E. Biennials				
Campanula americana	0.03	170		
Gaura biennis	0.08	25		
Gentianella quinquefolia	0.01	120		
Oenothera biennis	0.03	70	0.03	70
Oenothera clelandii			0.20	1050
Rudbeckia hirta			0.08	290
F. Other Forbs				
Allium cernuum	0.06	20	0.06	20
Anemone cylindrica	0.06	90	0.06	90
Anemone virginiana	0.08	50	0.08	50
Apocynum androsaemifolium	0.01	90	0.01	90
Apocynum cannabinum			0.06	90
Aquilegia canadensis	0.04	45	0.04	45
Arisaema triphyllum		3		

Asclepia purpurascens	0.01	2		
Asclepias amplexicaulus			0.03	5
Asclepias exaltata	0.10	14		
Asclepias tuberosa			0.10	12
Asclepias verticillata			0.03	12
Asclepias viridiflora			0.05	6
Aster laevis	0.06	130	0.06	130
Aster oolentangiensis	0.02	12	0.02	12
Aster prenanthoides	0.01	30	0.01	30
Aster sagittifolias	0.14	350	0.14	350
Aster sericeus			0.09	300
Aster shortii	0.09	210	0.09	210
Aster umbellatus	0.02	45		
Besseya bullii	0.03	110	0.03	110
Blephilia hirsuta	0.06	250		
Cacalia atriplicifolia	0.02	50		
Camassia scilloides		3		
Circaea lutetiana	0.07	14	0.07	14
Coreopsis palmata	0.03	25	0.03	25
Cyprepedium calceolus	trace	200	trace	200
Dodecatheon meadia	0.02	100	0.02	100
Eupatorium purpureum	0.10	240		
Eupatorium rugosum	0.01	35	0.01	35
Eupatorium sessilifolium	0.02	45	0.02	45
Euphorbia corollata	0.12	70	0.12	70
Gentiana flavida	0.04	350	0.04	350

Gentiana puberulenta	0.01	240	0.01	240
Geranium maculatum	0.02	3	0.02	3
Gerardia grandiflora			0.12	160
Geum canadense	0.06	110	0.06	110
Helianthemum canadense			0.00	2
Helianthus occidentalis			0.02	15
Helianthus strumosus	0.03	6	0.03	6
Heliopsis helianthoides	0.18	45	0.18	45
Heuchera richardsonii			0.05	140
Hieracium longipilum			0.01	40
Hieracium scabrum			0.00	1
Liatris aspera	0.14	70	0.14	70
Lilium michiganiense	0.05	20		
Lilium philadelphicum			0.00	2
Lobelia spicata			0.01	200
Lysimachia ciliata	trace	100	0.00	100
Monarda fisulosa	0.03	90	0.03	90
Monarda punctata			0.05	200
Napaea dioica	0.54	135		
Penstemon gracilis			0.02	320
Penstemon grandiflorus			0.02	12
Phlox pilosa			0.19	220
Phryma leptostachya	0.06	9		
Physalis virginiana			0.03	11
Polemonium reptans	0.22	145		
Polygonatum biflorum	0.02	9		

Polytaenia nuttallii	0.05	6	0.05	6
Ranunculus fascicularis	0.03	12	0.03	12
Ratibida pinnata	0.12	120	0.12	120
Sanicula marilandica	0.18	32		
Scrophularia lanceolata			0.01	60
Senecio pauperculus			0.04	170
Silene stellata	0.13	210	0.13	210
Smilacena racemosa	0.19	6	0.19	6
Smilacena stellata			0.08	4
Solidago flexicaulus	0.04	125		
Solidago rigida	0.06	100	0.06	100
Solidago speciosa	0.12	530	0.12	530
Taenidia integerrima	0.06	16	0.06	16
Thalictrum dasycarpum	0.05	14		
Thalictrum dioicum	0.10	35		
Triosteum perfoliatum		3		
Veronicastrum virginicum	0.05	1500		
Viola sagittata			0.00	4
Zizia aptera	0.06	20	0.06	20
Zizia aurea	0.06	34		

Table 2. Analysis of variance of 1-m^2 species (a) richness and (b) diversity with % sand (four levels), light (three levels), and year (three levels) as factors. Only data from quadrats planted with the Mesic Mix were used. All interaction terms were calculated. There are 798 degrees of freedom for error. F values shown are based on Type III sum of squares.

a. Richness

	df	F	P
Overall model	798	29.52	0.0001
Soil	2	141.62	0.0001
Light	2	12.75	0.0001
Year	2	140.95	0.0001
Soil x Light	4	2.66	0.0318
Soil x Year	4	19.06	0.0001
Light x Year	4	0.66	0.6215
Soil x Light X Year	8	1.41	0.1884

b. Diversity

	df	F	P
Overall model	798	31.40	0.0001
Soil	2	97.29	0.0001
Light	2	0.35	0.7067
Year	2	185.37	0.0001
Soil x Light	4	4.47	0.0014
Soil x Year	4	27.84	0.0001
Light x Year	4	0.37	0.8326
Soil x Light X Year	8	2.38	0.0154

Table 3. Analysis of variance of 1-m^2 species (a) turnover, (b) recruitment, and (c) loss with soil (loamy, silt loam, fine silt loam), light (three levels), and Year (1993-1994, 1994-1995) as factors. Only data from quadrats planted with the Mesic Mix were used. All interaction terms were calculated. There are 532 degrees of freedom for error. *F* values shown are based on Type III sum of squares.

a. Turnover between years

	df	*F*	*P*
Overall model	17	33.33	0.0001
Soil	2	187.92	0.0001
Light	2	9.46	0.0001
Year	1	105.30	0.0001
Soil x Light	2	5.12	0.0005
Soil x Year	2	15.19	0.0001
Light x Year	2	1.03	0.3583
Soil x Light X Year	4	1.54	0.1882

b. Recruitment between years

	df	*F*	*P*
Overall model	17	42.39	0.0001
Soil	2	173.29	0.0001
Light	2	6.75	0.0013
Year	1	137.50	0.0001
Soil x Light	2	7.84	0.0001
Soil x Year	2	87.36	0.0001
Light x Year	2	2.29	0.1025
Soil x Light X Year	4	1.31	0.2655

c. Losses between years

	df	*F*	*P*
Overall model	17	9.02	0.0001
Soil	2	32.19	0.0001
Light	2	2.88	0.0572
Year	1	5.24	0.0224
Soil x Light	2	1.12	0.3459
Soil x Year	2	27.08	0.0001
Light x Year	2	1.46	0.2327
Soil x Light X Year	4	1.53	0.1919

Table 4. Analysis of variance of species richness with light availability (three levels) and year (three levels) as factors for four soil classes. *F* values shown are based on Type III sum of squares.

Soil Class		df	*F*	*P*
"Sandy Loam"	Light	2	2.1	0.13
	Year	2	29.2	0.0001
	Light X Year	4	1.9	0.10
	Error	399		
"Loam"	Light	2	1.1	0.32
	Year	2	10.0	0.0001
	Light X Year	4	0.3	0.88
	Error	222		
"Silt Loam"	Light	2	4.8	0.0001
	Year	2	51.3	0.0001
	Light X Year	4	1.2	0.29
	Error	252		
"Silt"	Light	2	17.3	0.0001
	Year	2	186.1	0.0001
	Light X Year	4	2.5	0.04
	Error	324		

Table 5. The species are listed according to the direction of their change between Year 1 and Year 3 in mean position along %sand and % direct PPFD (light) gradients. Significant differences between means are shown, first for %sand, followed by % direct PPFD (two-tailed t-test: ø > 0.05, * ≤ 0.05, ** ≤ 0.01, *** ≤ 0.001).

1. Shifted toward increasing sand
    a. Shifted toward increasing light
        i. Annual and biennial forbs
            Amphicarpaea bracteata ***, ø
            Gaura biennis ***, **
        ii. Potential nitrogen fixers
            Amphicarpaea bracteata ***, ø
            Baptisia lactea var. *lactea* ***, ***
            Desmodium illinoense ø, ø
            Dalea purpurea ø, ø
            Dalea candida **, *
        iii. Other perennial forbs
            Aster oolentangiensis **, ø
            Aster umbellatus ø, ø
            Circium lutetiana ø, *
            Coreopsis palmata ø, ø
            Eupatorium sessilifolium **, ø
            Euphorbia corollata ***, ø
            Geum canadense **, ø
            Heliopsis helianthoides ø, ø
            Lysimachia ciliata ø, ø
            Polytaenia nuttallii *, ø
            Ratibida pinnata **, ø
            Silene stellata ***, ***
            Solidago rigida **, ø
            Veronicastrum virginicum ø, ø
            Zizia aptera ***, *
        iv. C$_3$ grasses
            Bromus kalmii ***, ***
            Elymus canadensis *, ***
            Elymus villosus *, ø
        v. C$_4$ grasses
            Andropogon geradii ***, ø
            Schizachyrium scoparium ***, ø
    b. Shifting toward decreasing light
        i. Annuals and Biennials
            Campanula americana ***, ø

       Oenothera biennis ***, ⌀
ii. Potential Nitrogen fixers
       Desmodium canadense ⌀, ⌀
       Desmodium glutinosum ***, ⌀
iii. Other perennial forbs

       Aquilegia canadensis ***, ⌀
       Aster prenanthoides ***, ⌀
       Aster laevis ***, ⌀
       Besseya bullii ***, ***
       Eupatorium rugosum ⌀, ⌀
       Geranium maculatum ⌀, ⌀
       Helianthus strumosus ***, ***
       Ranunculas fascicularis ***, ⌀
       Solidago speciosa **, ***
iv. C$_3$ grasses
       Elymus hystrix ⌀, ***
       Elymus virginicus ***, **
v. C$_4$ grasses
       [none]

1. Shifted toward decreasing sand
   a. Shifted toward increasing light
      i. Annual and biennial forbs
        [none]
      ii. Potential nitrogen fixers
        Amorpha canescens ***, ***
      iii. Other perennial forbs
        Cacalia atriplicifolia ⌀, ⌀
      iv. C$_3$ grasses
        Cinna arundinacea ***, ⌀
      v. C$_4$ grasses
        Sporobolus heterolepis ⌀, ⌀
   b. Shifting toward decreasing light
      i. Annuals and Biennials
        [none]
      ii. Potential Nitrogen fixers
        [none]
      iii. Other perennial forbs
        Arisaema triphyllum ⌀, ⌀
        Eupatorium purpureum ⌀, ⌀
        Napeae dioica **, ⌀
        Polemonium reptans ⌀, ⌀

Figure 1. Changes in total cover for the first three years of the restoration experiment are shown for four % sand classes. The first three classes were planted with the mesic seed mix, the fourth class was planted to the xeric seed mix. The graphs show total cover for (a) all planted species, (b) forbs vs. graminoids, (c) C_3 vs. C_4 graminoids, (d) annual vs. biennial herbs, (e) potential N-fixing species, (f) four leaf-width classes, and (g) three leaf-height classes.

Figure 2. Mean species richness for Year 1, Year 2, and Year 3 is graphed against four % sand classes.

Figure 3. Mean species diversity ± 1 s.d. is graphed by year for four % sand classes.

Figure 4. Means for between-year turnover, loss, and recruitment are graphed against pairs of adjoining years (Years 1 and 2, Years 2 and 3) for (a) four soil texture classes and (b) three light availability classes.

Figure 5. The mean position of 42 common species were plotted along gradients of % direct PPFD and % sand using data from (a) Year 1, (b) Year 2, and (c) Year 3 of the study. The null mean position is indicated by an x.

Figure 6. Average niche breadth ± 1 s.d. is graphed against three years for gradients of (a) % sand and (b) % direct PPFD.
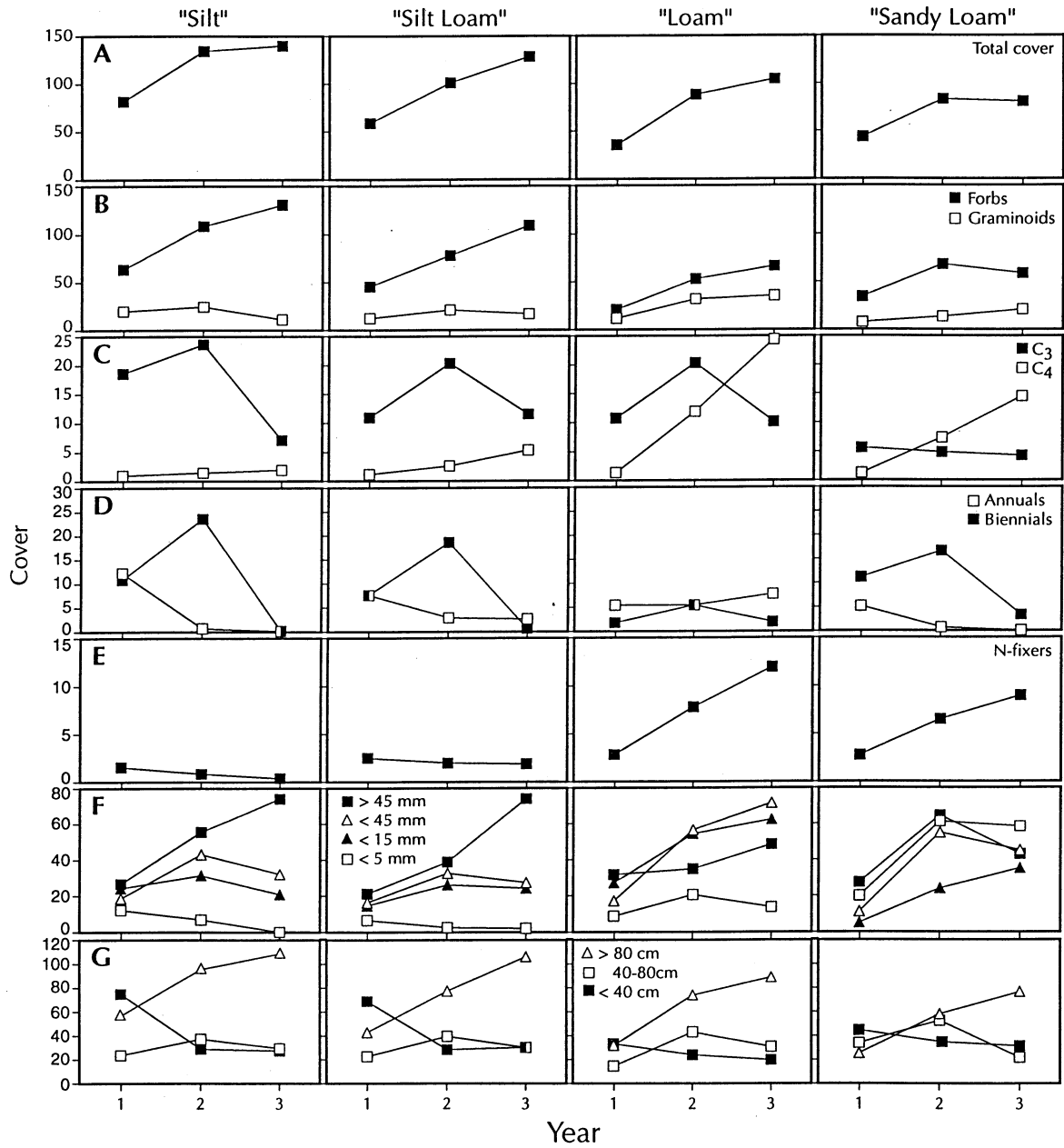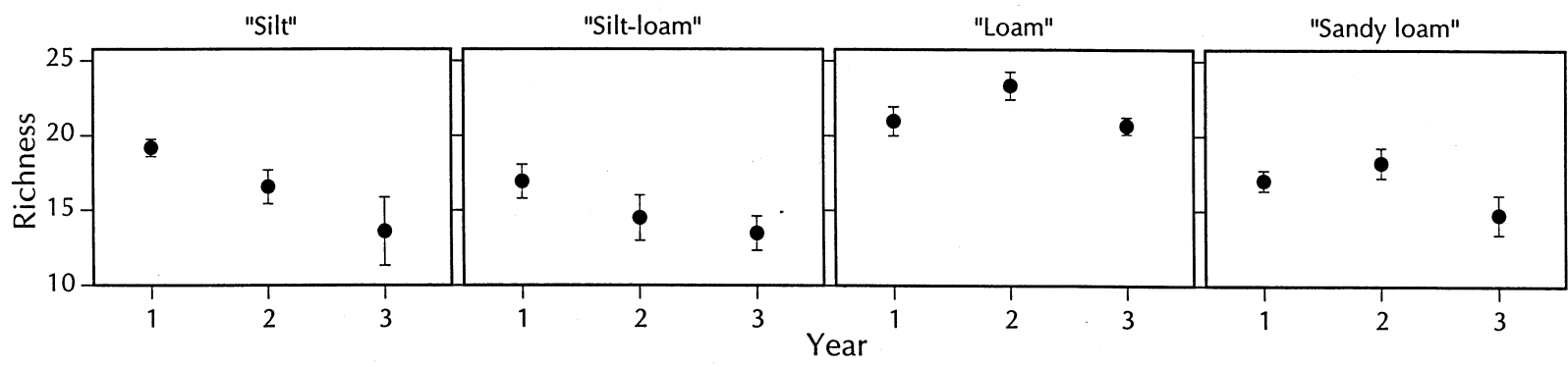
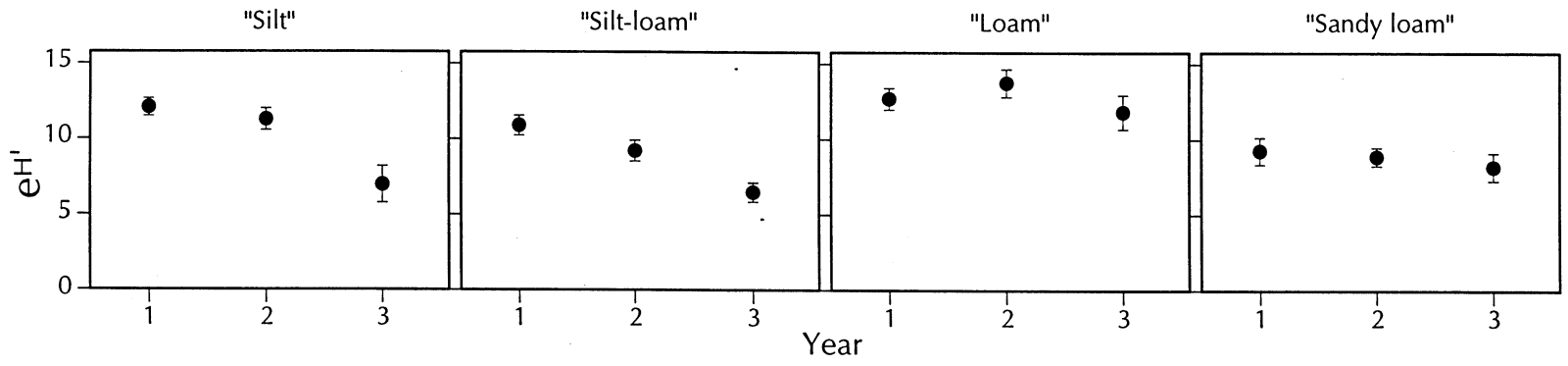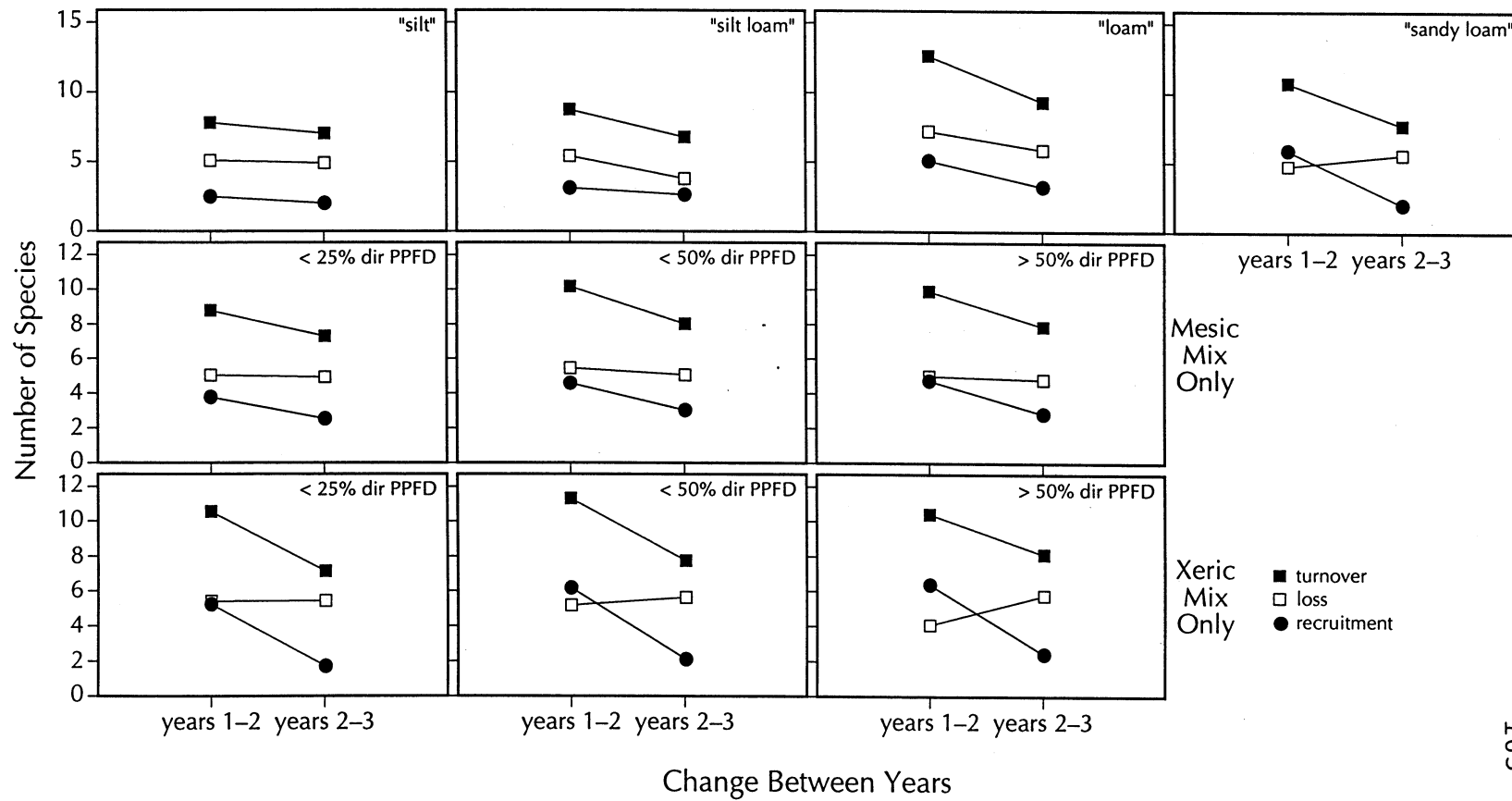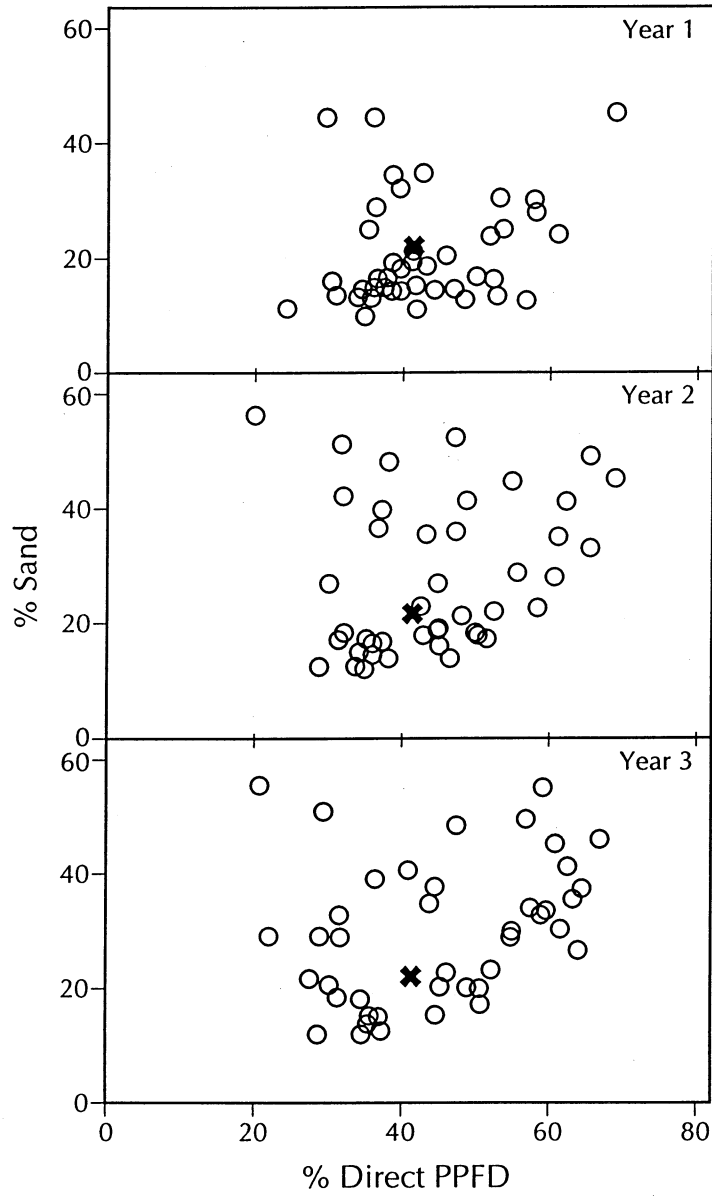**Figure 1**

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Figure 2

Figure 3

Figure 4

Figure 5

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Figure 6