EFFECTS OF OVERSTORY STAND DENSITY AND FIRE ON GROUND LAYER VEGETATION IN OAK WOODLAND AND SAVANNA HABITATS

John B. Taft[1]

[1] Plant Ecologist,Illinois Natural History Survey, Champaign, IL
JBH is corresponding author; to contact, call (217) 244-5046 or email at taft@inhs.uiuc.edu

Abstract.—Vegetation changes underway in oak woodland and savanna communities in the eastern and midwestern United States, primarily a result of reduced fire frequency or fire absence, include increased tree density and shading and loss of species diversity in the ground layer. However, some habitats, particularly on dry-mesic to xeric sites, retain considerable restoration potential, and insights are needed for directing management efforts, such as with prescribed fire, where they can be most effective. This paper examines overstory and ground layer interactions in flatwoods, barrens, and dry-mesic woodland habitats, together with fire effects, and highlights structural characteristics relevant to ecological condition and restoration potential.

In nested vegetation sample plots throughout Illinois, patterns of ground layer diversity were strongly related to levels of tree density at several study sites. At these sites, with increasing tree density, or "thicketization," the diversity of ground layer species and plant functional groups declines. Where this pattern was lacking suggests two possibilities: tree density has yet to become a limiting factor for ground layer species and functional group diversity, or, more typically, tree density has progressed to the point where remaining ground layer species are sparsely distributed, shade-tolerant, and relatively indifferent to levels of tree density. The pattern of ground layer species attrition with increasing thicketization is interpreted as a signal for productive restoration opportunities compared to the latter, low diversity condition. Efforts to restore these former communities with reintroduction of fire have shown promise. Use of fire on sites even with extensive thicketization seems to improve overstory structure and ground layer diversity; however, in these cases, the soil seed bank may be limited following prolonged periods of stand closure.

Interactions between overstory and ground layer vegetation also were examined for ordered patterns of plant functional group losses (community disassembly) with increasing tree density. Documenting ordered patterns along the structural gradient of tree density provides additional insights regarding ecological condition and restoration potential of sites or habitats. Functional groups that appear most sensitive to thicketization and are the first to decline with extended fire absence are herbaceous vines (relatively scarce), perennial grasses, sedges, and perennial forbs. While opportunities remain to restore aspects of oak woodland and savanna habitats, the attrition pattern suggests a limited time frame for the full restoration of ground layer diversity, even in dry to xeric sites.

INTRODUCTION

Oak-dominated savanna, barrens, and woodland habitats occur throughout North America but have undergone extensive habitat loss and degradation, particularly as a result of declining fire frequency and fire absence, and are considered imperiled ecosystems (Anderson et al. 1999, Abrams 2005). Restoring these communities has become a priority for conservation agencies and habitat managers. The prairie-forest transition zone (Anderson 1983), a region centered on Illinois and overlapping with the leading edge of the "prairie peninsula" (Transeau 1935), provides opportunities for testing the restoration potential of oak woodland and savanna-like habitats. While about 55 percent of the landcover of Illinois was prairie in the early 1800s (Szafoni et al. 2002), the remaining lands primarily were forest, woodland, and savanna. These vegetation types formed a heterogeneous mosaic; wooded habitats were most prevalent in dissected terrain and prairie predominated where slopes were less than 4 percent (Anderson 1991). Fires that contributed to the maintenance of prairie also maintained the structural and compositional characteristics of savanna and woodland habitats (Nuzzo 1986, Taft 1997, Anderson and Bowles 1999). This fire history, while seemingly in the distant past, is within the life-span of some long-lived trees still standing (e.g., bur [*Quercus macrocarpa*], white [*Q. alba*], and post oaks [*Q. stellata*]). The open-grown form of many of these veteran trees serves as a reminder of the more open structure of woodlands and savannas in the pre-settlement period. In some cases, burning of woodlands was a practice that continued into the early 20th century, when it was strongly discouraged and disparaged as a "savage custom" (Miller 1920). However, once fire frequency declined, many of these stands quickly underwent closure, or "thicketization" (Archer et al. 2004, Breshears 2006), resulting in conversion of prairies and savannas to woodlands and then forests.

Some savanna and woodland habitats in the prairie-forest transition zone on seasonally dry sites such as flatwoods and barrens demonstrate a degree of resistance to change during long fire-free intervals. The great majority of floristic diversity in these habitats is in the ground layer (Taft 1997); consequently, they provide an opportunity to examine the patterns of influence of overstory structure on ground layer composition and diversity for evidence of interactions that may be absent in less ecologically stressful habitats, where extended periods of fire absence have resulted in prolonged ground layer shading (e.g., Hutchinson et al. 2005).

Interactions between overstory and ground layer vegetation in forests and woodlands can be reciprocal, with overstory influencing ground layer and ground layer influencing successful regeneration among tree species (Gilliam and Roberts 2003). Using flatwoods, barrens, and dry-mesic woodlands as examples, this paper will focus on how overstory structure in woodland and savanna-like habitats is related to and possibly affects patterns of ground-layer species diversity and composition. Maintaining a species pool at a given habitat can be influenced by both regional and local processes and involves a balance of processes at each scale (Huston 1999). Local factors that tend to decrease diversity include competition (Huston 1994), such as from woody overstory species in savanna-like habitats (Peterson and Reich 2008), an effect that could be ameliorated by regional interactions promoting species exchanges among habitats (Ricklefs and Schluter 1993). However, habitat fragmentation would tend to limit species exchanges while ecological islands such as dry to xeric habitats also would limit the types of species that could become established. Consequently, it is expected in the highly fragmented prairie-forest transition zone (e.g., Schwartz 1997) that with thicketization, especially in dry to xeric sites, the interaction between woodland/savanna overstory and ground layer vegetation would be manifested as a pattern of species loss, or attrition, in the ground layer. Ground layer species in forest habitats also can be very diverse (Gilliam 2007); however, forest species generally adapted to mesic conditions could not be expected to compensate for attrition of species in closed dry savanna and woodland habitats, particularly in fragmented landscapes.

Under the framework in the current study, situations where tree density and ground-layer species diversity are found to be inversely related would provide a signal, perhaps a finite opportunity, of restoration potential and an indicator where management with prescribed fire could be focused. A significant regression of tree density on ground layer diversity ($P < 0.05$) will be referred to as fitting the post-fire species attrition hypothesis. This hypothesis is based on the concept of plant functional groups, which are assemblages of species with a shared set of attributes that may include morphological and physiological characteristics, ecological roles, resource use, and response to disturbance (Symstad 2002). Diversity in functional groups has been shown to be closely linked with ecosystem functioning and stability, and can serve as an indicator of community integrity (Hooper and Vitousek 1997, Tilman et al. 1997, Mason et al. 2003). Monitoring the density of plant functional groups shows promise as a rapid assessment technique in prairies for evaluating habitat integrity, as it is highly correlated with species richness and estimates of floristic integrity (Sivicek 2007). It is expected that the diversity of plant functional groups would decline with stand closure. This pattern will be referred to as the post-fire functional group attrition hypothesis.

Where such a pattern is lacking would suggest one of two null hypotheses: 1) relatively stable condition where

Table 1.—Summary of habitat type, sites name, sample intensity (0.05-ha circular tree plots), and fire history for sites examined in this study. Most data are baseline, preburn data. INAI = Illinois Naural Areas Inventory sites.

Community Type[a]	Site name	Plot #	Baseline fire treatments	Citations
Flatwoods (INAI)	Reckers Woods	8	none	Taft et al. 1995
Flatwoods (INAI)	Chip-O-Will Woods	8	none	Taft et al. 1995
Flatwoods (INAI)	Posen Woods	8	none	Taft et al. 1995
Flatwoods (INAI)	Wms Creek Woods	8	none	Taft et al. 1995
Flatwoods (INAI)	Jackson Slough	8	none	Taft et al. 1995
Flatwoods (INAI)	Lake Sara Flatwoods	10	20 yrs, annual	Taft et al. 1995
Flatwoods	Mt. Vernon	23	none (preburn)	Taft 2005
Dry Barrens (INAI)	Gibbons Creek	15	none (preburn)	Taft and Solecki 2002
Dry Barrens (INAI)	Forest Service	8	none	Taft and Solecki 2002
Woodland[b]	Beaver Dam SP	12	1-3 burns	Taft 2006
Woodland[b]	Beaver Dam SP	15	none	Taft 2006

[a] Community classification follows White and Madany (1978)
[b] Community classification follows White and Madany (1978), with revisions.

tree density has yet to limit ground layer diversity; or, more typically 2) the progression of thicketization to the point where remaining ground layer species are shade-tolerant and indifferent to levels of tree density. The differences in these alternative null states can be readily distinguished by evidence of thicketization and the extent of herbaceous species in the ground layer vegetation. Sites fitting the second null model would be densely shaded stands with few herbaceous species, a predominance of woody species, and substantial bare ground. Although quite rare, null condition 1 would be optimal in open-woodland and savanna habitats; the negative attrition profile would indicate greater opportunities for restoration compared with null condition 2. The attrition pattern would suggest an existing heterogeneous stand structure with gaps containing more and different ground layer species (e.g., Leach and Givnish 1999, Peterson and Reich 2008) compared with areas with greater tree density. Consequently, with the attrition pattern, the species pool retains shade-intolerant taxa that are responding, albeit negatively, to stand thicketization. Attempting restoration at closed stands where these species are absent would rely on diversity found off-site (limited by habitat fragmentation and ecological condition) or among the selected species residing in the soil seed bank that could be stimulated with fire treatments.

METHODS AND DATA SOURCES

Vegetation Sampling

Data for the following habitat descriptions and analyses were collected employing similar vegetation sample methods involving stratified-random distribution of nested sample units with 0.05-ha circular plots for trees (≥ 6 cm diameter at breast height [d.b.h.]), 0.005-ha subplots for shrubs and saplings (> 50 cm tall), and 12 to 25 ground-layer sample quadrats (primarily 1/4-m^2; one study [Taft 2005] with ½-m^2 quadrats) on a transect within each tree plot. The data come from several sources (Table 1). Habitat characterization for flatwoods is based on a quantitative survey of vegetation and soils at 50 plots (0.05-ha) sampled among six sites on the Illinoian till plain (Taft et al. 1995). All six sites are recognized by the Illinois Natural Areas Inventory ([INAI], White 1978) as high quality habitats. Data from an additional site, Mt. Vernon Flatwoods ([MVF], Taft 2005), also are used. Data for barrens were recorded from a pair of sites in southern Illinois monitored since 1989 as part of a fire effects study (Taft 2003) and include more recent unpublished data. The INAI recognized the fire treatment site, Gibbons Creek Barrens (GCB), as a high quality barrens remnant. The fire-free reference site, Forest Service Barrens (FSB), was similar in many ways to the fire treatment site (Taft and Solecki 2002).

Data from dry-mesic woodland habitat were collected from six management units at Beaver Dam State Park (BDSP) in central Illinois, including three units with and three without recent burns as part of a fire management program (Taft 2006).

Habitat Descriptions

Dominant species and summary parameters for canopy, shrub/sapling, and ground layer strata are shown in Appendix 1, combining data from flatwoods (Taft et al. 1995), barrens (Taft and Solecki 2002), and woodland habitats (Taft 2006). Dominance is based on importance values calculated as the sum of two relative values (IV 200): basal area and density for trees, frequency and density for saplings and shrubs, and percent cover and frequency for ground layer species, including woody plants to 50 cm tall. The top-ranking 10, 15, and 50 species from canopy, shrub/sapling, and ground layer strata, respectively, are shown. Many species in the woody strata are present across habitats. By contrast, as an indication of dissimilarity among habitats in the ground layer stratum, only two species (Virginia creeper [*Parthenocissus quinquefolia*] and poison ivy [*Toxicodendron radicans*]) were found in all three habitats. Botanical nomenclature follows Mohlenbrock (1986) and community classification follows that developed for the Illinois Natural Areas Inventory (modified from White and Madany 1978). Eleven plant functional groups were recognized for the ground layer species in these habitats: ferns, annual/biennial forbs, herbaceous vines, legumes, perennial forbs, C3 perennial grasses (cool season), C4 perennial grasses (warm season), perennial sedges, shrubs, trees (seedlings to 50 cm), and woody vines.

<u>Flatwoods</u> - The flatwoods included in this study also are termed “southern flatwoods” (White 1978) or “post oak flatwoods” due to the predominance of post oak, a species accounting for about 57 percent of the IV. Oak and hickory species combined account for 93 percent of the IV in the canopy, but were relatively scarce in the shrub/sapling stratum. The shrub/sapling layer had just over 4,000 stems/ha (Appendix 1), an indication of thicketization.

Flatwoods are level woodlands (≤ ~2-percent slope) with claypan soils. Claypans (argillic horizons) are subsurface soil horizons characterized by a sharp increase in clay content compared to overlying soil horizons. Claypans can result in a perched water table in the spring; however, with evapo-transpiration during summer months, the surface soil horizons typically become very dry. These woodlands formerly were widespread on the Illinoian till plain (Telford 1926, Braun 1936, Aldridge and Homoya 1984) but have been reduced by extensive logging and land-use changes (Taft et al. 1995).

Flatwoods remnants can be instructive for examining overstory-ground layer interactions because variance in overstory structure and composition ordinarily attributable to degree of slope and aspect is reduced to variation in edaphic characteristics, such as soil nutrient content, depth to claypan, and soil available water holding capacity (AWC). For example, total density of woody stems is positively related to depth to claypan and particularly to soil AWC (Taft et al. 1995). Sites with more mesic soil conditions will be the fastest to undergo vegetation changes with fire absence and perhaps the most challenging to restore. Accordingly, stability in overstory structure and composition varies widely among flatwoods remnants with some demonstrating both structural and compositional instability, the typical condition for many oak woodlands (Abrams 1992, Moser et al. 2005). In contrast, some stands demonstrate compositional and structural stability with apparently sustainable levels of post oak regeneration. Differences can be traced to variance in soil parent materials. Unstable sites with poor oak recruitment and prolific regeneration of invading tree species tend to be found on relatively deeper soils with greater AWC. These tend to be soil types developed in loess deposits with a silty-loam texture. Structurally stable sites have been found on lacustrine deposits with considerable sand content in the surface soil horizons (about 40-50 percent) and, consequently, lower AWC (Taft et al. 1995).

At MVF (not included in Appendix 1), an old second-growth flatwoods, white oak was co-dominant with post oak. Tree density was 465/ha (≥ 6 cm d.b.h.), basal area was 24.7 m^2/ha, and sapling/shrub density was just over 7,000 stems/ha (Taft 2005), demonstrating considerable thicketization. Ground layer vegetation was very sparse and dominated by woody seedlings and vines; Virginia creeper, poison ivy, sassafras, riverbank grape (*Vitis riparia*), Mayapple (*Podophyllum peltatum*), and black oak accounted for more than half of the species occurrences. No grasses and only a single occurrence of one sedge was found in baseline samples.

Barrens - Barrens is a term applied to a wide range of physiographic and environmental conditions to describe distinctly different types of vegetation (e.g., Hutchison 1994, Bowles and McBride 1994). As the term is used in forested regions of the Midwest, barrens typically refer to a savanna-like community characterized by local assemblages of a prairie flora (White and Madany 1978). Today, barrens remnants occur primarily in dissected terrain on south- and southwest-facing aspects with shallow soils over bedrock (Heikens and Robertson 1995). During extended periods of fire absence, barrens tend to convert to closed woodland.

Baseline data from a pair of dry barrens in southern Illinois examined for a long-term fire effects study indicate that post oak was the dominant tree species, accounting for about 55 percent of the IV for trees (Taft and Solecki 2002). These sites, GCB (the fire treatment site) and FSB (a fire-free reference site), occur on shallow soils developed in loess and residuum over sandstone. Oak and hickory species combined accounted for 77 percent of the IV for trees. The size class distribution pattern for trees indicated compositional stability because post oak likely will continue to be dominant; however, prolific regeneration of post oak forming a strong reverse-J-shaped curve indicates a structurally unstable site and portends stand closure. Stem density for saplings and shrubs was just over 5,000 stems/ha, indicating thicketization was well underway (Appendix 1, pg. 38).

Dry-Mesic Woodland - Woodland habitat at BDSP, Macoupin County, IL, occurs primarily on rolling, dissected glacial moraines. Soils are developed in glacial till deposits and generally have a silty-loam texture (Tegeler 2004). Fire management units at Beaver Dam State Park included woodlands with one to three recent burns as well as unburned units. Oak and hickory species accounted for 49 percent of the total IV. Oak species were dominant in terms of basal area, but the high density of slippery elm (*Ulmus rubra*) and hackberry *(Celtis occidentalis*) made them prominent species as well. Overstory regeneration generally was a pattern of instability with little successful oak recruitment. Total shrub/sapling stem density was just over 14,000/ha, indicating advanced thicketization. Previously burned units had slightly lower tree density but slightly higher tree basal area compared to unburned units, much lower stem density in the shrub/sapling stratum, and higher ground-layer species density and diversity.

Perennial forbs are the most species-rich functional group in the ground layer of flatwoods, barrens, and woodland habitats in this study. However, the profiles of plant functional group importance in these habitats show a shift from woody vine dominance and near-equal secondary dominance of forbs, sedges, and grasses in flatwoods, to graminoid (grass and sedge) dominance in barrens and forb dominance in woodlands (Fig. 1).

DATA ANALYSIS

Data from canopy cover estimates made with a spherical densiometer and overstory structure were recorded in both flatwoods and barrens habitats. Correlations between canopy cover and total density of trees were positive, particularly in flatwoods ($r = 0.57$). However, tree density explained more of the variance in ground layer vegetation than did canopy cover ($r = -0.67$ vs. $r = -0.44$). Tree basal area was unrelated to ground layer diversity patterns in flatwoods, barrens, and woodland datasets. Consequently, tree density is used to examine the interactions between overstory and ground layer vegetation.

Interactions between overstory tree density and ground layer species and functional groups were examined with regression analysis; mean comparisons of tree density classes and ground layer parameters were done with ANOVA and Tukey post-hoc tests (SPSS ver. 10, Chicago, IL). Tree density classes of high, medium, and low levels were created for each habitat to examine trends among ground-layer functional groups. Tree density classes were formed by dividing the range of tree densities into equal thirds; in each case, mean differences

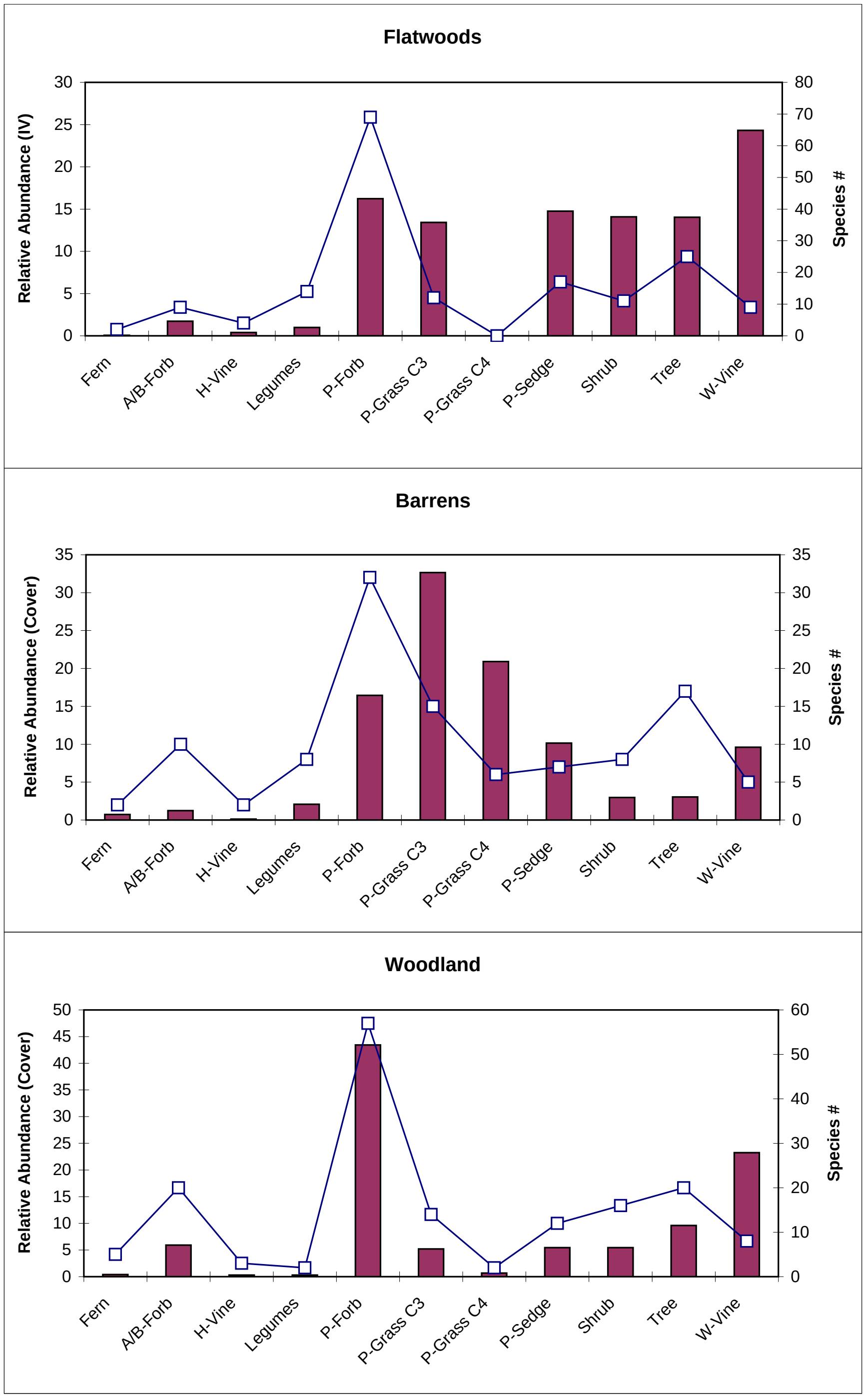

Figure 1.—Relative abundance (bars [left y axis]) and species richness (line and point data [right y axis]) of plant functional groups from vegetation sample data in flatwoods, barrens, and woodland habitats in Illiniois. A/B = annual/biennial, H = herbaceous, P = perennial, W = woody. Quadrat numbers for each community type were: flatwoods - 1,080, barrens - 276, and woodlands - 312.

in tree density classes were significant overall and with all pairwise Tukey post-hoc comparisons. Species density in the ground layer stratum is the average number of species per quadrat (generally, ¼ m^2). Species diversity is the Shannon-Wiener Index (H'). Functional group richness is calculated as the total number of plant functional groups in ground layer quadrat samples nested within tree plots.

RESULTS

Overstory-Ground Layer Interactions

Regression analysis of the interaction between tree density and ground layer diversity for all sample data combined from flatwoods, barrens, and woodland habitats showed no pattern. However, interactions were found between overstory and ground layer strata when individual community types were examined separately.

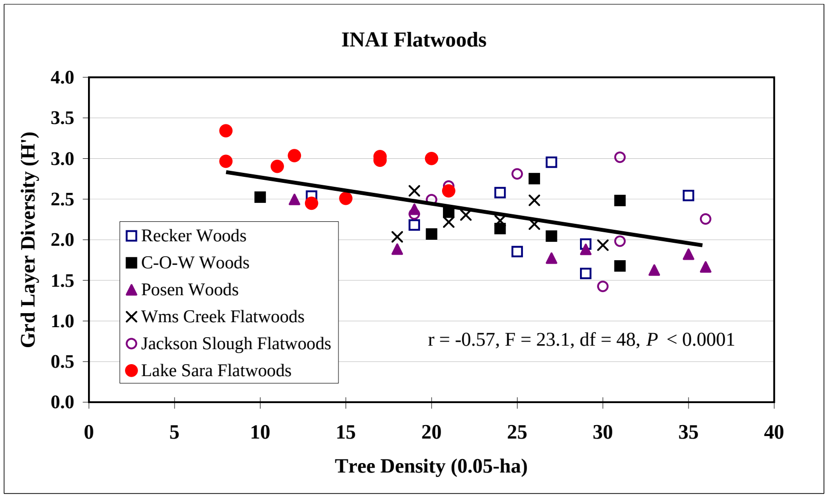

Figure 2.—Interaction between overstory tree density and ground layer diversity fitting the species attrition hypothesis for six flatwoods recognized by the Illinois Natural Areas Inventory (INAI). Ground layer diversity is the average Shannon-Wiener Index (H') from 12 (Lake Sara) to 25 quadrats for each tree plot. Tree density is based on stems ≥ 6 cm d.b.h.

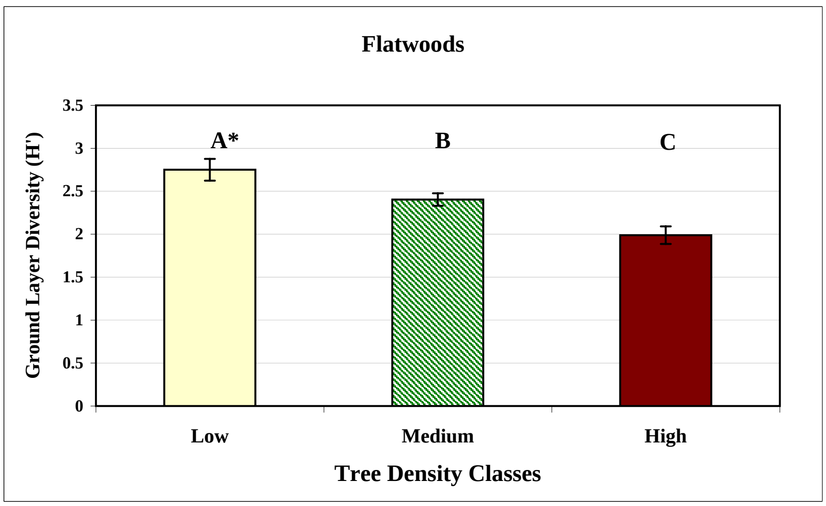

Figure 3.—Mean comparison of ground layer diversity (Shannon-Wiener Index [H') among tree density classes for six flatwoods recognized by the Illinois Natural Areas Inventory. The overall differences are significant (ANOVA: F = 11.6, df = 2, P < 0.0001); different letters indicate significant pairwise comparisons with Tukey post-hoc test (*difference between low and medium tree density is marginally significant [P = 0.055]). Error bars are SE.

Flatwoods

Survey of Six INAI Sites on the Illinoian Till Plain - Ground layer species diversity was inversely related to tree density (Fig. 2) on all plots from the six sites examined together and on four of the six sites examined separately. The two exceptional sites fit the null attrition model 2; these latter sites had the greatest mean soil AWC among flatwoods study sites. The overall pattern due to regression of tree density on ground-layer diversity (Fig. 2) fits the species attrition hypothesis (r = -0.57, F = 23.1, df = 48, P < 0.0001) and is made particularly strong by including Lake Sara Flatwoods (LSF), a site with an extensive fire history (20 years of nearly annual fire). Without the burned unit, the pattern is weaker but still significant (r = -0.37, F = 6.1, df = 38, P = 0.017). Mean comparisons of ground layer diversity (H') by tree density classes (low, medium, and high) were significantly different (Fig. 3), with the greatest diversity in the low tree density class. All pairwise comparisons also were different. (The difference between low and medium tree density was marginally significant [P = 0.055]).

Functional group richness also was inversely related to tree density (Fig. 4), but this pattern was true primarily at the community level. Only one individual site, Posen Woods, showed this pattern. Overall differences in functional group richness among tree-density classes were significant (Fig. 5). Functional groups proportionately more common in low- and medium-density portions of stands include nitrogen-fixing species (legumes), annual/biennial species, perennial forbs, perennial sedges, and perennial grasses. Woody functional groups (vines, shrubs, tree seedlings) were predominant in the high tree-density sites (Fig. 6).

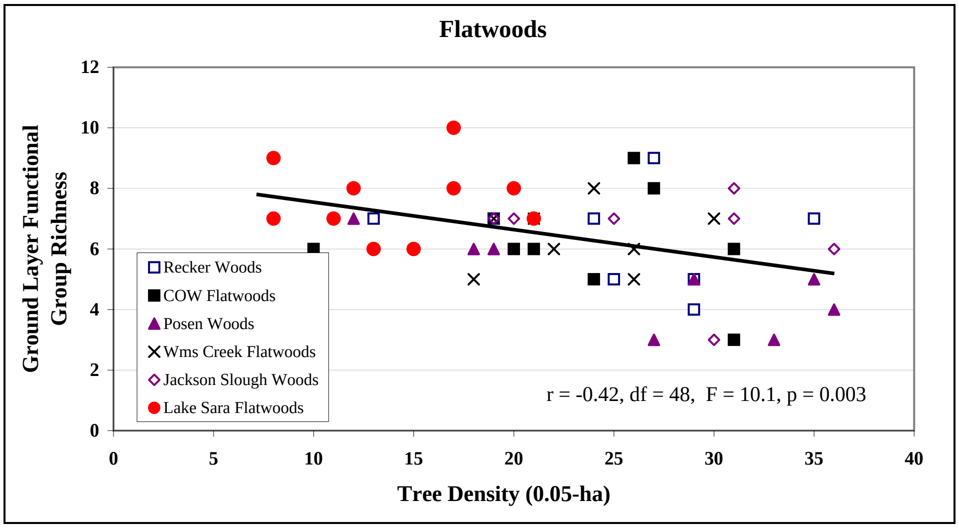

Figure 4.—Interaction between overstory tree density and ground layer functional group richness for six flatwoods recognized by the Illinois Natural Areas Inventory. The pattern fits the functional group attrition hypothesis. Functional group richness is the total count among sample quadrats for each tree plot (n = 12 for Lake Sara and n = 25 for all other sites). Tree density is based on stems ≥ 6 cm d.b.h.

Figure 5.—Comparison of average ground-layer functional group richness among tree density classes in flatwoods. Differences from mean comparisons are significant (ANOVA: $F = 5.8$, $df = 2$, $P < 0.006$). Different letters indicate significant differences in pairwise comparisons with Tukey post-hoc test. Error bars are SE.

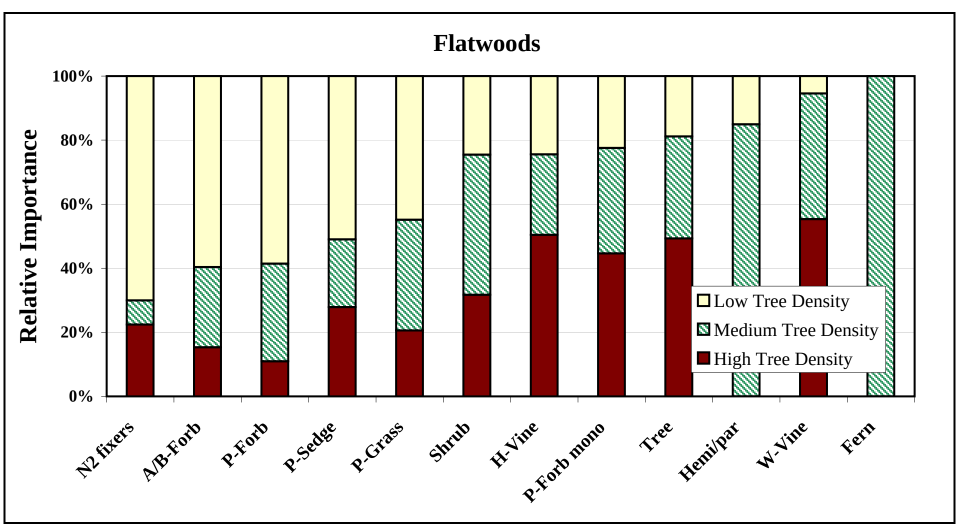

Figure 6.—Distribution of ground-layer functional groups proportionate to tree density classes in flatwoods. Tree density classes had significantly different means. N2 = nitrogen fixers, A/B = annual/biennial, H = herbaceous, P = perennial, Hemi/par. = Hemiparasites, W = woody.

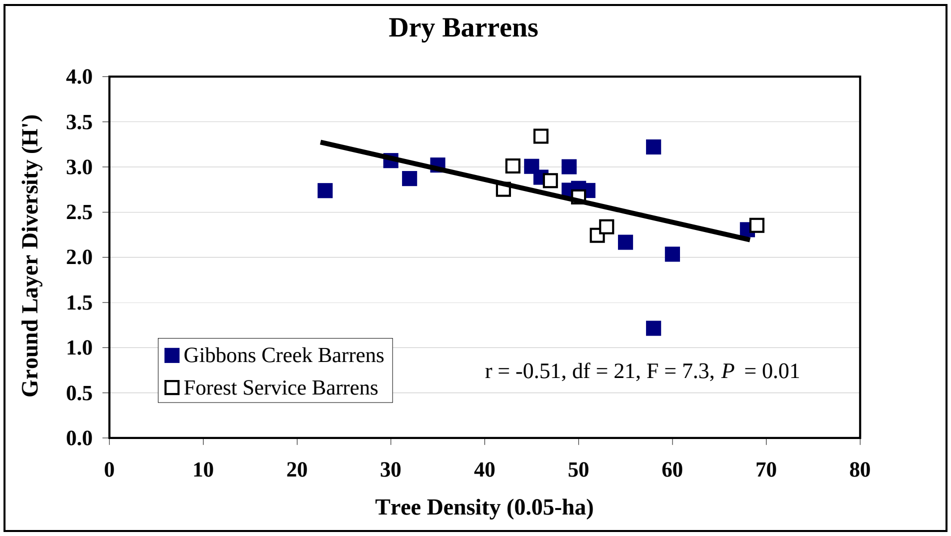

Figure 7.—Interaction between overstory tree density and ground layer diversity fitting the species attrition hypothesis from 23 plots sampled at Gibbons Creek and Forest Service barrens. Ground layer diversity is the average Shannon-Wiener Index (H') for each tree plot. Tree density includes stems ≥ 6 cm d.b.h.

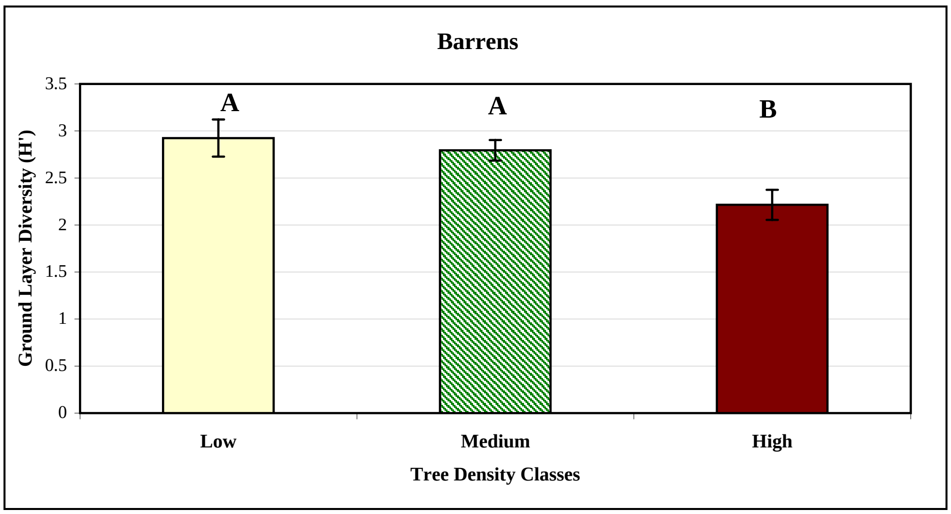

Figure 8.—Mean comparison of ground layer diversity (Shannon-Wiener Index [H']) among tree density classes in barrens sample data. The overall differences are significant (ANOVA: F = 5.4, df = 2, P = 0.01); different letters indicate significant pairwise comparisons with Tukey post-hoc test. Error bars are SE.

Mt. Vernon Flatwoods - Sample data from MVF are in contrast with most of the flatwoods dataset described above. At MVF there was no correlation between stand density and ground layer diversity. Fifteen of the 20 most frequent taxa in the ground layer were woody species. These conditions suggest null attrition model 2. A fire management study was conducted to determine restoration potential of this site (Taft 2005; see below).

Barrens

Gibbons Creek and Forest Service Barrens - Ground-layer species diversity trends lower with increasing tree density (Fig. 7). The pattern due to regression fits the species attrition hypothesis when baseline, preburn data from both sites are combined. Density of post oak alone, by far the dominant tree, explains even more of the variance in ground layer diversity ($F = 25.8$, $P < 0.001$). Differences in mean ground layer diversity among tree-density classes were significant with the greatest diversity in the low tree density class; however, there were no differences between low and medium tree-density classes (Fig. 8).

Functional group richness also trends lower with increased tree density (Fig. 9). Differences in functional group richness among tree-density classes were significant with the greatest richness in the low tree density class, though there were no differences between low and medium tree-density classes (Fig. 10). Functional groups proportionately more common in low density portions of stands are herbaceous vines, ferns, cool and warm season grasses, perennial forbs, and sedges (Fig. 11).

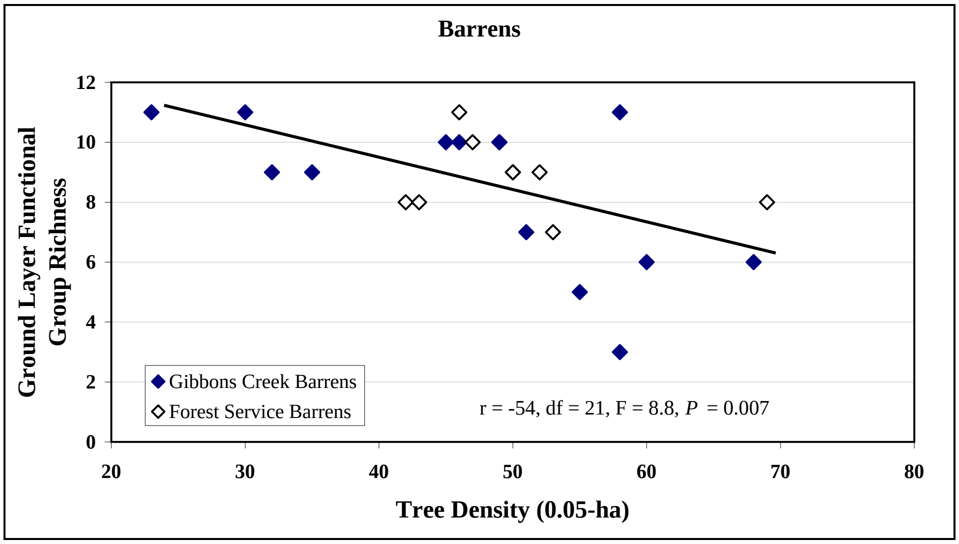

Figure 9.—Interaction between overstory tree density and ground-layer functional group richness in baseline (preburn) barrens sample data. The pattern fits the functional group attrition hypothesis. Functional group richness is the total count among sample quadrats for each tree plot (n = 12). Tree density is based on stems ≥ 6 cm d.b.h.

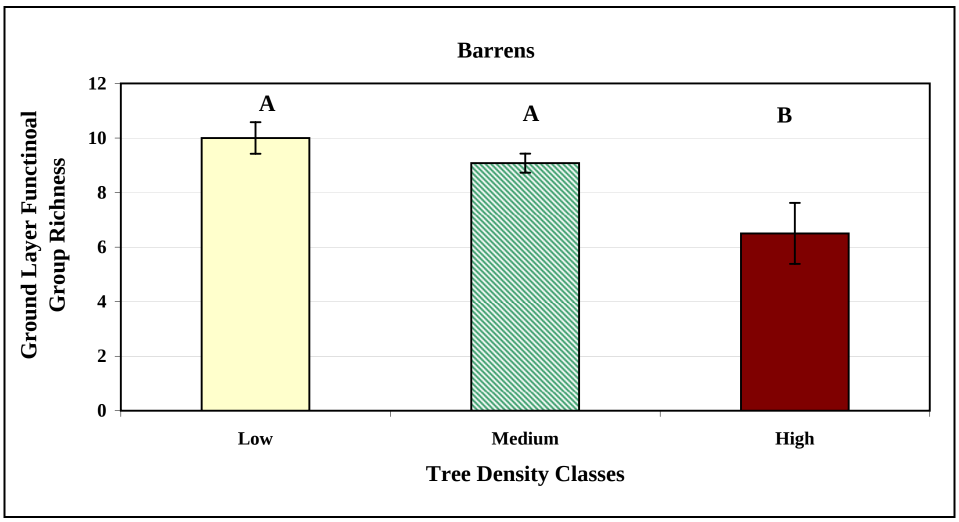

Figure 10.—Comparison of average ground-layer functional group richness among tree density classes in barrens. Differences from mean comparisons are significant (ANOVA: F = 6.2, df = 2, P = 0.008). Different letters indicate significant differences in pairwise comparisons with Tukey post-hoc test. Error bars are SE.

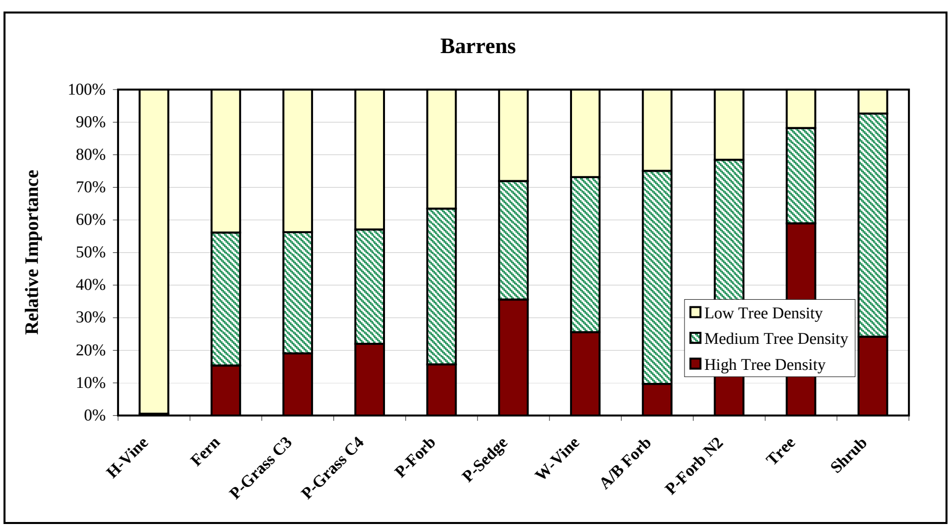

Figure 11.—Distribution of ground layer functional groups proportionate to tree density classes in barrens. Tree density classes had significantly different means. H = herbaceous, P = perennial, C3 (cool season), C4 (warm season), A/B = annual/ biennial, W = woody, N2 = nitrogen fixers.

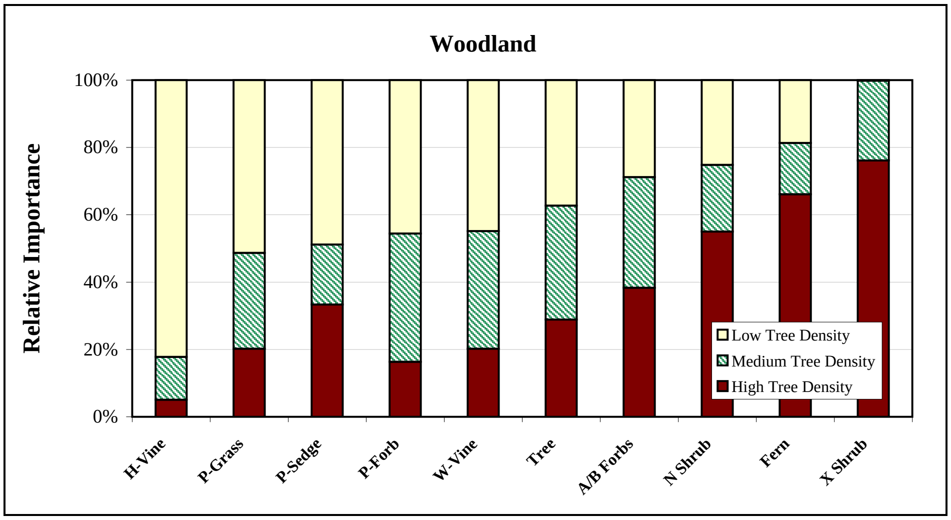

Figure 12.—Distribution of ground-layer functional groups proportionate to tree density classes in woodlands. Tree density classes had significantly different means. H = herbaceous, A/B = annual/biennial, P = perennial, W = woody, N = native, X = nonnative.

Figure 13.—Lake Sara Flatwoods (left) in Effingham County, IL, following a 20-year period of annual burns. Photo taken in July 1990. Note the absence of fire scars. Contrast with Mt. Vernon Flatwoods (right) in Jefferson County, IL, on the same soil series (Wynoose) but lacking recent fire. While tree densities (stems ≥ 6 cm d.b.h.) differ greatly (284 vs. 465 stems/ha), basal area is more similar (20.2 vs. 24.7 m^2/ha).

Dry-Mesic Woodland

Beaver Dam State Park - Among all sampled management units at BDSP, there is no correlation between tree density and ground-cover species density or diversity of ground-layer functional groups, suggesting null attrition model 2 with the extensive thicketization. Previously burned units show a weak pattern consistent with the species attrition hypothesis; however, the pattern due to regression is nonsignificant. Functional group richness also did not show a pattern of attrition with greater tree density. However, functional groups with affinity for low tree-density zones include herbaceous vines, perennial grasses, perennial sedges, perennial forbs, and woody vines (Fig. 12).

Fire Effects on Interactions Among Strata

Flatwoods - Lake Sara Flatwoods, a site with an extensive fire history, strengthened the species attrition pattern found among sample units with relatively high species diversity and low tree density. Ground-layer species density was over four times the mean species density for all other sites. LSF and MVF occur on the same soil series, Wynoose silt loam, but differ greatly in ground layer cover, composition, and diversity (Fig. 13). Following three burns at MVF, species density increased three-fold and tree density declined 26 percent; however, there was a 270-percent increase in density of stems in the shrub/sapling stratum (Taft 2005). Following three burns, there remained no discernable species attrition

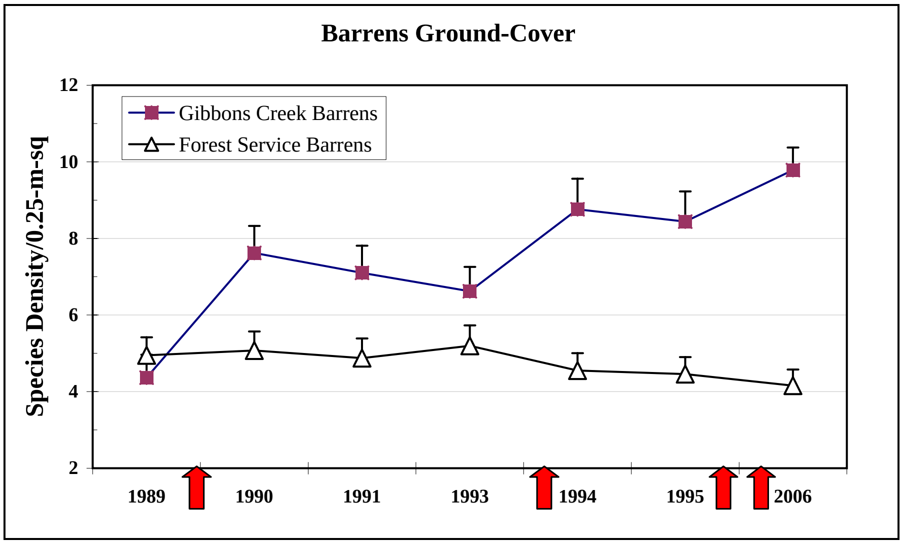

Figure 14.—Comparison of trends in ground-layer species density between a barrens remnant managed with prescribed fire (Gibbons Creek Barrens) and a fire-free reference unit (Forest Service Barrens) in Pope County, IL. Arrows indicate times of burns. Error bars are SE.

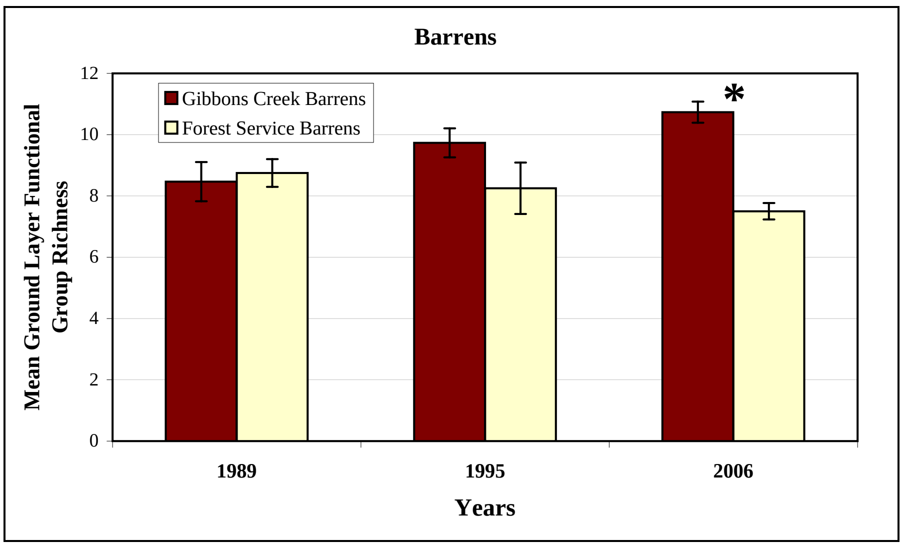

Figure 15.—Comparison of changes in mean functional group richness in fire treatment and fire-free reference units in dry barrens habitats. Two fire treatments occurred before 1995 and two after. * indicates significant difference (t-test: $t = 7.4$, $df = 21$, $P < 0.0001$). Error bars are SE.

pattern. The increase in ground layer diversity resulted primarily from species stored in the soil seed bank. Eight sedge species that were absent in baseline samples emerged following the burns, but perennial grasses dominant at other flatwoods remnants remained very sparse or absent.

Barrens - Following four burns over a 17-year period at GCB, ground layer species density more than doubled (Fig. 14), tree density declined 29 percent, shrub/sapling density declined 35 percent, and the pattern of ground-layer species attrition was strengthened compared to the baseline sample ($r = -0.70$ compared to $r = -0.51$), but only when the fire-free reference plots are included. Data from the fire treatment unit following four burns approximates null attrition model 1 with extensive percent cover of a rich herbaceous ground layer. The pattern of functional group attrition also was strengthened compared to the baseline sample data ($r = -0.68$ compared to $r = -0.54$), and made particularly strong when data from fire treatment and fire-free reference units are combined.

Not only do spatial patterns of tree density and ground layer diversity support the species attrition hypothesis, but long-term trends data from FSB, the fire-free reference site, also show gradual species losses over time (Fig. 14). Trends for mean functional group richness show a diverging pattern from nearly equal values in the baseline samples (1989) to widely and significantly divergent means in 2006 following 17+ years of fire absence at FSB and four burns at GCB (Fig. 15).

Predominantly declining functional groups at FSB include perennial grasses (C3 and C4 species combined for a 35-percent reduction in cover), sedges, woody vines, and perennial forbs. All functional groups declined in percent cover at FSB except for tree seedlings.

Dry-Mesic Woodland - Fire treatments at BDSP resulted in a significant decrease of tree density (5.6 percent) and a significant increase in ground-layer species density (17 percent). In fire-free reference units, there were a slight increase in tree density and a significant decline in ground-layer species richness compared to baseline samples 2 years earlier. As a result of these changes, an overall pattern consistent with the species attrition hypothesis developed; however, the pattern due to regression is relatively weak and non-significant (P = 0.14). Data from fire treatment units alone, which showed a weak but nonsignificant attrition pattern with the baseline data, show a significant inverse pattern in the relationship between tree density and ground-layer species density after an additional fire treatment (r = -0.57, F = 5.7, df = 12, P = 0.03).

DISCUSSION

A chief limiting factor for ground-layer species richness and cover in savanna habitats is light availability (Bray 1958, 1960, Leach and Givnish 1999, Peterson et al. 2007). However, available light is spatially and temporally heterogeneous and accurate assessment requires specialized equipment and considerations of several abiotic and biotic variables measured over time (Neufeld and Young 2003). In this study, tree density was tested as a factor for rapid and cost-effective assessment of the influence of overstory stand structure on ground-layer species diversity in savanna and woodland habitats. Tests were conducted at different ecological scales: across multiple habitats, within habitats, and within individual sites and management units. Patterns of overstory-to-ground layer interactions were obscured in this study when multiple habitat types, including sites with widely ranging ecological conditions, were examined collectively. Based on these datasets, the most appropriate ecological scale for examining patterns of overstory and ground layer interactions relevant to the species and functional group attrition hypotheses is within habitats and sites.

Results summarized here explore overstory-ground layer interactions as an indicator of ecological condition and restoration potential. The post-fire species attrition hypothesis and functional group attrition hypothesis predict that with increasing thicketization (overstory density) during extended periods of fire absence, ground-layer species diversity and the richness of plant functional groups will decline until a stasis is reached and remaining species are relatively indifferent to shade levels (null attrition model 2). Alternatively, with increasing fire, reduced tree density, and increased ground layer diversity (e.g., Taft 2003, Bowles et al. 2007, Peterson et al. 2007), the relations between tree density and ground-layer diversity may strengthen. Eventually, a temporary stasis might be reached where shade levels are not limiting to ground layer vegetation (null attrition model 1).

These results suggest a sequence of three developmental stages with fire absence in savanna and open woodland habitats relevant to ecological condition and restoration potential: 1) null attrition model 1, where tree density has yet to alter ground layer patterns of diversity; 2) post-fire species attrition where patterns of tree density are inversely related to ground layer diversity; and 3) null attrition model 2, where tree density (thicketization) has progressed to the stage where primarily only shade-tolerant ground layer species remain (e.g, MVF, unburned portions of BDSP). While there is potential for restoration of some aspects of habitats resembling null attrition model 2, full restoration may not be possible without species augmentation at some sites due to seed bank attrition (Bond 1984). In contrast, sites fitting null model 1 and the post-fire species attrition model merit consideration as management priority sites.

The pace of thicketization with fire absence can be attributed to edaphic resource availability (Taft et al. 1995, Peterson et al. 2007). Among the flatwoods examined here, sites fitting null attrition model 2 had the greatest AWC. Likewise, savanna habitats on deep, rich soils are particularly imperiled because they have fewer resource limitations (e.g., available moisture) compared to dry-to-xeric sites and readily convert to forests with extended fire absence (Nuzzo 1986, Anderson and Bowles 1999).

Applications of prescribed fire in oak savannas and woodlands in the prairie-forest transition zone, particularly repeated burns, consistently result in reduced tree density and increased ground layer species richness and diversity (White 1983, Taft 2003, Bowles et al. 2007). Consequently, development of the species attrition pattern where formerly absent (i.e., null model 2) would indicate successful treatment. The loss of the attrition pattern with fire management where it once occurred potentially would suggest the development of null attrition model 1.

In addition to the spatial pattern of decline among ground layer species with stand thicketization, long-term trends data at a fire-free reference barrens community (FSB) suggest that species loss can be a gradual and ongoing process. Perennial grasses and sedges showed the greatest decline with long-term fire absence at FSB. Similar patterns during long fire-free intervals can be expected in savanna and woodland habitats throughout the prairie-forest transition zone. Functional groups most affiliated with lower tree density in flatwoods, barrens, and woodland habitats in descending average rank order are: herbaceous vines, cool-season perennial grasses, perennial forbs, warm-season perennial grasses, perennial sedges, and nitrogen-fixing species. (In barrens, these species are most strongly affiliated with intermediate tree-density zones.) Herbaceous vines (e.g., crested bindweed [*Polygonum cristatum*], wild yam [*Dioscorea villosa*], small passion flower [*Passiflora lutea*], and carrion flower [*Smilax lasioneuron*]) were relatively scarce in all datasets (absent in Appendix 1, pg. 38).

Based on data summarized here, ordered disassembly (Zavaleta and Hulvey 2004) of savanna/woodland ground layer with thicketization begins with declines among perennial grasses, sedges, perennial forbs including herbaceous vines, and nitrogen-fixing species. A degree of spatial heterogeneity in stand structure contributes to overall site diversity because plant functional groups are partitioned into differentially shaded zones, for example with warm-season grasses in the most open sites and forbs most abundant in semi-shaded zones (Leach and Givnish 1999, Peterson et al. 2007). Similar results are found in the present study with lower diversity most pronounced in the high tree-density zones. Such trends can help guide interpretation of site conditions and the degree of needed restoration for recovery of ground layer diversity.

The soil seed bank is an important refuge for ground layer diversity (Taft 2003), particularly where there is extensive habitat fragmentation. However, the abundance of viable seeds likely declines over time. Bond (1984) and Bond and van Wilgen (1996) described a post-fire seed attrition hypothesis that predicts seed availability following fire would decline in the seed bank depending on the time frame for action by seed predators, decay, and disease. The restoration of sedges at MVF but not grasses or legumes (Taft 2005) and the recovery of C3 grasses but not C4 grasses at GCB (Taft 2003) suggest some species and functional groups may not persist in the seed bank for extended periods.

The question has been raised as to whether it is too late to restore oak communities in the eastern United States using prescribed fire except on the driest sites (Abrams 2005). While there remain opportunities for restoring woodland and savanna-like habitats in the prairie-forest transition zone, particularly remnants on dry to xeric sites, spatial and long-term trends in these communities suggest at least structural and in some cases compositional instability in the overstory. In addition, ground layer diversity continually declines during long periods of fire absence. In a highly fragmented landscape such as the Midwest, where species immigration opportunities are limited, the time frame for restoring the full compliment of species and plant functional groups in ground layer vegetation of oak woodland and savanna-like habitats appears to be limited.

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APPENDIX 1

Dominant species examined for this study from flatwoods, barrens, and woodland habitats in Illinois. The dominant species are the top ranking 10, 15, and 50 species from canopy, shrub/sapling, and ground cover strata, respectively, from combined lists for all three habitats. Summary values for each stratum and habitat are shown. IV 200 is sum of two relative values (e.g., basal area and density for trees). FG = Functional Group, af = annual forb, pf = perennial forb, pg C3 = perennial grass (cool season), pg C4 = perennial grass (warm season), ps = perennial sedge. * = nonnative species.

	FLATWOODS	BARRENS	WOODLAND	
CANOPY STRATUM				
- Top 10 ranking species	IV 200	IV 200	IV 200	
Quercus stellata	114.8	109.9	13.5	
Ulmus rubra	3.0	-	41.3	
Ulmus alata	-	35.5	-	
Quercus velutina	14.9	0.3	20.0	
Carya ovata	10.9	4.4	16.5	
Quercus alba	5.9	0.6	23.2	
Quercus marilandica	17.3	6.9	-	
Celtis occidentalis	-	-	24.2	
Carya texana	2.5	15.1	-	
Carya glabra	0.6	14.6	-	
% of IV	**85.0**	**93.7**	**69.4**	
Summary Data				
Tree Density/ha	464.0	975.0	796.0	
Basal Area (m^2/ha)	23.1	18.1	25.8	
SHRUB/SAPLING STRATUM				
-Top 15 ranking species	IV 200	IV 200	IV 200	
Ulmus alata	-	44.7	-	
Ulmus rubra	7.0	-	30.4	
Rubus allegheiensis/pen.	29.6	-	0.5	
Sassafras albidum	20.4	-	8.1	
Quercus stellata	7.8	17.8	-	
Carya ovata	13.3	7.2	3.7	
Prunus serotina	15.5	4.6	3.8	
Fraxinus americana	2.9	10.3	9.9	
*Rosa multiflora**	2.0	-	20.4	
Quercus velutina	11.1	10.6	0.3	
Celtis occidentalis	2.5	-	19.5	
Carya texana	7.1	13.6	-	
Symphoricarpos orbiculatus	-	13.7	7.0	
*Lonicera maackii**	-	-	16.9	
Quercus marilandica	9.5	5.2	-	
% of IV	**64.3**	**63.8**	**60.2**	
Summary Data				
Shrub/Sapling Density/ha	4,004	5,323	14,196	
GROUND LAYER SPECIES				
- Top 50 species, combined habitats	IV 200	IV 200	IV 200	FG
Acalypha gracilens	2.19	3.52	-	af
Impatiens capensis	-	-	4.13	af
Pilea pumila	-	-	2.52	af

continued

Appendix 1 continued

	FLATWOODS	BARRENS	WOODLAND	
Asplenium platyneuron	-	3.21	-	fern
Helianthus divaricatus	18.39	15.12	-	pf
Sanicula odorata	-	-	22.98	pf
Eupatorium rugosum	-	-	8.49	pf
Circaea lutetiana	-	-	6.59	pf
Helianthus strumosus	-	-	5.17	pf
Polygonum virginicum	-	-	3.63	pf
Galium pilosum	-	3.50	-	pf
Antennaria plantaginifolia	-	3.41	-	pf
Geum canadense	-	-	3.37	pf
Parthenium integrifolium	3.10	-	-	pf
Viola sororia	-	-	3.08	pf
Phryma leptostachya	-	-	2.68	pf
Euphorbia corollata	-	2.40	-	pf
Solidago ulmifolia	-	-	2.25	pf
Smilacina racemosa	-	-	2.14	pf
Danthonia spicata	1.51	34.01	-	pg C3
Dichanthelium laxiflorum	-	16.39	-	pg C3
Cinna arundinacea	9.83	-	-	pg C3
Agrostis scabra	7.86	-	-	pg C3
Dichanthelium acuminatum	7.84	-	-	pg C3
Dichanthelium boscii	-	4.74	-	pg C3
Dichanthelium linearifolium	-	3.57	-	pg C3
Festuca obtusa	-	-	2.66	pg C3
Bromus pubescens	-	-	2.06	pg C3
Schizachyrium scoparium	-	21.19	-	pg C4
Sorghastrum nutans	-	3.26	-	pg C4
Andropogon gerardii	-	2.65	-	pg C4
Carex artitecta	-	12.71	-	ps
Carex pensylvanica	9.69	-	-	ps
Eleocharis verrucosa	6.76	-	-	ps
Carex festucacea	6.26	-	-	ps
Carex hirsutella	4.99	-	-	ps
Carex blanda	-	-	2.36	ps
Carex radiata	-	-	1.92	ps
Rubus allegheniensis	13.59	-	-	shrub
Rubus flagellaris	7.53	-	-	shrub
Rosa carolina	-	2.63	-	shrub
Ulmus rubra	-	-	11.10	tree
Quercus stellata	3.65	1.82	-	tree
Sassafras albidum	4.45	-	-	tree
Celtis occidentalis	-	-	3.33	tree
Cercis canadensis	-	-	1.99	tree
Parthenocissus quinquefolia	30.60	12.57	24.54	w vine
Toxicodendron radicans	5.04	1.55	2.17	w vine
Vitis riparia	-	-	2.86	w vine
Smilax hispida	-	-	2.14	w vine
% of IV	**71.64**	**74.13**	**61.12**	
Summary Data				
Species Density (1/4-m^2 quadrat)	2.79	4.65	6.51	
Species Diversity (H')	2.33	2.67	2.02	