Effects of Fire on Invasion and Community Structure of a Southern Indiana Cedar Barrens

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Introduction

Cedar barrens and glades are floristically related forest openings that occur on shallow soil over bedrock (often limestone) and support species adapted to extremes of light, temperature, and moisture (12). These areas are significant floristically and ecologically because they support species (some rare) of varying geographical distributions in unusual combinations.

In Indiana both glades and barrens occur on south-, southwest-, or west-facing slopes (1,4). When underlain by very shallow, azonal soils these areas are usually termed glades (9). They are generally incapable of supporting woody vegetation except in bedrock crevices where eastern redcedar (*Juniperus virginiana*) establishes (5). Although cedar is the most abundant woody species, prairie grasses and forbs dominate the openings. Areas with soil deep enough to allow substantial establishment of cedar are termed barrens (7) and often require fire to prevent tree invasion.

Fire suppression and cultivation have reduced Indiana barrens and glades to remnants (4), thereby causing some species to form small, disjunct populations. Continued fire suppression and subsequent forest encroachment could cause Indiana barrens and glades to disappear, resulting in extirpation of many species with restricted distributions. Little, however, is known about how forest closure is affecting glade species distribution and abundance, or how to manage and preserve the glade and barrens habitat.

Barrens and glades are distributed throughout the Central Basin of Tennessee (12, 34), the Big Barrens region of Kentucky (8), the east-central and southwestern Missouri Ozarks (11, 22), and northward across the Ohio River into the southern portions of Illinois (23, 26), Indiana (1, 4, 19, 21), and Ohio (40). Extensive presettlement grasslands, related to Indiana barrens, existed on limestone karst topography in the Big Barrens region of Kentucky (8). After settlement there, fire suppression caused a rapid shift to forest vegetation. Although little is known about Indiana barrens relative to their southern counterparts, it is thought that presettlement barrens in Indiana were also widespread, and that the same process of forest invasion occurred here (4). Deam (10), although aware of barrens in southern Indiana, appeared to underrepresent their flora when collecting species and constructing range maps.

Recently increased attention has focused on recognizing barrens and glades of biological significance, determining the flora they support, and preserving and managing the best remnants (1, 4, 19, 21). Quantitative studies are needed to characterize processes causing barrens closure and to determine how to best manage for glade-like habitat. Specifically, the optimal fire frequency for discouraging woody vegetation encroachment and encouraging the more restricted glade species needs to be determined. This paper describes a study on the effects of forest encroachment and fire on Leavenworth Barrens Nature Preserve, a limestone cedar barrens in Crawford County, with recommendations for intermittent controlled burns to maintain the site for barrens habitat.

Objectives

In response to the need for quantitative ecological work in Indiana cedar barrens and glade communities, Holcomb Research Institute (with partial support from the Divi-

sion of Nature Preserves, Indiana Department of Natural Resources) initiated a monitoring study in 1985 at Leavenworth Barrens Nature Preserve (LBNP). The purpose of this study was to determine management practices that will (1) maintain openness of the barrens and (2) encourage persistence of glade species. Specific objectives included:

(1) determining the effects of a spring 1985 burn on LBNP plant communities, and formulating recommendations on use of fire for preserving the integrity of cedar barrens;
(2) describing the cedar barrens community by means of multivariate analyses and by relating environmental conditions, tree species structure, and herb-layer data to each other;
(3) relating the cedar barrens at LBNP to other high-quality cedar barrens and glades in the Midwest and southeast; and
(4) establishing a permanent grid system for future monitoring studies.

Study Site

Leavenworth Barrens Nature Preserve (LBNP), in Crawford County, Indiana, is a patchwork of four units (Figure 1). The 60-acre North Unit, located about one mile north of Leavenworth (T3S, R2E, S31) in the Harrison-Crawford State Forest, was the study site for this project. The site is floristically valuable, containing several rare species including the state-endangered glade endemic *Hypericum dolabriforme*, until recently thought to be extirpated from Indiana (1,3).

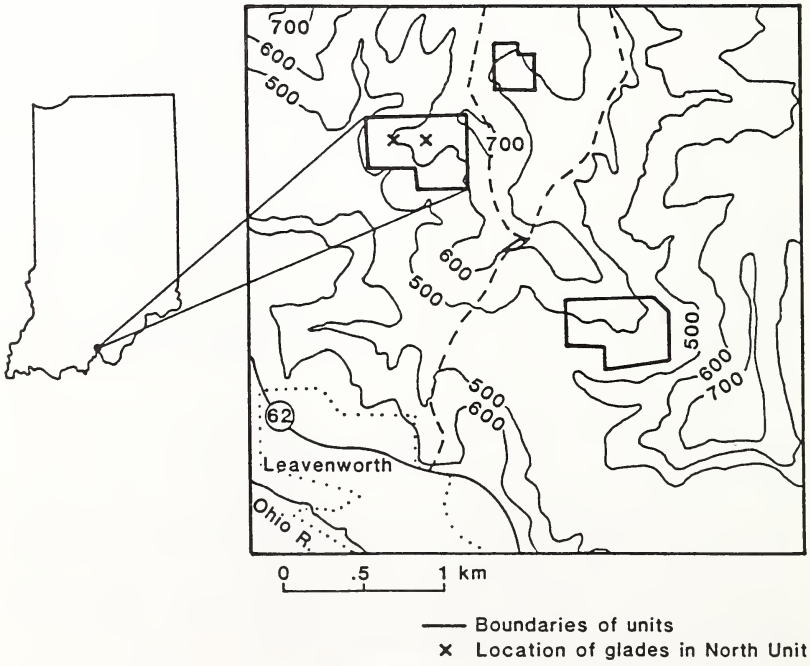

FIGURE 1. Location of Leavenworth Barrens Nature Preserve (LBNP) in Crawford County near the Ohio River in southern Indiana. This report details research in and around two glade-like openings (marked by x's) in the North Unit.

LBNP is one of a few Indiana barrens found in the Crawford Upland Physiographic Province (4); most presettlement barrens in the state are farther east in the Mitchell Plain (21). The LBNP substrate is Wellston silt loam (6-18 percent slopes), a well-drained soil formed from sandstone and siltstone and underlain by alternating layers of Mississippian shale, sandstone, and limestone (25,39). Wellston silt loams often support oak-hickory forest (24). At LBNP, outcroppings of limestone and shallow soil favor communities dominated by herbaceous plants. Soils of the Wellston series are usually about 130 cm deep (39); soil depth at LBNP was generally greater than 30 cm.

The North unit contains two openings (termed "glades" in this paper), located on and either side of an old logging road on a southwest-sloping ridge, that grade to closed glade, open woods, and closed woods (Figure 1). The east and west glades—currently a little over 1 ha and 2 ha, respectively—have decreased in size because of woody encroachment (4). To prevent further closure of the openings and encourage persistence of glade flora, the Indiana Department of Natural Resources burned portions of both openings in March 1985.

Methods

Surveying

We constructed a 25 m × 25 m grid system in the North Unit of LBNP in 1985 using a transit, stadia rod, and measuring tape. Permanent metal rebars and associated wooden stakes marked the 75 grid points (Figure 2). The grid is rectilinear on a plane

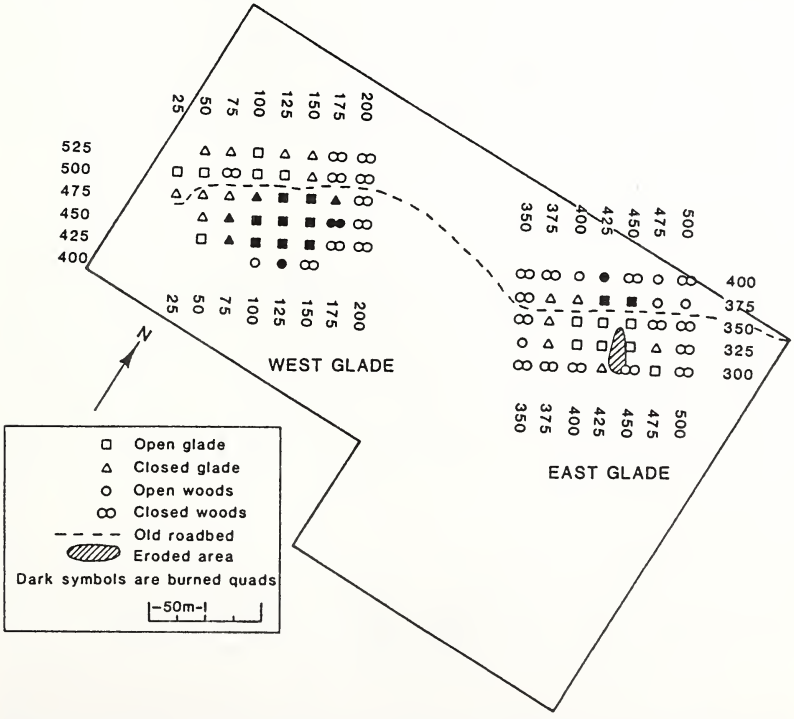

FIGURE 2. LBNP grid map showing eroded area, old logging road, and cover types at each grid point.

projection because the surveying incorporated corrections for slope. The grid, located relative to the Nature Preserve concrete marker at the northeast corner of the unit and the road leading into the openings, is rotated about 30 degrees from cardinal direction in order to follow the major ridge where the open glades are located.

Community Sampling

An initial species reconnaissance was undertaken on July 2-3, 1985. We sampled the plant community extensively on three trips to LBNP: July 8-10 (trees, shrubs, herbs, cover type), August 26-28 (herbs), and October 9-10 (late-flowering herbs). The species and diameter at breast height (dbh) were recorded for all woody stems $\geq$ 2.5 cm dbh occurring in a 100 m^2 circular plot (radius = 5.64 m) centered on each grid point. (This information is referred to as tree data). Percent cover, designated as cover class [0-1% (1), 1-7% (2), 7-25% (3), 25-50% (4), 50-75% (5), 75-93% (6), 93-100% (7)], was recorded for all herb and woody species with stems < 2.5 cm dbh in 10 m^2 circular plots (radius = 1.78 m) centered on the grid points (herb-layer data). Maximum cover achieved by each species was used in subsequent analyses.

Species difficult to identify were marked on the July trip for future identification. We collected plant vouchers for 110 species, largely grasses, legumes, and composites. Nomenclature for species identification follows Gleason and Cronquist (16), while Gleason (15), Gleason and Cronquist (16), and Graves (17) were used for keying. All vouchers were compared with specimens in the Friesner Herbarium at Butler University.

We also recorded cover type at each grid point and approximated borders of cover types between grid points. Cover types were unburned open glade and burned open glade ($\leq$ 25% canopy), unburned and burned closed glade (between 25% and 50% canopy), burned and unburned open woods (between 50% and 75% canopy), and closed woods (> 75% canopy). Closed glade and open woods intergraded but closed glades had more vertical layers (e.g., more shrubs) than did open woods, and cedar was more dense than in open glades.

Soil Sampling

Surface soil samples were collected from each grid point on August 26-28, 1985. The samples were analyzed for pH with a Fisher portable pH meter and a combination electrode in a solution of soil and 0.01 M $CaCl_2$ (36). For analysis of 11 elements (P, K, Ca, Mg, B, Mn, Fe, Cu, Zn, S, Al), samples from similar cover types were combined into 15 composite samples. These samples were sent to the Feed and Fertilizer Laboratory, Louisiana State University (Baton Rouge) where they were wet-ashed with perchloric and nitric acids for elemental analysis. Total, P, B, and S were determined with Technicon Autoanalyzers; samples were analyzed for K with a flame photometer; an atomic absorption spectrophotometer was used for determination of levels of total Ca, Mg, Mn, Fe, Cu, Zn, and Al.

Analytical Methods

Data were analyzed on the Butler University VAX-VMS system with @ORD (27) and SPSS-X (37) software. Multivariate analyses were applied to the community data (using @ORD) to classify and ordinate samples and species, as follows.

We used DECORANA (detrended correspondence analysis) to order quadrats by their dissimilarity in species composition (based on herb-layer cover class), and to order species by their dissimilarity in distribution over quadrats. DECORANA is an ordination technique that is generally successful in removing the arch distortion characteristic of some other ordination methods (13,18). Overlays of environmental data (cover type,

soil data, tree basal area, tree density, and elevation) and correlations of environmental data with ordination axis scores facilitated interpretation of ordination results.

TWINSPAN (two-way indicator species analysis), a polythetic divisive technique (13,14), classified quadrats into various groups according to indicator species (species that best separate groups of quadrats). Further divisions on each subgroup produced smaller subgroups.

Discriminant analysis distinguished burned and unburned glades according to linear combinations of species abundance (38), thus maximizing distances between these two discrete cover types. Diversity was measured by species richness and evenness (33).

Results and Discussion

Flora of Leavenworth Barrens Nature Preserve

Two striking floristic features of LBNP are its diversity and its high proportion of native species. With 162 vascular species sampled (plus three fruticose lichens), LBNP has more species than are reported from most other glades and barrens. For example, Baskin and Baskin (7) reported 148 herbaceous vascular plants from five cedar glades in the Big Barrens region of Kentucky; however, the largest number in any single glade was 79 compared to the 107 herbaceous species at LBNP. Out of 313 plots in 10 cedar glades of central Tennessee, Pearsall et al. (32) found 140 taxa. Quarterman (34) found a comparable number of species (166) when she sampled 22 glades. (She also found 191 species in glade woods.) Although our rather large species list may reflect inclusion of several cover types and sampling of a large total area (750 m^2) at one site, high diversity may also be an inherent property of LBNP and one indication of its value as a natural area. Of the 107 herbs at LBNP, over 80% are native perennials. Only 4-6 species (depending on interpretation) have been introduced, or only about 3% of the flora, confirming LBNP as a high-quality site. Blue Licks, a cedar glade in Battlefield State Park, Kentucky, is comparable to LBNP, having six introduced taxa (9). Other representations of introduced taxa in Kentucky glades are somewhat higher, ranging from 13% to 25% (5,7,20).

The 162 vascular plant taxa represent 101 genera and 48 families. Compositae have the greatest number of representatives (34 species), followed by Gramineae (15 species), Leguminosae (15 species), and Rosaceae (10 species). Over two-thirds of the flora are herbaceous (107 taxa), representing 31 families. Most characteristic glade species were found largely in open and closed glade cover types.

LBNP vegetation has distinct affinities to cedar glades outside Indiana. Of 155 taxa that appeared in sampling quadrats at LBNP, 67 species (43.2%) were listed as constituents of two or more cedar glades in Missouri (11,22), Illinois (23,26), Tennessee (6,31,32), and Kentucky (5,7,9,20); and 36 species (23.2%) were listed in four or more of these studies. *Hypericum dolabriforme* represents the only cedar glade endemic found at LBNP (6) and is one of 10 species rare to Indiana that may be found at LBNP (Table 1).

Herb species quadrats supported between 6 and 38 species, averaging 20.4 species per 10 m^2 area. Species richness was greater in glades (11-38 species, mean 24.5) than in woods (6-26 species, mean 15.2); this difference was highly significant ($t = 7.16$, $p < 0.001$). However, evenness was similar among glades and woods. Among glades, closed glades had greater species richness (28.3 vs. 21.4, $t = 3.83$, $p < 0.001$) and greater evenness ($p < 0.001$) than open glades. In comparisons of burned vs. unburned open glades and open vs. closed woods, no differences were evident in either diversity measure.

TABLE 1. Rare species at LBNP.

Species	Status in Indiana*
Aster oblongifolius	Endangered
Galactia volubilis var. *mississippiensis*	Endangered
Hypericum dolabriforme	Endangered‡
Liatris squarrosa	Rare
Linum sulcatum	Endangered**
Pinus virginiana	Rare‡‡
Rudbeckia fulgida	Endangered**
Sisyrinchium angustifolium	Endangered**
Spiranthes tuberosa	Endangered
Zizia aptera	Endangered**

* After Bacone and Hedge (3), updated by Indiana Division of Nature Preserves.
** Not seen or sampled in 1986.
‡ Status changed from extirpated to endangered after rediscovery (1).
‡‡ Probably planted at LBNP.

Ordinations of the Herb-layer Vegetation

Herb-layer species at LBNP appeared to be distributed largely in response to the degree of openness of their habitat. A cover-type overlay on a DECORANA ordination shows that the first axis of variation (with eigenvalue = 0.416) clearly separated quadrats in closed woods from quadrats in open glades (Figure 3). Both closed glade and open

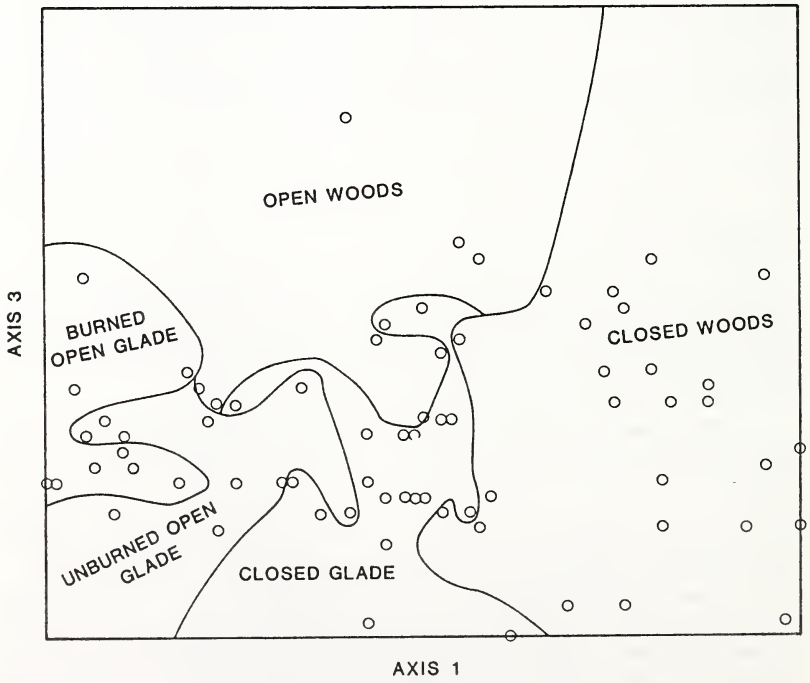

FIGURE 3. DECORANA ordination of herb species found in five or more quadrats at LBNP. Circles show location of quadrats in ordination space defined by axes 1 and 3. Lines separate different cover types.

woods cover types occupied intermediate locations on the first and second axes, but were clearly distinct on axis 3 (Figure 3).

Herb species composition was influenced primarily by the amount of woody cover and the relative dominance of *Juniperus virginiana*. Tree basal area varied strongly and monotonically along axis 1 of the herb ordination ($r = 0.74$, $p < 0.001$). *J. virginiana* relative dominance varied inversely ($r = 0.68$, $p < 0.001$) so that all areas with greater than 80% *J. virginiana* dominance were placed on the left 60% of this ordination.

Closed woods appeared to form an especially distinct group clearly differing from open woods and all types of glades. Species placement on DECORANA ordinations suggests that at LBNP a few woody species were characteristic of the herbaceous stratum in closed woods, as compared to glade species. Particularly associated with closed woods were the understory shrub *Symphoricarpos orbiculatus*, the understory herb *Polygonatum biflorum*, the vines *Rhus radicans*, *Dioscorea quaternata*, and *Parthenocissus quinquefolia*, and several tree species present in the herb layer of closed forests (*Celtis occidentalis*, *Cercis canadensis*, *Acer saccharum*, *Ostrya virginiana*, *Carya glabra*, and *Prunus serotina*). All species listed above were placed on the right 30% of the DECORANA first axis.

Herb species composition differed between glade areas burned in the spring of 1985 and unburned areas. Quadrats separated partially along the first axis of DECORANA ordinations, with some additional distinctions along subsequent axes (Figure 3). Burned quadrats were less similar to other areas of LBNP than were unburned areas, which occupied an intermediate position on axis 1, suggesting that burning has favored open conditions. Species on the extreme left of axis 1, suggesting an association with burning, included *Sorghastrum nutans*, *Solidago rigida*, *Liatris spicata*, *Polygala ambigua*, and *Desmodium rigidum*. *L. spicata* does not appear harmed by fire, which increases its success in burned areas (28,30).

In terms of herb species composition, quadrats typed as closed glade and open woods represented intermediates. Ordinations did not separate these two cover types until the third axis (eigenvalue = 0.168) (Figure 3), suggesting fairly subtle differences between them. Open woods were characterized by *Lespedeza intermedia*, *L. procumbens*, *Stylosanthes biflora*, and *Helianthus divaricatus*, while closed glades included *Geum virginianum*, *Scutellaria incana*, and *Oxalis stricta*.

Quadrat location was closely related to scores on the second DECORANA axis (eigenvalue = 0.201). Quadrats located in the eastern part of the gridded area tended to be located above the western quadrats on axis 2 (Figure 4). The separation was clearer in glades (open and closed) and open woods than in closed woods. Eastern quadrats were located farther uphill; elevation, therefore, showed a strong relationship with axis 2 ($r = 0.51$, $p < 0.001$).

These ordination patterns may also reflect environmental variables other than woody vegetation cover and burning (29). Other ordinations revealed that surface soil pH varied significantly with axis 2 ($r = 0.32$, $p < 0.001$) as did the concentrations of seven elements (P, Fe, Ca, K, Mg, B, and S). The heterogeneity of east and west glades may therefore be exerting some influence on soil chemistry. The third axis pattern of closed glade vs. open woods also reflects soil pH ($r = -0.50$, $p < 0.001$); from closed glade to open woods, pH changes from over 7 to less than 4.5. Lower soil pH can be expected in open woods areas where tannins from oak leaves tend to acidify the soil. The relationship of other environmental variables (aspect, slope angle, soil texture, and other drainage factors) to ordination patterns may be significant enough to merit further exploration.

Classifications of the Herb-layer Vegetation

Classification of herbaceous communities at LBNP confirms ordination results and provides additional insights into environmental influences and species groups. Two-way

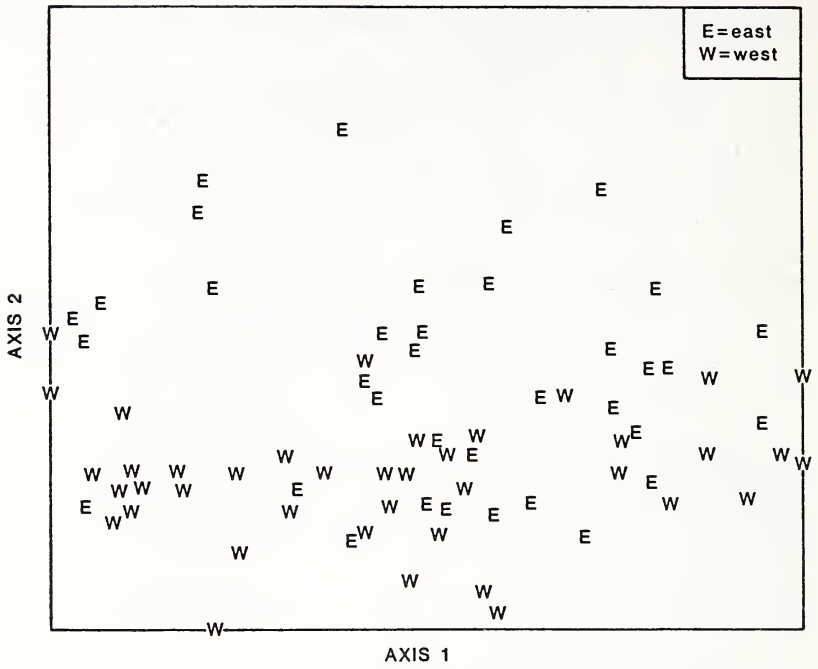

FIGURE 4. Overlay of quadrat location (east or west glade) onto first and second axes of DECORANA ordination of herb data.

indicator species analysis (TWINSPAN), which clusters groups of both samples and species, was used.

The initial TWINSPAN division separated nearly all woods quadrats (open and closed) from all open glade quadrats. Closed glade quadrats were placed on both sides of this initial division. Legumes were a conspicuous component of open glades at LBNP; two legumes indicated open glades (*Cassia fasciculata* and *Strophostyles umbellata*). The initial TWINSPAN division, when plotted on the DECORANA ordination, split the first axis in two (Figure 5).

The second level of division continued to separate quadrats based on the degree of openness of the vegetation. A set of open glade quadrats characterized by the prairie grass *Sorghastrum nutans* was distinguished from a group of open and closed glade quadrats, with a *Panicum* species and *Rosa carolina* as indicators (Figure 5). Species richness was considerably higher in the latter group (19 vs. 27 per quadrat). The division was also primarily between east and west glades (see Figure 4). *S. nutans* characterized the uphill, eastern glade. Again, the east vs. west differences may have been due to unmeasured environmental differences in moisture regime.

The other level-two division separated closed woods quadrats, characterized by three vines (*Parthenocissus quinquefolia*, *Rhus radicans*, and *Dioscorea quaternata*) and an understory herb (*Viola* sp.) from more open communities indicated by *Potentilla* sp. *Danthonia spicata*, and *Vaccinium stamineum*. The latter quadrat group included several intergrading cover types. This level-two division fell primarily across the first axis of the DECORANA ordination, which summarized species response to site openness.

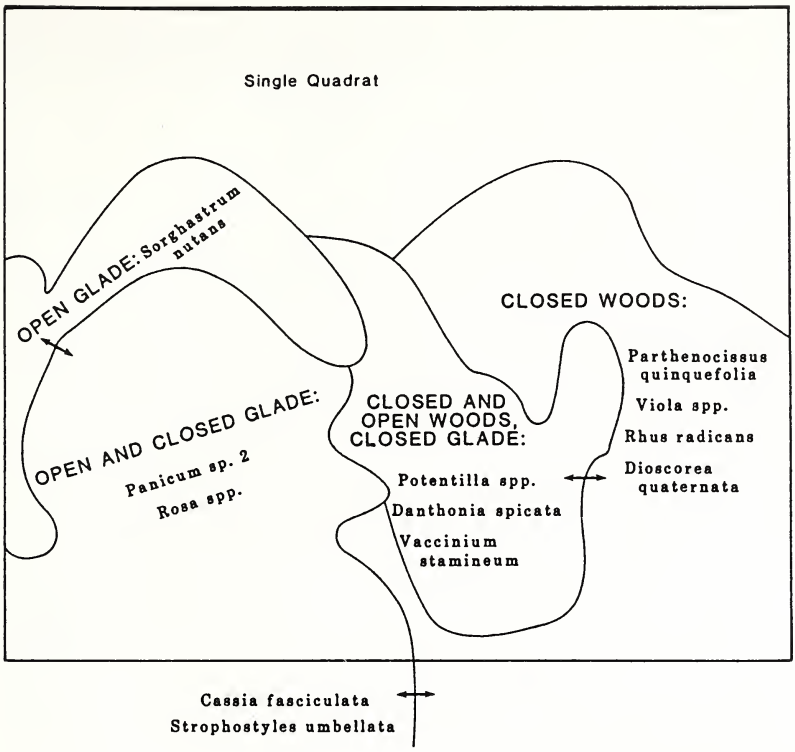

FIGURE 5. Plot of major TWINSPAN classification groups onto first two axes of DECORANA ordination of herb samples. The first division is shown at the bottom of the graph and second divisions within the ordination by arrows. Indicator species for each division are shown.

At the third level of TWINSPAN division (Figure 6), burning became an important criterion for separation of open glades. Open glade quadrats divided into burned open glade (group A, indicator: *Liatris spicata*) and unburned open glade (group B, indicators: *Cornus florida*, *Helianthus divaricatus*), both with 19 species per quadrat. A TWINSPAN analysis on glade quadrats only (not shown) demonstrated burning effects to be second only to the degree of openness. In this second analysis, *L. spicata* and *Panicum* sp. characterized burned areas while *Sassafras albidum*, *Smilax glauca*, and *Acer rubrum* characterized unburned areas.

Another level-three division separated the mixed open glade/closed glade group into open glade (group C: *Liatris spicata*, *Lespedeza virginica*, 24 species per quadrat) vs. more diverse closed glade (group D: *Rhamnus caroliniana*, *Cornus florida*, *Rhus copallina*, 29 species per quadrat) (Figure 6). *C. florida* was the key indicator of closed glade in analyses excluding woods quadrats also (not shown). The significance of woody species in the herb layer suggests that woody plant invasion, turning open glade into closed glade, has important effects on herb species composition in general.

Woody species were also important indicators of an herb species division within closed woods (Figure 6). *Acer saccharum* indicated a group of quadrats (G) with low species richness (15 per quadrat), while *Fagus grandifolia* and three other species

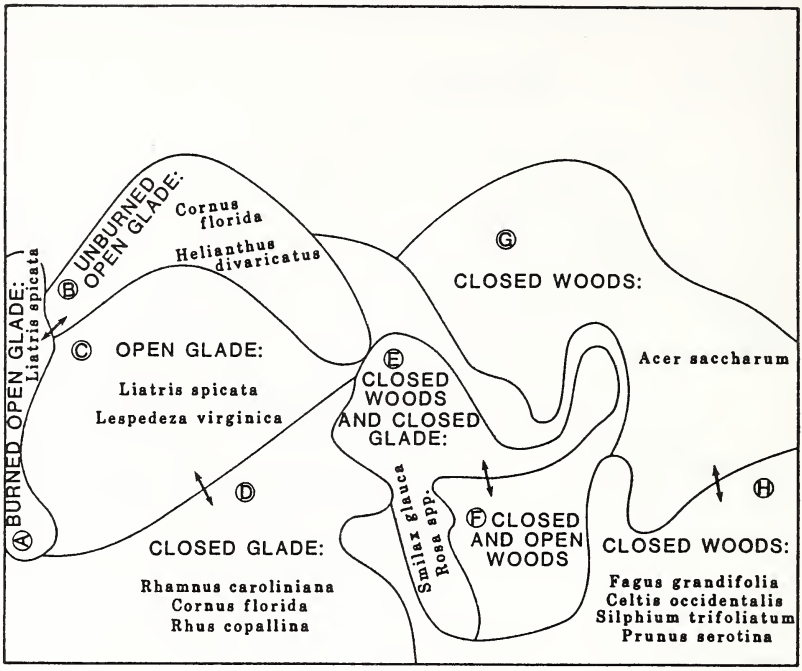

FIGURE 6. Plot of less major TWINSPAN classification groups onto first two axes of DECORANA ordination of herb samples. The third level of division is shown, with indicator species for each division.

characterized another group (H) with higher species richness (20 species per quadrat) than G. Finally, another third-level division separated closed glade (E) from open woods (F) quadrats.

Effects of Fire

We separated burned and unburned glade quadrats (all glades or just open glades), using discriminant analysis (not shown). Perfect classification was possible with knowledge of scores from 12-20 species, depending on the analysis. Fifteen herbs showed a preference for burning in a t-test ($p < 0.1$), seven of which were species with glade affinities. Several of the plants at LBNP (*Andropogon gerardi*, *Cassia fasciculata*, *Gaura biennis*, *Rudbeckia hirta*) also showed a positive response to fire in a southern Illinois barrens (2), where they either increased markedly in frequency after burning or had high frequency values (> 20%) in a burned area. LBNP glade elements exhibited slightly more of a preference for burning than did the prairie elements, but neither group showed a preference significantly greater than did herbs in general (Table 2). Although most herbs at LBNP (83.7% of the glade species and 85.0% of all woody species) showed no substantial preference for areas burned in 1985, the ten species typical of glades, barrens, and prairies that showed a preference were significantly more abundant in burned quadrats. Initial findings thus indicate a positive response to fire for some species typical of open habitats. Other glade and prairie plants may require more than a growing season to establish themselves in previously burned areas. Follow-up community sampling may reveal higher frequencies or greater abundance of glade and prairie species in burned open glades.

TABLE 2. Summary of herbaceous glade, herbaceous prairie, and woody species at LBNP, showing preference for burned and unburned environments.[1]

	No. Glade[2] Species	No. Nonglade Species	
Preference for Burned Areas	7	6	$x^2 = 2.02$ d.f. = 1 $p < 0.25$
Preference for Unburned Areas	0	2	
	No. Prairie[3] Species	No. Nonprairie Species	
Preference for Burned Areas	7	6	$x^2 = 0.010$ d.f. = 1 $p > 0.9$
Preference for Unburned Areas	1	1	
	No. Woody Species	No. Nonwoody Species	
Preference for Burned Areas	2	13	$x^2 = 9.97$ d.f. = 1 $p < 0.005$
Preference for Unburned Areas	7	2	

[1] Preference is significant using t-test, $p < 0.1$.
[2] Based on (5,6,7,9,11,20,22,23,26,31,32).
[3] Based on (8,35).

Intermittent fires may arrest invasion of woody species while at the same time allowing for establishment of glade species in the areas opened up. Additional studies should provide a suitable framework for determining the optimal fire frequency.

Some woody species (e.g., *Cornus florida*, *Juniperus virginiana*, and *Quercus alba*) were excluded by fire (Table 2). *J. virginiana* was particularly affected by the 1985 burn; we observed 14 dead tree-sized individuals in burned glade quadrats vs. three in unburned quadrats. Dead/alive ratios were highest for the smallest size classes of *J. virginiana*—i.e., those most vulnerable to fire. In a southern Illinois barrens (2), prescribed burning also decreased the abundance of *J. virginiana* and other tree species.

In time, lack of periodic burning may allow complete closure of the glades by mixed hardwood forest. In TWINSPAN analyses (Figure 6), *Cornus florida* is an indicator species for unburned open glades (vs. burned open glades)—and all indicator species for a group of closed glades are small, invading tree species. Classification of tree-sized individuals, based on relativized basal area (29), generated groups of closed glade quadrats with invading hardwoods (*C. florida* and *Sassafras albidum*) and woods quadrats characterized by canopy hardwoods (*Quercus spp.*, *Liriodendron tulipifera*, *Carya glabra*). Open glades in this classification contained only *J. virginiana* and *Pinus virginiana* as woody indicator species. Woods and closed glades also had greater tree species diversity than open glades (29). Other evidence for invasion into glades includes shifts to larger size classes for tree species found in both glades and woods.

Progressive invasion of open glades at LBNP parallels the successional processes that Quarterman (34) hypothesized for Tennessee cedar glades. Unlike the deeper-soil LBNP, Tennessee glades feature large rock outcrops that prevent complete canopy closure. LBNP is ecologically similar to the Big Barrens region of Kentucky (8) and southern

Illinois barrens (2), both of which contained large open areas only during a history of repeated burning. In the absence of controlled burning, these characteristics may make LBNP vulnerable to rapid and complete forest closure.

Summary

A floristic and community summary of Leavenworth Barrens Nature Preserve, a northern example of a limestone cedar barrens, shows high floristic diversity including rare species with high affinities to more southerly limestone glades. Comparisons with other cedar glades support the assessment of LBNP as a high-quality natural area.

Ordination and classification of one-year herb-layer abundance values reveal that composition of the herbaceous community is strongly related to the degree of shading by woody species. Plants most typical of glades, barrens, and prairies occur in the most open habitat. While forested portions of LBNP add to its overall diversity, woody encroachment into open glade-like areas excludes species most typical of cedar glades.

Initial findings indicate that controlled burning is a useful tool for maintaining barrens habitat. At least ten herbaceous glade and prairie species were significantly more abundant in burned quadrats than in unburned areas, while fire discouraged or excluded some woody species. Without controlled burns, progressive forest invasion may completely close the glade-like openings of LBNP. While fire is important to the integrity of the site, the optimal frequency and timing necessary to favor particular elements remain to be investigated.

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