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Soil Properties and Soil Nitrogen Dynamics of Prairie-like Forest Openings and Surrounding Forests in Kentucky's Knobs Region

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ABSTRACT.—Herbaceous communities located within forest openings increase plant species diversity of forests in the Knobs Region of Kentucky. Although these grass-dominated communities are protected and managed for rare plant species conservation, it is unclear how soil conditions may delineate the grassland-forest boundary. We compared soil chemical and physical properties and soil nitrogen pools and transformations of three forest openings with those in the surrounding forest and the wooded edge separating the grassland and forest communities. Soil pH, extractable cations, bulk density and silt content were higher in openings compared to forest soils and extractable phosphorus was lower. In forest-opening grasslands, total soil nitrogen and the availability and production of plant-available N were 25 to 50% of levels in adjacent forest. Soils of the woody edge were similar to the surrounding forest. Our results suggest that the presence of these calcareous glade openings is highly correlated with edaphic conditions, so that efforts to expand rare plant habitat may be constrained by the distinct soils of these forest openings.

INTRODUCTION

Isolated herbaceous communities situated within forest openings are an important component of plant diversity in the eastern deciduous forests of North America (Quartermann *et al.*, 1993; Anderson *et al.*, 1999). These openings have various possible origins. They can be stable, spatially-discrete communities whose extent is controlled by edaphic conditions, successional communities originating from natural disturbance or human land use practices or communities resulting from the combination of preexisting edaphic conditions that are further modified by canopy or soil disturbance (Baskin *et al.*, 1994). Within Kentucky, forest-opening communities are a conservation concern because they contain locally rare plant species threatened by land conversion, land degradation and woody plant encroachment. Statewide, 51 species of state or federally threatened plant

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species are found within such openings (Kentucky State Nature Preserves Commission, 1996).

Although unique soil conditions may control the extent and composition of some forest-opening communities (Anderson *et al.*, 1999), the focus of most studies in these communities has been floristic (Baskin and Baskin, 1973, 1975, 1978). Major difference in soils of the opening and the forest could have a strong influence on the extent and successional trajectory of forest opening communities. If edaphic conditions control the location and extent of forest openings, the border between the herbaceous and forest community should be relatively stable, corresponding to a relatively abrupt change in parent material type or profile depth and associated changes in soil chemical and physical properties (Kalisz and Boettcher, 1990). In contrast, where the openings are formed by forest canopy disturbance, woody vegetation should readily reinvade herbaceous communities following fire, drought, wind damage or other perturbations. In such cases, biotically mediated soil processes (*i.e.*, nitrogen turnover, nutrient uptake and organic matter stabilization) will shift with species composition and litter inputs across the forest to grassland ecotone (Jenny, 1980; Daniels *et al.*, 1983; Rhoades and Coleman, 1999; Rhoades *et al.*, 2000).

Where fire suppression or other land conversion has resulted in woody plant encroachment into forest openings, forest-opening communities may expand relatively rapidly following mechanical felling of trees growing at the periphery of these openings. In contrast, where the boundary between herb-dominated forest openings and the adjacent forest corresponds to abrupt parent material transition (Kalisz and Boettcher, 1990; Boettcher and Kalisz, 1991), forest clearing may not be sufficient to promote expansion of the herbaceous species associations. In either case, without consideration of the linkage between vegetation communities and chemical or physical soil factors, efforts intended to favor expansion of unique plant species into newly cleared or expanded openings may fail.

The overall objective of this study was to compare soil chemical and physical properties and soil nitrogen dynamics across the ecotone between forest openings and adjacent forest. Large differences in soil chemical conditions between the openings and surrounding forest may provide insight regarding the historic extent of the herbaceous communities and, thus, help delineate vegetation management activities aimed at maintaining or expanding the glade openings.

METHODS

Site description.—We studied a group of three forest openings located in Kentucky's Knobs Region on the western border of the Bluegrass section of the Interior Low Plateaus Physiographic Province (Quarterman *et al.*, 1993; Fig. 1). The study site is located at the Bernheim Arboretum and Research Forest, in the southern extreme of Bullitt County (37°52'N; 85°35'W) near its border with Nelson County. The openings are on south-facing slopes associated with calcareous shale interbedded with dolomite of the Silurian lower Laurel formation (Kepferle, 1969). The series of openings corresponds to a band of soils mapped as Caneyville-Rock outcrop or Caneyville-Beasley-Rock outcrop complexes and classified as fine, mixed mesic Typic Hapludalfs (Soil Conservation Service Staff, 1986). Together these soil groups cover about 5% of Bullitt County.

In Kentucky's Knobs Region on the "driest situations, where limestone outcrops exist," Braun (1950) described "xerophytic red cedar communities and occasional typical prairie patches" amidst the surrounding deciduous forest. Such openings are currently classified as either limestone glades (Evans, 1991) or xeric limestone prairies (Baskin *et al.*, 1994). At the Bernheim forest, "glade" openings were noted on land deed boundaries surveyed in the

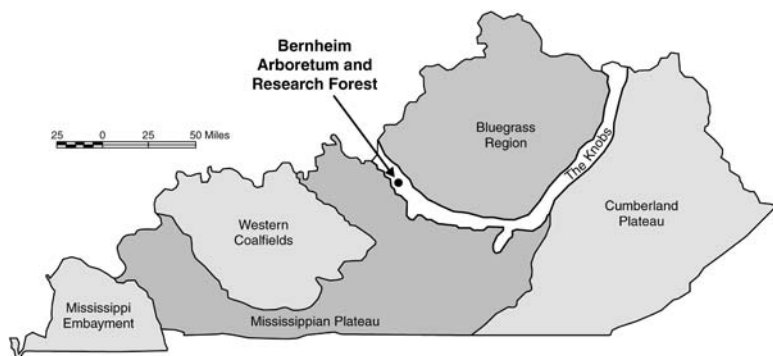


FIG. 1.—Study site location at the Bernheim Research Forest and Arboretum within Kentucky's Knobs Physiographic Region

1780s (Dickson and Kollath, 2001). The three forest openings were visible on 1928 aerial photographs. Presently, the 0.25 to 0.30 ha openings are the only herbaceous-plant-dominated hillside communities known within the 6500 ha Bernheim Research Forest.

The openings are dominated by the grasses *Schizachyrium scoparium* (Michx.) Nash and *Sporobolus vaginiflorus* Torr. and to a lesser extent by *Panicum capillare* L. and *Danthonia spicata* L. Common forbs include *Scutellaria parvula* Michx., *Lithospermum canescens* Michx., *Croton monanthogynus* Michx., *Hypericum dolabriforme* Vent. and *Echinacea simulata* McGregor. The openings also contain the state-listed threatened plants *Viola septemloba* Le Conte var. *egglesonii* (Brainerd) McKinney and *Spiranthes magnicamporum* Sheviak (Kentucky State Nature Preserves Commission, 1996).

Juniperus virginiana L. is the most abundant tree scattered within the forest openings and within both the edge and forest communities (Table 1). In addition to *J. virginiana*, the overstory community of the forest surrounding the openings is codominated by *Fraxinus americana* Marshall, *Acer saccharum* Marshall, *Quercus muehlenbergii* Engelm. and *Pinus virginiana* Miller. *Cercis canadensis* L. and *Rhamnus caroliniana* Walter. are common midstory species within all three community types.

Surface features differ between the forest openings and the surrounding habitats. Large exposures of rock are absent from the openings, whereas gravel, cobble or bare soil cover about 60% of the openings. Exposed rock and soil are absent from forest sites and cover only 13% of the wooded edge.

Study design.—Each of three sites was partitioned into the following habitat types arranged in concentric zones: (1) opening, (2) woody edge and (3) surrounding forest. The openings were round to elliptical; distance from the center of the openings to the woody edges ranged from 15 to 50 m. The woody edge formed a 5- to 10 m-wide band. Two transects originating at the opening center and radiating through the edge and into surrounding forest were located at each opening site ($n = 6$ transects). In each opening, transects were stratified into opposing halves of the opening then oriented along randomly selected radii (i.e., 1 to 180° or 181 to 360°). Along each transect, sample plots were located (1) midway between the opening center and the woody edge, (2) centered within the wooded edge and (3) 20 m beyond the edge within the surrounding forest ($n = 6$ plots per vegetation zone).

Chemical and physical soil properties.—The chemical and physical properties of opening and surrounding forest soil profiles were sampled and analyzed by depth increments extending

TABLE 1.—Density, stem diameter and basal area of tree species found within openings, edge and forest¹. Measurements from 5 m by 5 m plots (n = 12 per zone). Species listed comprise 80 to 85% of the total stem density

Vegetation zone	Density stems/ha	Mean diameter cm	Basal area m ² /ha
Opening			
<i>Juniperus virginiana</i>	315.2	10.1	2.9
<i>Rhamnus caroliniana</i>	121.2	5.3	0.4
<i>Cercis canadensis</i>	109.1	5.6	0.2
<i>Pinus virginiana</i>	60.6	16.6	1.3
Edge			
<i>Cercis canadensis</i>	606.9	6.1	2.1
<i>Juniperus virginiana</i>	400.0	12.9	6.6
<i>Quercus muehlenbergii</i>	206.9	6.3	0.8
<i>Rhamnus caroliniana</i>	165.5	5.0	0.3
<i>Pinus virginiana</i>	96.6	24.4	5.1
<i>Acer saccharum</i>	82.8	8.2	0.7
<i>Fraxinus americana</i>	82.8	5.8	0.3
Forest			
<i>Juniperus virginiana</i>	535.7	14.1	11.0
<i>Acer saccharum</i>	192.9	6.9	1.1
<i>Ostrya virginiana</i>	192.9	4.9	0.5
<i>Fraxinus americana</i>	171.4	8.5	1.4
<i>Cercis canadensis</i>	171.4	7.3	0.8
<i>Quercus muehlenbergii</i>	142.9	9.9	1.6
<i>Cornus florida</i>	142.9	7.4	0.6
<i>Diospyros virginiana</i>	64.3	10.6	0.6
<i>Pinus virginiana</i>	50.0	19.0	1.7
<i>Fagus grandifolia</i>	42.9	5.4	0.1

¹ Trees: ≥ 3 cm diameter at 1.7 m height

to rock, impenetrable clay or the maximum soil corer length (50 cm). For each opening and adjacent forest site, two cores were collected at both transect plots (n = 12 cores per habitat type) using a 5-cm diameter slide hammer corer (Giddings Co., Ft Collins, CO). Each core was divided into 10-cm increments, samples were then weighed, air-dried, sieved (2000 μ m mesh) and analyzed for pH (Thomas, 1996), Mehlich-III extractable phosphorus and cations (Mehlich, 1984) and total soil N (by LECO CHN 2000 dry combustion). For each 10-cm depth increment sample, the oven dry mass (24 hours at 105 C) of a 10 g subsample was used to calculate the bulk density of each sample layer. Soil bulk density was used to convert nutrient concentrations to area-based measurements. Soil texture was measured with the Bouyoucos hydrometer method (Gee and Bauder, 1986). The color of air-dried samples was quantified beneath a uniform indoor light source using a Munsell color book (Kollmorgen Instruments, Baltimore, MD).

Soil nitrogen dynamics.—Since no single measure consistently characterizes soil N cycling (Binkley and Hart, 1989), we assayed various components of the soil N cycle. We evaluated both rapidly changing pools of plant available N (NO_3^- and NH_4^+) and two different assays of the production of mineral N. Plant available soil nitrogen (NO_3^- and NH_4^+) and net production of these N forms were measured in March, June and October 2000. On each

collection date, two subsamples were composited from plots oriented along transects in each opening, edge, forest site ($n = 6$ composited samples per vegetation zone). Mineral soils were sampled after removing forest or grass litter. Within the opening and edge zones, samples were collected at the mid-point between individual grass clumps.

Samples of the top 10 cm of mineral soil were collected with a 5-cm diameter corer, transported within a plastic cooler, refrigerated at 4 C and processed within 48 h. An initial 10-g subsample of fresh soil was extracted with 50 ml of 1 M KCl and analyzed for NO_3^- and NH_4^+ by colorimetric spectrophotometry (Bundy and Meisinger, 1994). A second subsample was oven-dried at 105 C for 24 h to determine the gravimetric soil moisture content. A third set of 10-g subsamples was incubated for 14 d at 26 C at field capacity (Binkley and Hart, 1989). Field capacity was approximated as the gravimetric water content of a subsample wetted to saturation then allowed to drain for 12 h (gravimetric moisture content of about 50%). After 14 d, the incubated subsamples were extracted with 50 ml of 1 M KCl and analyzed as described above. Net mineralization was calculated as the change in NO_3^- plus NH_4^+ and net nitrification as the change in NO_3^- between initial and incubated extracts.

An anaerobic incubation was also conducted to complement the assay of aerobic mineralization just described (Bundy and Meisinger, 1994). This procedure estimates the net production of NH_4^+ released from readily decomposable organic matter plus the N contained within microbial biomass. A 20-g subsample of fresh soil was waterlogged with 50 ml of deionized water and incubated at 40 C for 7 d. Fifty ml of 2 M KCl extractant was added to the saturated incubations and the analysis proceeded as described above.

Soil CO_2 efflux provides an integrated index of root and microbial respiration. It was quantified during March and June 2000 using an *in situ* infrared gas analyzer fitted with a soil chamber (PP Systems, Haverhill, MA). The change in chamber CO_2 concentration during a 120-s period was used to calculate soil CO_2 efflux. The CO_2 measurement chamber was located directly on the mineral soil surface after clearing away surface detritus. The chamber was located to avoid rocks, soil cracks and grass clumps and loose soil was packed around the chamber base to seal against leaks. Two flux measurements, located 20 cm apart, were taken within each sample plot along the opening, edge, forest transects ($n = 12$ readings per vegetation zone per date). A corresponding soil temperature measurement (5-cm depth) was taken near the CO_2 chamber during each flux measurement.

Statistical analysis.—The three vegetation zones (openings, edge, forest) were compared using a mixed analysis of variance model with the vegetation zone as a fixed effect and the individual site ($n = 3$) and the zone by site interaction as random effects (SPSS Inc., Chicago, IL). Significant differences between vegetation zones means were identified using Tukey's LSD means separation test at a $P = 0.05$ significance level.

RESULTS

Chemical and physical soil properties.—Both chemical and physical soil properties differed between the openings and surrounding forest. Overall, soils in the forest openings were more alkaline and contained more calcium and less phosphorus than surrounding forests. For the upper 10 cm, forest soil pH was more than one unit lower than opening soil pH (Fig. 2a). The pH profile was relatively uniform within the upper 50 cm of forest-opening soil (range: 8.1 to 8.5); across that same depth, soil pH increased from 7.1 to 8.1 beneath forest vegetation (Fig. 2a). Extractable Ca^{2+} was four- to five-fold greater within the openings than in forest soils throughout the sample profile (Fig. 2b). Calcium increased with depth in both the openings and the surrounding forest, but the depth effect was greater within the openings. Neither Mg^{2+} nor K^+ differed between forest and opening. Extractable soil P and

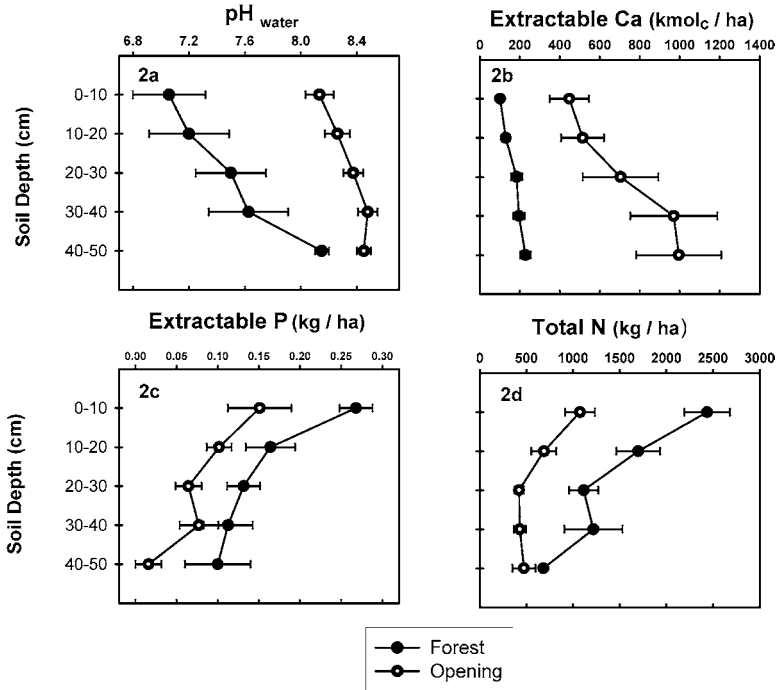


FIG. 2a–d.—Chemical properties of forest and forest-opening soil profiles. Data are means from three forest and forest-opening pairs and horizontal bars represent 1 SE of the mean ($n = 12$). Closed and open circles represent forest and forest-opening soils, respectively

total soil N stocks were both lower in openings than in forests throughout the upper 30 cm of mineral soil (Figs. 2c, d).

Soils of the forest openings were pale yellowish-brown with little indication of A horizon formation or surface organic matter accumulation (2.5 Y 4/4 mode in 0–10 cm depth). In comparison, the surface of the forest soils was much darker (10 YR 3/3 mode in 0–10 cm depth) and the color discrepancy extended to below 40-cm ($P \leq 0.02$). The bulk density of opening soils was significantly greater than that of forest soils throughout the upper 50-cm (Fig. 3a; $P \leq 0.02$). Opening soils contained more silt and less clay in the upper 10 cm (Fig. 3b; $P \leq 0.05$); the pattern was consistent throughout the upper 30 cm. Clay content increased with depth in the forest soils, but was uniform with depth in the openings. Sand content did not differ between the two habitat types.

Soil nitrogen dynamics.—Soil nitrogen pools and transformation rates also differed between the openings and surrounding forest. Forest soils consistently had more plant available N and greater production of mineral N than forest-opening soils (Table 2). Averaged across dates, extractable soil NH_4^+ and NO_3^- were nine- and two-fold higher in forests than in openings ($P \leq 0.001$ and $P \leq 0.08$, respectively). Mineralization and nitrification rates were both about twice as high in forests as in openings ($P \leq 0.001$ and $P \leq 0.01$, respectively). Anaerobic production of NH_4^+ in forest soils exceeded that in openings more than seven-fold ($P \leq 0.001$). Ammonium represented a greater proportion of the total plant available

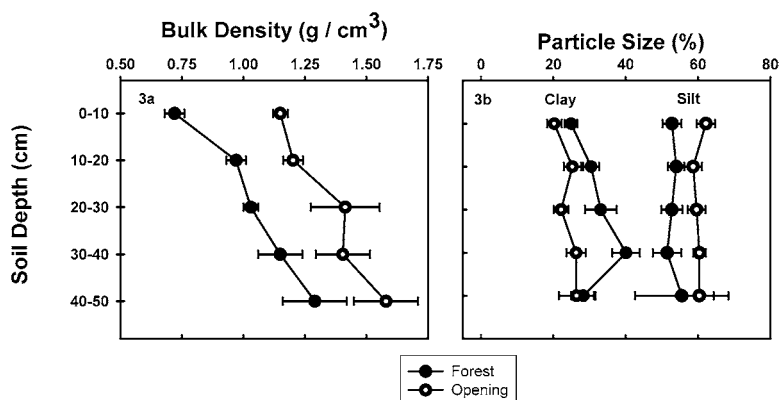


FIG. 3a–b.—Physical properties of forest and forest-opening soil profiles. Data are means from three forest and forest-opening pairs and horizontal bars represent 1 SE of the mean ($n = 12$). Closed and open circles represent forest and forest-opening soils, respectively

soil N pool in forest soil; there was twice as much extractable NH_4^+ as there was NO_3^- in forest soil. Conversely, the openings contained 2.5-fold more NO_3^- than NH_4^+ .

Edge soils were intermediate between opening and forest for all soil N parameters. Edge soils contained 65% and 80% of the levels of extractable NH_4^+ and NO_3^- , respectively, found in forest soils. Opening soil produced inorganic N at about one half the rate of forest soils, whereas soils within the edges mineralized and nitrified at more than 80% of the forest rates.

Soil C efflux was also lower in the interior of the openings compared to forest sites (Table 3). Averaged over two sample dates, soil respiration was 2.3 times greater in the forests compared to the openings ($P \leq 0.001$). Edge soils released soil C at 1.5 times the rate measured within openings ($P \leq 0.012$) and at 65% of the average forest rate. Soil temperature followed an inverse pattern, with opening soils 3.9 and 2.4 °C higher than forest and edge soils ($P \leq 0.001$ for both), respectively. Within forest openings, average soil moisture was 64% of that in the forest.

DISCUSSION

This study documents the unique nature of the soils beneath isolated forest-opening grasslands of Kentucky's Knobs Region. The forest-opening grasslands are nutrient-poor relative to neighboring forests, as well as to other North American grass-dominated ecosystems. Inorganic N pools and net N transformation rates in the forest opening averaged 25 and 50% of levels in adjacent forest. The forest openings averaged 1 μg of inorganic N/g of soil compared to about 4 μg N/g in Kansas tallgrass prairie (Blair *et al.*, 1998) and 2 μg N/g in Western Kentucky barrens grasslands (Rhoades *et al.*, 2002). Production of inorganic N in Bernheim grass-dominated openings was one-third of that mineralized in Kansas tallgrass prairie soils (Blair *et al.*, 1998).

We measured a sharp transition in physical and chemical soil properties and in biologically-mediated soil processes across the grassland to forest ecotone. An abrupt transition between sedimentary parent material types may explain the location and extent of the distinct Bernheim forest-opening communities (Birkeland, 1984; Boettcher and Kalisz,

TABLE 2.—Nitrogen availability in opening, edge and forest soils. Within columns, similar letters indicate that vegetation type averages are equal based on Tukey's means separation test [mean and (SE); n = 6 per date per zone; α = 0.05]. *F* statistic and significance levels based on ANOVA with log-transformed data

Vegetation zone	Plant available N pools ($\mu\text{g N/g}$)		Aerobic N transformations ($\mu\text{g N/g/14 d}$)		Anaerobic N index ¹ $\mu\text{g NH}_4\text{/g/7 d}$
	NH ₄ -N	NO ₃ -N	Mineralization	Nitrification	
Opening					
March	0.15 (0.1)	1.01 (0.2)	6.74 (1.0)	6.36 (1.0)	
June	0.35 (0.2)	0.10 (0.1)	0.82 (0.5)	0.97 (0.4)	
October	0.84 (0.2)	0.42 (0.1)	1.61 (0.7)	2.24 (0.7)	
Average	0.30 c (0.1)	0.76 b (0.2)	4.90 b (0.8)	4.78 b (0.8)	6.60 c (2.0)
Edge					
March	1.33 (0.3)	0.92 (0.2)	10.33 (1.2)	9.10 (1.1)	
June	1.83 (0.3)	1.28 (0.5)	2.98 (1.2)	3.50 (1.2)	
October	3.57 (0.9)	1.37 (0.4)	6.97 (2.3)	5.17 (1.6)	
Average	1.79 b (0.3)	1.05 ab (0.2)	8.54 a (1.0)	7.51 a (0.9)	23.77 b (4.2)
Forest					
March	2.61 (0.7)	1.44 (0.3)	15.92 (1.3)	13.85 (1.8)	
June	1.25 (0.2)	0.89 (0.4)	3.85 (1.0)	2.99 (1.3)	
October	4.62 (0.9)	1.56 (0.5)	5.50 (0.9)	3.26 (1.6)	
Average	2.77 a (0.5)	1.33 a (0.2)	10.30 a (1.4)	8.49 a (1.5)	48.20 a (3.1)
<i>F</i> -test Statistic					
Vegetation Zone ²	20.0***	2.6*	7.2***	3.9**	28.7***
Site ³	4.1**	1.1	3.6**	3.0	0.1
Vegetation Zone $\times$ Site	1.5	0.8	0.8	1.1	0.7

¹ Anaerobic incubations conducted in March only
² Significance levels: * ≤ 0.1 , ** ≤ 0.05 , *** ≤ 0.001
³ The site factor evaluates differences among the three individual study sites

1991). Within Kentucky's Knobs Region, geologic strata are bedded horizontally and soil parent material shifts with small changes in elevation or topography (Kepferle, 1969; Soil Conservation Service, 1986). The forest openings are confined to a narrow elevational band and appear to correspond to localized areas where softer calcareous shale is exposed between outcrops of more durable dolomite. Upslope of the openings, soils formed from Devonian shale support tree species common to more acidic conditions (*i.e.*, *Quercus alba* L., *Q. montana* Willd. and *Q. velutina* Lam.) (Homoya, 1999). The slopes below the forest openings are dominated by species common to mesic calcareous sites, especially *Q. muehlenbergii*, *Aesculus glabra* Willd and *Celtis occidentalis* L. The consistent differences in silt content, bulk density and extractable Ca²⁺ throughout the upper 50 cm suggests a distinct sedimentary origin of grass-dominated openings and forest soils. Although the general location of the forest openings can be approximated from their topographic position, the extent of the openings cannot be precisely delineated from surface features.

The extent and location of the forest openings may correspond to a stable parent material boundary, though soil movement may have contributed to formation of the edaphic discontinuity between the forest openings and their surroundings by exposing lower soil horizons. For example, soil pH and extractable Ca²⁺ in the upper 10 cm of the openings

TABLE 3.—Soil CO₂ efflux, soil temperature (5 cm depth) and gravimetric soil moisture [means and (SE); n = 12 per zone per date]. Within columns, similar letters indicate that vegetation type averages are equal based on Tukey's means separation test ($\alpha = 0.05$). *F* statistic and significance levels based on ANOVA

Vegetation zone	Soil respiration g CO ₂ m ⁻² h ⁻¹	Soil temperature C	Soil moisture %
Opening			
March	0.22 (0.0)	17.04 (0.5)	20.5 (0.0)
June	0.79 (0.1)	21.04 (0.5)	29.4 (0.0)
Average	0.34 c (0.0)	17.84 a (0.5)	22.3 b (0.0)
Edge			
March	0.38 (0.0)	14.63 (0.4)	29.0 (0.0)
June	0.98 (0.1)	18.67 (0.7)	36.6 (0.0)
Average	0.50 b (0.0)	15.43 b (0.4)	30.5 a (0.0)
Forest			
March	0.51 (0.0)	12.50 (0.4)	35.6 (0.0)
June	1.29 (0.1)	16.79 (0.2)	32.9 (0.0)
Average	0.77 a (0.1)	13.93 c (0.3)	34.7 a (0.0)
<i>F</i> -test Statistic			
Vegetation Zone ¹	17.4***	26.2***	14.0***
Site ²	0.9	28.7***	0.5
Vegetation Zone × Site	0.4	1.9	2.3

¹ Significance levels: *** ≤ 0.001

² The site factor evaluates differences among the three individual study sites

matches the values found at lower depths in forest soil profiles (Figs. 2a, b). Scars from gully erosion are common on the slopes near the Bernheim forest openings and throughout the Knobs Physiographic Region (Soil Conservation Service Staff, 1971). Overgrazing was a common historic source of soil loss and fence remnants surrounding the forest openings and the accounts of local residents indicate that the forest openings once supported livestock. It is unlikely that the openings ever underwent agricultural tillage due to their small size and poor fertility. Previous land use may have aggravated soil erosion, however 1928 aerial photography demonstrates that the perimeter of the isolated openings has been relatively stable for at least 75 y.

The amount and production of plant-available soil N are significantly lower in the forest openings compared to the surrounding forest and also to the woody edge. This gradient in soil N fertility relates to differences in litter quantity and quality across the grassland to forest boundary; the response of soil conditions to shifts between forest and grassland vegetation is concentrated at the soil surface (Daniels *et al.*, 1983; Rhoades and Coleman, 1999). It is possible that soil N availability is tied to a shifting forest-grassland boundary as the extent of the openings fluctuates following fire, clearing or some other canopy disturbance. However, historic aerial photography and subsurface differences in physical and chemical soil properties suggest that, although it is possible that the openings resulted from historic disturbance, it is more likely that they developed as a result of natural edaphic conditions that were then potentially altered by human activities.

Management considerations.—Threats of habitat loss and degradation are conservation concerns for the forest openings of Kentucky's Knobs Region. The limited acreage under

protection has led to attempts to maintain and expand forest openings to enhance habitat of unique plant species. Typical management of forest openings involves a combination of mechanical stem removal and prescribed burning (Packard and Mutel, 1997; Anderson *et al.*, 2000). These practices effectively alter the light, temperature and moisture conditions of the currently wooded edge and shift species dominance from woody to herbaceous species.

Although many common grass and forb species will respond rapidly to increased site resources, it is unclear how canopy removal will influence populations of locally rare species currently present within the forest openings (*i.e.*, *Viola septemloba* var. *egglestonii*, *Spiranthes magnicamporum*). If these species require the unique nutrient-poor conditions found within the forest openings, canopy removal alone may not be sufficient to increase their effective habitat. Soil N availability and turnover will respond relatively rapidly to management manipulations as litter from the grass-dominated community replaces forest litter. However, soil pH, extractable cations and P are expected to respond much more slowly to overstory removal. Our results suggest that significant edaphic differences between forest openings and surrounding forests may limit the expansion of the openings beyond their current extent.

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