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Forest Vegetation and Soil Patterns Across Glade-forest Ecotones in the Knobs Region of Northeastern Kentucky, USA

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ABSTRACT.—The Crooked Creek Barrens Preserve in the northeastern Knobs region of Kentucky contains an aggregation of species-rich grass and forb-dominated glade openings surrounded by secondary forest. Encroachment of woody species and invasion by non-native species threaten the rare forbs and sedges of the glades. The locations of these plant assemblages are commonly known to correspond to the unique properties of their underlying soils, yet few studies consider how soil factors may influence habitat conservation or restoration. This study describes vegetation and soil properties across the glade-edge-forest transition of three individual glade openings. *Juniperus virginiana* was the most abundant woody species within the glade openings. *Juniperus virginiana*, *Quercus stellata*, *Fraxinus americana* and *Cercis canadensis* co-dominated the edge-forest boundary. Glade surface soils had dramatically higher pH (2 units) and lower extractable soil P (50% less) than forest soils. Also, total soil N content and net mineralization rates were significantly lower in glades than in forest or edge soils. The highly erodable nature of alkaline shale sediments appears to have contributed to the current location and extent of the glade openings. These findings suggest that management efforts to enhance rare plant habitat by expanding the glade openings should be accompanied by monitoring of soil changes following clearing. Further study should assess whether glade species of conservation concern are restricted to the nutrient-poor alkaline soils within extant glade openings or if they readily colonize the more nutrient-rich habitat of the cleared edge.

INTRODUCTION

The Knobs Region is a horseshoe-shaped band of hills that surrounds the rolling plains of the Bluegrass Region of Kentucky and extends into southern Indiana and Ohio. The “knob”-shaped hills formed where resistant limestone or sandstone overlay erosion-prone shale (Peck and Pierce, 1966). Alternating shale, limestone and sandstone sediments produce a pattern of soils with contrasting chemical and physical boundaries separated

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along abrupt boundaries. The region's complex soils, in conjunction with the varied topography and land-use patterns, contribute to the diversity of Knob plant communities.

Grass- or forb-dominated forest openings, classified as either "glades" (M. Evans Kentucky State Nature Preserves Commission, pers. com.) or "xeric limestone prairies" (Baskin *et al.*, 1999) are a unique feature of the region. These openings, referred to as glades in this paper, are situated on various interbedded alkaline substrates including clay shale, dolomite and limestone (Peck and Pierce, 1966). Early geologic surveyor John Locke (1838) described the "bald hills" or "buffalo beats" of Knobs in Adams County, Ohio, as "quite a paradise for the botanist." Locke (1838) also noted that sparse forest and glade openings corresponded to areas where the dolomitic, clay shale-derived soil "is often almost barren of trees, and produces some peculiar prairie-like plants as the prairie docks, wild sunflowers, scabish [*Scabiosa* spp. of the Dipsacaceae family], rudbeckias, &c." Fifty-one species of state- or federally-threatened plant species are currently found within such openings across Kentucky (Kentucky State Nature Preserves Commission, 2000).

In Kentucky, the herbaceous communities of glades have become a conservation priority because they contain locally-rare plant species threatened by land conversion, land degradation and woody plant encroachment. In addition to identifying and protecting glade communities, natural area managers in Kentucky have initiated activities aimed at maintaining or expanding the unique plant assemblages. Where fire suppression or other land-use practices have resulted in woody plant encroachment into glades, herbaceous glade flora may expand relatively rapidly following mechanical removal of trees growing at the periphery of these openings. In contrast, where the boundary between glades and the adjacent forest is fixed by an abrupt parent material transition (Boettcher and Kalisz, 1991; Rhoades and Shea, 2003; Rhoades *et al.*, 2004), forest clearing may not be sufficient to promote expansion of the herbaceous species.

Although edaphic factors are known to determine the location and spatial extent of glade openings and soil processes may determine the outcome of management activities, information linking glade plant communities and underlying soil properties is scarce. This study characterizes the differences in soil conditions of three glade openings and the surrounding forest in the Knobs Region of Kentucky to provide insight regarding the stability of the herbaceous communities and to guide vegetation management aimed at maintaining or expanding their spatial extent.

METHODS

SITE DESCRIPTION

This study was conducted at the Crooked Creek Barrens State Nature Preserve (CCB) in the northeastern Knobs Region in Lewis County, Kentucky (Fig. 1). The Kentucky State Nature Preserves Commission (KSNPC) protects and manages the site. CCB (38° 38' N; 83° 35' W) is 4 km south of the Ohio River, south of the limit of Pleistocene glaciation, near the border between the Appalachian Plateau and the Interior Low Provinces (Braun, 1950). CCB is also 20 km south of the prairie-like openings at Lynx Prairie in Adams County, Ohio (Braun, 1928; Boettcher and Kalisz, 1991).

Soils at the site weathered from soft clay shale and silty dolomite of the upper Crab Orchard formation (Peck and Pierce, 1966). The soils classify as mesic Typic Hapludalfs of the Beasley-Shrouds complex (Jacobs, 2004), and surface soils are neutral to moderately alkaline (Karathanasis, 1992). Average annual precipitation and temperature are 1281 mm and 13.9 C, respectively (National Climatic Data Center, 2001).

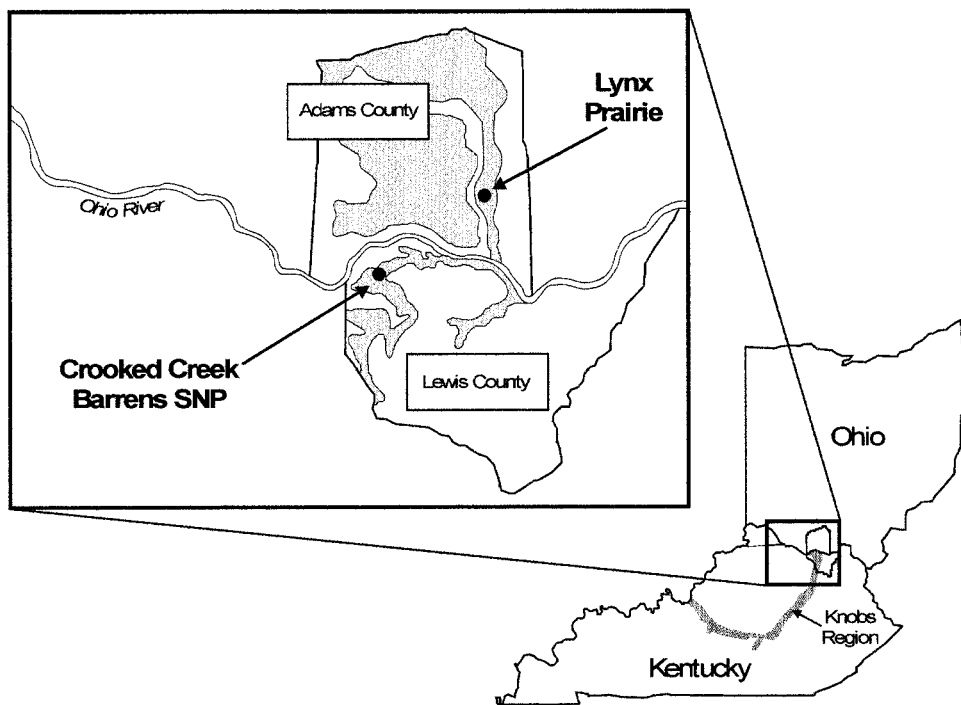


FIG. 1.—Location of Crooked Creek Barrens State Nature Preserve in Lewis County, Kentucky, and Lynx Prairie in Adams County, Ohio (modified from Rexroad *et al.*, 1965). Shaded area demarks the extent of Silurian sediments

There are six glade openings in the 141 ha preserve that range in area from 500 to 8000 m². The complex of glades contains the following Kentucky-listed threatened or endangered sedges, grasses and forbs: *Carex juniperorum* Catling, Crins and Reznicek, *C. rugosperma* Mack., *C. tetanica* Schkuhr., *Bouteloua curtipendula* (Michx.) Torrey, *Castilleja coccinea* (L.) Sprengel, *Liatris cylindracea* Michx., *Prenanthes alba* L. and *Agalinis auriculata* (Michx.) S.F. Blake (KSNPC, 2000). Nomenclature follows Gleason and Cronquist (1991) and Kartesz (1994). The long-term management objectives for CCB are to maintain and increase native species diversity and abundance within the glade-forest complex by reversing woody tree encroachment, soil loss and exotic species invasion across the preserve site (KSNPC, 2001).

STUDY DESIGN AND SAMPLING DETAILS

This study characterizes three discrete openings at CCB that are located within 1000 m of each other on the flanks of the central knob (Hymes Knob). The largest and smallest glades are approximately 0.8 and 0.1 ha, respectively (Table 1). The largest glade also has the steepest slopes (15–35%); slope of the other two glades is 5 to 15%. Two glades are situated on the south and southwest side of the knob and the third faces north.

Sampling was designed to quantify differences in woody species composition and soil properties across the grassland-forest ecotone. We partitioned each individual glade site into concentric habitat types: glade opening, woody edge and interior forest. At each glade site, five sample transects were randomly located. Transects extended radially from the glade

TABLE 1.— Tree and seedling density within Crooked Creek Barrens habitat types. Species list reports > 80% of total stem density per habitat

Habitat	Trees (≥ 2 cm DBH)	Density (stem/ha)	Relative density	Seedlings	Density (stem/ha)	Relative density
Glade Interior	<i>Juniperus virginiana</i>	283.0	0.79	<i>Juniperus virginiana</i>	849.1	0.53
	<i>Quercus stellata</i>	37.7	0.11	<i>Cornus drummondi</i>	150.9	0.09
				<i>Fraxinus americana</i>	113.2	0.07
	Habitat total	358.5		<i>Ostrya virginiana</i>	94.3	0.06
				<i>Diospyros virginiana</i>	84.9	0.05
				<i>Viburnum prunifolium</i>	75.5	0.05
				<i>Amelanchier arborea</i>	66.0	0.04
				Habitat total	1594.3	
Glade edge	<i>Juniperus virginiana</i>	400.0	0.29	<i>Amelanchier arborea</i>	1114.3	0.16
	<i>Cercis canadensis</i>	200.0	0.15	<i>Ostrya virginiana</i>	1085.7	0.16
	<i>Quercus stellata</i>	171.4	0.13	<i>Viburnum rufidulum</i>	914.3	0.13
	<i>Fraxinus americana</i>	85.7	0.06	<i>Cornus drummondi</i>	685.7	0.10
	<i>Acer rubrum</i>	85.7	0.06	<i>Juniperus virginiana</i>	685.7	0.10
	<i>Quercus marilandica</i>	85.7	0.06	<i>Fraxinus americana</i>	514.3	0.07
	<i>Quercus alba</i>	85.7	0.06	<i>Cercis canadensis</i>	485.7	0.07
	<i>Acer saccharum</i>	57.1	0.04			
	<i>Quercus velutina</i>	57.1	0.04	Habitat total	6971.4	
	Habitat total	1371.4				
Forest edge	<i>Cercis canadensis</i>	652.2	0.19	<i>Amelanchier arborea</i>	4429.3	0.26
	<i>Quercus stellata</i>	489.1	0.15	<i>Viburnum prunifolium</i>	2038.0	0.12
	<i>Fraxinus americana</i>	380.4	0.11	<i>Viburnum rufidulum</i>	1413.0	0.08
	<i>Amelanchier arborea</i>	298.9	0.09	<i>Cornus florida</i>	1114.1	0.07
	<i>Viburnum rufidulum</i>	271.7	0.08	<i>Fraxinus americana</i>	1114.1	0.07
	<i>Cornus florida</i>	244.6	0.07	<i>Cornus drummondi</i>	1005.4	0.06
	<i>Juniperus virginiana</i>	190.2	0.06	<i>Ostrya virginiana</i>	1005.4	0.06
	<i>Ostrya virginiana</i>	190.2	0.06	<i>Quercus alba</i>	978.3	0.06
				<i>Juniperus virginiana</i>	597.8	0.04
	Habitat total	3369.6		<i>Cercis canadensis</i>	597.8	0.04
				Habitat total	16929.3	
Forest interior	<i>Fraxinus americana</i>	214.3	0.11	<i>Viburnum prunifolium</i>	1222.2	0.12
	<i>Cercis canadensis</i>	214.3	0.11	<i>Amelanchier arborea</i>	1023.8	0.10
	<i>Quercus stellata</i>	190.5	0.09	<i>Fraxinus americana</i>	896.8	0.09
	<i>Acer saccharum</i>	166.7	0.08	<i>Ostrya virginiana</i>	817.5	0.08
	<i>Cornus florida</i>	150.8	0.08	<i>Cornus florida</i>	785.7	0.08
	<i>Juniperus virginiana</i>	134.9	0.07	<i>Acer saccharum</i>	722.2	0.07
	<i>Sassafras albidum</i>	111.1	0.06	<i>Cercis canadensis</i>	690.5	0.07
	<i>Quercus velutina</i>	103.2	0.05	<i>Cornus drummondi</i>	642.9	0.06
	<i>Quercus alba</i>	103.2	0.05	<i>Viburnum rufidulum</i>	507.9	0.05
	<i>Ostrya virginiana</i>	103.2	0.05	<i>Sassafras albidum</i>	500.0	0.05
	<i>Viburnum rufidulum</i>	95.2	0.05	<i>Quercus alba</i>	452.4	0.05
	<i>Amelanchier arborea</i>	95.2	0.05	<i>Juniperus virginiana</i>	428.6	0.04
	<i>Cornus drummondi</i>	71.4	0.04	<i>Prunus serotina</i>	357.1	0.04
	Habitat total	6020.3		Habitat total	10015.9	

interior for 50 to 60 m, through the wooded edge and into the surrounding forest. The abrupt shift in stem density, canopy height and species composition was used to differentiate woody edge habitat from the interior forest. To describe the species pattern near the perimeter of the glade in greater detail, the edge zone was divided into two adjacent 5 by 5 m plots denoted as "glade edge" and "forest edge" located on either side of the grassland-forest border.

Tree species composition, basal area and stem density were evaluated in 5-m wide belt transects that extended the length of each habitat zone along each radial transect. Diameter of stems ≥ 1 cm diameter was measured at 1.4 m height (tree class). Woody stems < 1 cm diameter were tallied by species (seedling class). Herbaceous vegetation and ground cover classes [*i.e.*, forb, graminoid, bare ground, litter and "other" (including coarse downed wood and woody plants)] were quantified by line intercept at 1 m intervals within each habitat type along the radial transects.

Soil analyses defined chemical and physical properties and soil nitrogen cycling gradients across the vegetation ecotone. Soils were collected along each transect at the midpoint of the glade, edge, and forest habitat types. Samples of mineral soil were taken with a 5 cm-diameter slide-hammer corer. Total C and N, soil pH (Thomas, 1996), Mehlich-III extractable phosphorus and cations (Mehlich, 1984) and soil texture were analyzed on 10-cm increments to 30-cm depth. Samples were oven-dried (60 C for 48 h), weighed and ground before total soil C and N analysis by dry combustion (LECO CNS-2000; St Joseph, MI).

We compared plant-available soil nitrogen pools (NO_3^- and NH_4^+) and the production of these N forms across habitat types in July 2000. Samples of the top 10 cm of mineral soil were collected with a 5-cm diameter hand corer, transported within a plastic cooler, refrigerated at 4 C and processed within 48 h. An initial subsample was extracted with 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 calculate the gravimetric soil moisture content. Another set of 15-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 freely drain for 12 h (gravimetric moisture content of about 50%). After 14 d, the incubated subsamples were extracted with 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^- before and after incubation.

Soil properties from the three habitat types (glade, edge, forest) were compared using a mixed analysis of variance model with habitat type as a fixed effect and individual glade site and habitat type by site interaction as random effects (SPSS Inc., Chicago, IL). Significant differences among habitat type means were identified using Tukey's LSD means separation test at a 0.05 significance level. Variables were log-transformed before analysis where required to meet assumptions of normality or homogeneity of variance.

RESULTS

The glade openings were dominated by grasses (30 to 53% cover), with forb cover ranging from 10 to 40% of the ground surface (Table 1). Grass cover was evenly divided between *Andropogon gerardii* Vitman and *Schizachyrium scoparium* (Michx.) Nash. Prairie dock (*Silphium terebinthinaceum* Jacquin.) was the most common forb species, comprising 70% of forb cover and 6 to 40% of total cover in the three glades. Blazing star [*Liatrix cylindracea* Michx. and *L. spicata* (L.) Willd.] represented 14% of the forb cover in the glade openings. Bare soil covered 23 and 37% of the area in two glades but was absent from the third glade. There were no rock outcrops within the three glades.

Grass cover declined to 17% in the 5-m section of glade adjacent to the forest edge and was 4.5 and 1.5% within the forest edge and forest interior, respectively. Similarly, forb cover

decreased to 14.3% in the glade edge, 3.4% in the forest edge and 0.0% in the forest interior. Extent of bare soil declined to 7.1 and 5.7%, respectively, in both glade and forest edge and to 0.5% in forest interior as leaf litter cover increased. Coarse wood and leaf litter covered 12 and 81%, respectively, of the surface in the forest zone.

The glade openings contained five tree species compared to 25 species in the forest interior. *Juniperus virginiana* L. was the most abundant woody species in the glade openings (79 and 53% of trees and seedlings, respectively; Table 2). Glade edge also was dominated by *J. virginiana*, where the species reached its highest density. Density and relative abundance of *J. virginiana* trees declined in the forest edge and interior. *Quercus stellata* Wang., *Fraxinus americana* L., *Cercis canadensis* L. and *Diospyros virginiana* L. were also present within the glade openings. Combined, *Q. stellata*, *F. americana* and *C. canadensis* represented 31 to 45% of tree stems in forest and edge habitats.

Seedlings of seven tree species were found within the three glade openings, which was half the number found in edge and forest zones. *Juniperus virginiana* was the most abundant seedling species in the glade interior but declined in absolute and relative density with distance from the glade opening (Table 2). Like total number of seedlings, *Fraxinus americana* seedling density was 2- and 10-fold higher in forest edge than in glade edge and glade opening, respectively. *Quercus stellata*, *Q. alba* L. and *Q. velutina* Lam. seedlings were present in all zones of the glade-forest transition, but the density of these and other oak species (*Q. rubra* L., *Q. marilandica* Muench., *Q. muehlenbergii* Engelm.) was low. Relative density of *Acer saccharum* Marsh. and *Cornus florida* L. seedlings and stems increased in forest edge and in interior sites.

Midstory species represented 56 to 70% of all seedlings found in edge and forest zones and 30% of those found within the glade openings. Eight midstory species occurred in all four zones. Seedlings of *Amelanchier arborea* (Michx.) Fernald, *Ostrya virginiana* (Mill.) K. Koch and *Cornus drummondii* Meyer were common across the glade-forest transition, but larger individuals of these species (stems ≥ 2 cm) were scarce or absent. In contrast, *Cercis canadensis* was common in tree plots, but seedlings of this midstory species were rare.

Both chemical and physical soil properties differed between glade openings and surrounding forest. Overall, soils in the glades had higher pH and contained less extractable P and more extractable cations than surrounding forests. The pH of glade soil was two units higher than that of forest soil throughout the sample profile (Fig. 2a). The amount of extractable soil P in the surface 10 cm of the glades was only about half of that found in the forest and edge soils, and it remained significantly less throughout the sampled depth ($P < 0.001$; Fig. 2b). Extractable Ca^{2+} , Mg^{2+} , and K^{+} were 2-, 1.7- and 1.2-fold higher in the surface of the glade soils than in forest soils ($P < 0.05$).

Soil N fertility was lower in glade openings than in forest or edge. Total N content of glade surface soils (Fig. 2c) was 60% of that measured in forest or edge ($P < 0.004$), and the C:N ratio was significantly higher ($P < 0.02$; Fig. 2d). Net mineralization rates decreased by 98%, from $3.7 \mu\text{g N} / \text{g} / 14 \text{ d}$ in forest and edge sites to $0.06 \mu\text{g N} / \text{g} / 14 \text{ d}$ within glade soils ($P < 0.05$). Similarly, net nitrification within the glades was one-half that measured in the other two zones. The higher C:N and lower total N content of the glade soils suggests that both lower organic matter quantity and quality explain the reduced net N transformation rates.

Glade soils were classified as silty clay loams throughout the 30-cm sample profile. In contrast, the texture of forest and edge soil profiles changed from silty clay loams in the surface 10-cm to silty clays in the lower depths. Clay content increased from 26% in the top 10 cm to 43% at depth in forest soils, but remained relatively constant (33%) throughout the glade profiles. A dense clay layer (up to 52% clay) occurred at the 30 cm depth in both forest and edge sites, but was absent from glade soils. Mean surface texture was comparable

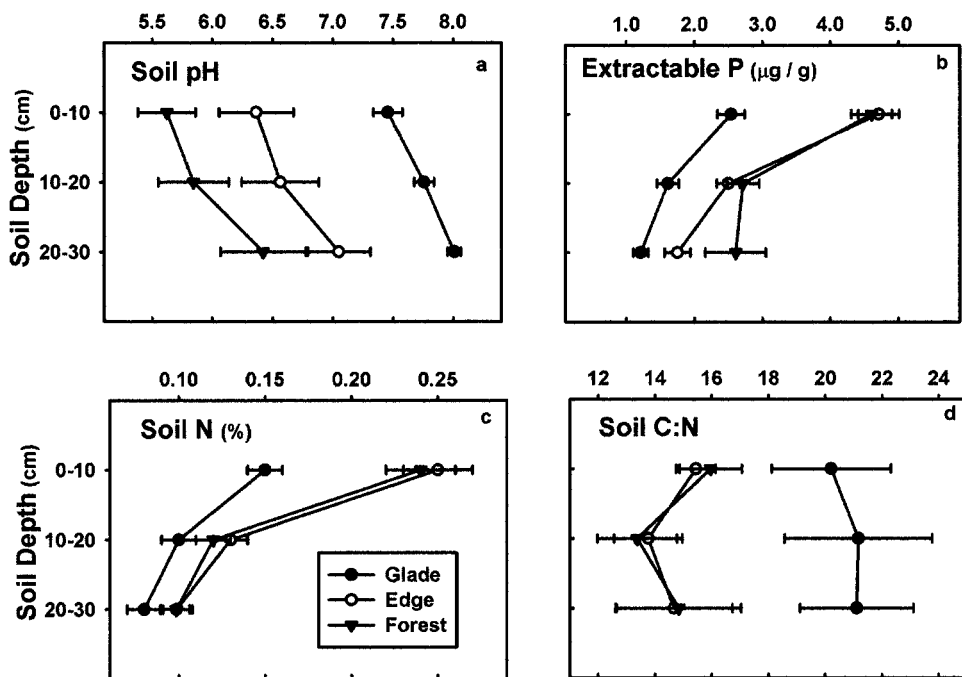


FIG. 2.—Soil pH (a), Mehlich III-extractable soil P (b), total soil N (c) and C:N (d) with depth at Crook Creek Barrens State Nature Preserve. Data are means and 1 SE from three glade opening sites ($n = 15$ per depth per habitat type)

between the three habitat types, but in the glades the 10–20 and 20–30 cm depths had significantly less clay ($P < 0.05$) and more silt ($P < 0.01$) than either forest or edge soils.

DISCUSSION

There was a sharp decline in soil N and P fertility and an abrupt increase in soil pH and extractable cations across the transition from forest into the glade openings. Soil in the wooded edge, less than five m from the glade perimeter, was similar to interior forest soil and distinct from glade soil. Similar soil gradients have been described across grassland-forest ecotones of alkaline glades in the western Knobs region of Kentucky (Rhoades *et al.*, 2004) and in the Knobs and Outer Bluegrass transition of southeastern Ohio (Boettcher and Kalisz, 1991). As at CCB, plant-available N, total soil N and extractable P in three western Knobs glades were half that measured in adjacent edge or forest (Rhoades *et al.*, 2004). At both the Ohio and Kentucky sites, soil pH, extractable cations, silt content and bulk density were significantly higher in glade openings than in forest or edge soils (Boettcher and Kalisz, 1991; Rhoades *et al.*, 2004).

The change in edaphic conditions and the extent of the glade openings may correspond to sharp boundaries between distinct sedimentary parent material types (Boettcher and Kalisz, 1991; Rhoades *et al.*, 2004). At CCB and throughout the Knobs Region, geologic strata are bedded horizontally and soil parent material shifts with small changes in elevation or in topography (Peck and Pierce, 1966). For example, glade openings in the western Knobs are confined to a narrow elevational band and appear to correspond to localized

areas of alkaline shale exposed between dolomite outcrops (Rhoades *et al.*, 2004). Upslope of the western Knobs openings, soils formed from Devonian black shale support tree species common to more acidic conditions (*i.e.*, *Quercus alba*, *Q. montana* Willd and *Q. velutina*) (Homoya, 1999). Slopes below the forest openings are dominated by species common to mesic calcareous sites, especially *Q. muehlenbergii*, *Aesculus glabra* Willd and *Celtis occidentalis* L. In southeastern Ohio, vegetation shifts abruptly from prairie-like grasslands to pine-hardwood forest in areas where calcareous parent material abuts acidic sediments. In contrast, where the dolomitic parent material extends beyond the perimeter of the glade opening, grass-dominated vegetation grades into cedar-hardwood forest, and the soil transition is more gradual (Boettcher and Kalisz, 1991). These studies demonstrate that sharp transition between parent material types generate abrupt soil chemical and physical gradients and result in relatively stable borders between the herbaceous and forest communities. At CCB in contrast, where the Crab Orchard shale underlies both the glade openings and most of the surrounding forestland, it is unlikely that a change in parent material type delimits the current glade boundaries.

Soil erosion associated with land clearing may be an alternative explanation for the genesis of these glade openings. Gully erosion and patches of exposed soil are common within CCB glade openings, and the incidence of bare ground and soil loss increases with slope. Early land and forest surveyors noted the erosive tendency of Crab Orchard shale-derived soil (Locke, 1838): 'if it lies on a steep declivity, it is liable, after the trees are removed, to slip in large avalanches, blasting entirely the prospects of the husbandman.' The current abundance of *Juniperus virginiana* and *Quercus stellata* at CCB and the surrounding area resulted from periodic forest clearing that has occurred since the time of European settlement. By the early 1900s, there was "scarcely any" uncut timber remaining in Lewis County and a *J. virginiana*-dominated "old-field type" had become abundant (Holmes and Hall, 1909). In nearby Adams County Ohio, Braun (1928) also noted extensive "cedar barrens" following land clearing for cultivation and grazing. Long-time local residents recall the open aspect of cleared land in the CCB area during the early decades of the 20th Century and the subsequent increase in *J. virginiana* density as cultivated acreage declined after World War II (R. Nash, pers. comm.).

By exposing lower soil horizons, soil erosion may generate the unique edaphic conditions within the CCB glades. In general, soil properties at the surface of the glades were similar to those of lower forest soil layers. For example, clay, extractable P and total soil N contained in the surface 10 cm of glade soils were equal to that measured in adjacent forest soils at the 20–30 cm depth. In the two glades with extensive bare soil, clay, extractable P and total N and C changed little with depth compared to forest soil profiles. The flattest glade had the lowest extent of bare soil and, similar to forest soils, the most well-developed soil profiles.

EDAPHIC CONSIDERATIONS FOR GLADE MANAGEMENT AT CROOKED CREEK PRESERVE

Although soil erosion may have contributed to the formation of the glades at the CCB site, these areas contain plant assemblages that are unique in the region. Restricting livestock and recreational vehicle traffic since the preserve was established in 1999 has begun to slow soil erosion. More recently, Kentucky State Nature Preserves Commission managers have begun to employ a combination of mechanical stem removal and prescribed burning in order to maintain and expand CCB glade openings to support a diverse glade flora. This will slow encroachment by woody plants and should enhance production and cover of the dominant herbaceous species and warm-season grasses, *Andropogon gerardii* and *Schizachyrium scoparium* (Hulbert, 1988; Knapp *et al.*, 1998). For example, following forest clearing surrounding a series of alkaline glade openings in Kentucky's western Knobs

Region, herbaceous biomass and forb cover equaled or surpassed that of the original glade openings (Rhoades and Shea, 2003). The dense herbaceous cover within the expanded glade openings should contribute to soil protection.

Although locally-common grass and forb species will rapidly colonize expanded edge habitat, it is unclear how canopy removal will influence soil conditions or populations of less common glade species. In glades of Kentucky's western Knobs, soils of the cleared edge remained significantly more nutrient-rich and acidic than glade openings 2 y following tree removal and the occurrence of glade indicator plants was lower (Rhoades and Shea, 2003). At CCB, the response of soil conditions following mechanical clearing is unknown. Future studies should assess the population dynamics of species currently restricted to the glade openings and should compare their success in the nutrient-poor glades with that in the relatively nutrient-rich cleared edge habitat.

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