

Vegetation and soils of a serpentine barren in western North Carolina¹

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MANSBERG, L. AND T. R. WENTWORTH (North Carolina Natural Heritage Program, North Carolina Department of Natural Resources and Community Development, Raleigh, NC 27611 and Department of Botany, North Carolina State University, Raleigh, NC 27695-7612). Vegetation and soils of a serpentine barren in western North Carolina. *Bull. Torrey Bot. Club* 111: 273-286. 1984.—Vegetation of a pine-savanna on an olivine-serpentine outcrop is described. Soil characteristics, community structure, species composition, species richness, and representation of life-forms and geographic areas are discussed and compared with those of oak-mixed hardwood vegetation growing on mica gneiss slopes in the same area. The pine-savanna differs from the oak-mixed hardwoods in the following ways: canopy closure is incomplete, whereas a closed canopy is observed on mica gneiss; the pine-savanna has somewhat fewer species; hemicryptophytes and chamaephytes are more important life-forms in the flora of the pine-savanna than in that of the oak-mixed hardwood type; the flora of the pine-savanna displays an affinity with that of midwestern regions of the United States, represented by a disjunct element (6%), whereas the oak-mixed hardwood type is more closely allied with southern Appalachian flora; the serpentine soils are more variable morphologically, are higher in cation exchange capacity and percentage base saturation, and are lower in acidity, the ratio of calcium to magnesium, and difference in water retention between -33 and -1500 kPa. The pine-savanna is physiognomically similar to vegetation occurring elsewhere on serpentine, particularly in the northwestern United States, and contains range disjunctions and morphological variants such as typify serpentine vegetation on many continents. It appears to be a stable edaphic climax as are some of the other barrens, limestone cedar glades, and prairie-like communities occurring outside the prairie region proper.

Key words: olivine; savanna; serpentine; pine barren.

Variations in topography, mineral content, and physical properties of parent rock often account for regional differentiation in vegetation (Kruckeberg 1969b, Cole 1980, Wentworth 1981). The relationship of plant distribution to soil parent material is particularly well illustrated by the striking aspect of vegetation on soils developed from ultramafic rocks. These rocks, which in-

clude peridotite and dunite, contain less than forty percent silica and are rich in iron and magnesium. Serpentine, in its strictest sense, refers to a small group of layer silicate minerals, most of which are products of the hydrothermal alteration of ultramafic igneous rocks, though the term is generally used to refer to ultramafic rocks containing the mineral olivine and the soils derived from them.

Numerous edaphic and environmental factors associated with serpentine sites interact to produce conditions adverse to plant growth. Unfavorable physical properties of serpentine soils, such as shallowness and stoniness (Rune 1953) or low plant extractable water, may actually limit plant growth. The chemical properties of serpentine soils, however, are currently regarded as the most critical limitations to plant growth. Most serpentine soils are relatively high in iron

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and magnesium and low in silica; many contain low levels of calcium. A calcium–magnesium ratio unfavorable for plant growth has been detected in many serpentine soils, particularly in the northwestern United States (Kruckeberg 1954, Walker 1954, Proctor 1971). Some serpentine soils also contain high levels of nickel, chromium, and cobalt because of the presence of accessory minerals like chromite and the frequent substitution of magnesium by other metals.

The physiognomic and taxonomic uniqueness of serpentine-based vegetation has been amply documented (cf. Proctor and Woodell 1975). Attributes which distinguish serpentine vegetation from that of surrounding soils include: sparse cover with much intervening barren ground, dwarfing and xerophytism, and an enriched flora which is almost always unique for the region and which contains a number of endemics, ecotypes, morphological variants, and range disjunctions (Pichi-Sermolli 1948, Kruckeberg 1954, 1969a,b, Whittaker 1954a,b, 1960, Proctor and Woodell 1975).

Most investigations of serpentine areas in the eastern United States have been floristic studies of the “barrens” in southeastern Pennsylvania and northern Maryland (Harshberger 1903, Pennell 1910, 1912, 1930, Wherry 1963). Radford (1948) surveyed the flora occurring in North Carolina and Georgia on olivine deposits within the gneissic belt of the southern Appalachians. He recognized several communities or dominance types associated with various topo-edaphic situations. A more detailed ecological study of serpentine vegetation was conducted by Miller (1977) in southeastern Pennsylvania.

In this paper, we characterize the vegetation of the Buck Creek serpentine barren in Clay County, North Carolina, with regard to structure, composition, species richness, and representation of life-forms and geographic areas. We then compare it to the vegetation of nearby sites having similar topography and macro-climate but different soil parent material. We conclude with a brief comparison of the vegetation of this serpentine barren with that of other serpentine sites in North America and various barrens and prairie-like areas in the eastern United States.

Materials and Methods. STUDY AREAS.

The Buck Creek serpentine barren and comparative sites near Standing Indian Mountain are located on the western side of the Nantahala Mountain Range, north of the Blue Ridge and south of the Unaka Mountains (Fig. 1). The Nantahala River provides the principal drainage for the region. West- and northeast-facing slopes above Buck Creek constitute the barren, which is located on the largest peridotite outcrop in North Carolina (Pratt and Lewis 1905). Our study examined the west-facing slope, an area about 6 ha in extent. The landform is unique for the region—a discrete, largely convex-surfaced knob projecting from the base of a larger slope. This topographic form results because the intrusive peridotites are more resistant to weathering than the surrounding rocks (Pratt and Lewis 1905).

Extensive accounts of the geology of the Buck Creek peridotite are given by Pratt and Lewis (1905), Hunter (1941), and Hadley (1949). Approximately 90 per cent of the main body of the deposit is relatively unaltered olivine and serpentinized dunite. Many pegmatites cut through the dunite and account for veins of such alteration and weathering products as actinolite, vermiculite, and chlorite. Some veins contain minor amounts of corundum.

The study area has remained undisturbed since 1932 when major portions of the “barrens” were acquired by the U.S. Forest Service. Corundum was mined from the deposit between 1875 and 1906. A brief period of prospecting occurred around 1943. Cuts and pits made on the west-facing part of the dunite outcrop are still visible today, but the major ones are outside the study area. Minor prospecting scars within the study area, however, may contribute to microhabitat heterogeneity already induced by the mineral veins mentioned above. No significant fires have occurred for at least 40 years.

Slopes of similar topography, aspect, and elevation approximately 9 km from the serpentine barren and bordering the Nantahala River in Standing Indian Wildlife Management Area, Macon County, were chosen for comparative study. Parent material of the substrate on the comparative sites is mica gneiss (Hatcher 1976).

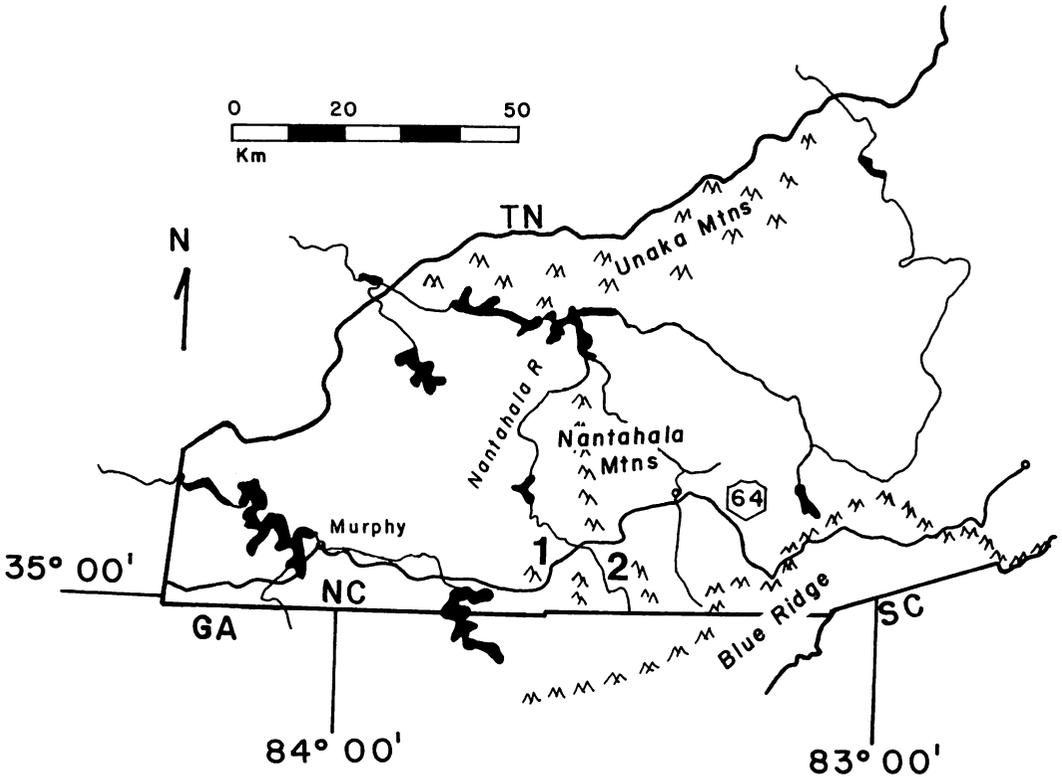


Fig. 1. Location of study areas in western North Carolina. (1) Serpentine area. (2) Mica gneiss comparative sites.

Average annual precipitation recorded over a ten-year period at the Coweeta Experiment Station (17 km from the Buck Creek barrens and 10 km from Standing Indian) was 1770 mm. The lowest monthly mean occurred in October (99 mm), the highest in February (203 mm). Mean monthly temperatures at the same station were 4°C in January and 22°C in July, with an average annual temperature of 13°C. Mean monthly evaporation was highest for July, 110 mm. Annual evaporation averaged 866 mm (U.S. Department of Commerce 1961).

There are no recent soil surveys for the counties that include the two study areas. In a survey of Clay County (U.S. Department of Agriculture 1941), the Buck Creek serpentine area is mapped as Porter's Loam, which develops from gneissic parent material. Our examination of soil morphology, through sample boring and pit excavation, suggests a different classification (Mansberg 1981). On many areas of the

serpentine slope thick, very dark loam epipedons of high base saturation and percent organic matter (see Results) were observed. Equally high base saturation for C-horizon materials (92.8%) suggests that this soil is a Mollisol. Although Mollisols have not yet been recorded for North Carolina (S. Buol, pers. comm.), we have tentatively classified the serpentine soil as a coarse loamy, mixed, mesic, Lithic Hapludoll. The soil profile varies greatly over the serpentine slope, a fact probably directly related to the presence of veins of accessory minerals which weather at different rates and produce soils of differing physical and chemical properties. Bedrock occurs at depths ranging from 23 to 42 cm. After periods of heavy rain we observed a perched water table above the bedrock in some soil pits, suggesting that pockets of moist soil alternate with better-drained areas.

Soil morphology on the mica gneiss slope is not as variable as that on the serpentine; soils are uniformly well-drained, and the

entire solum averages about 60 cm in depth. It is likely that this is a loamy-skeletal, mixed, mesic Typic Dystrachrept, possibly in the Brandywine series, though in places solum shallowness suggests a Lithic Dystrachrept.

The study areas are located in the Oak-Chestnut Forest Region described by Braun (1950) and in the Appalachian Oak Forest as mapped by Küchler (1964).

FIELD SAMPLING. Sampling was conducted in the early summer of 1979. Eleven 20 × 20 m (0.04 ha) quadrats were located at regular intervals along 3 transects running parallel to the azimuth of the serpentine slope. Since non-serpentine study slopes were much smaller in extent, only one or two quadrats could be placed on each. Extensive reconnaissance in the region revealed that the west-facing, knob-like landform is very rare. We therefore obtained a sample consisting of only five quadrats off serpentine. Site information collected at each quadrat included elevation, aspect, degree of slope, average depth of the upper (A) soil horizon, and canopy height.

Two means of assessing species importance were used. We made a complete stem count of trees and shrubs (the latter defined by a mature height ≥25 cm) within each 0.04 ha quadrat. Diameter at breast height (dbh) was recorded for every tree stem ≥1.27 cm dbh. Stems <3 m tall were counted as saplings. Individuals <30 cm tall were considered seedlings (with the exception of *Pinus rigida*, where 19 cm was used as the cut-off height) and counted with herbaceous species as described below. Relative density and relative basal area for each canopy species were summed within each quadrat, divided by two, and then averaged over the quadrats of each sample. The resulting mean importance value (maximum equals 100) and a percentage constancy value provided estimates of species dominance and presence in the canopy of each vegetation type.

We also arranged 10 meter-square subquadrats at 1 m intervals on alternate sides of a tape running downslope through the center of each 0.04 ha quadrat. Within these subquadrats we estimated for each species the percentage of ground area covered by living parts occurring in a column projected vertically upward from the ground to a height of 2 m. The 10 subquadrat cover

estimates were then averaged to give a single cover estimate for each species in each 0.04 ha quadrat. Following the stand count and subquadrat cover estimation, each quadrat was examined for additional species. Nomenclature for most species follows Radford *et al.* (1964). Hitchcock and Chase (1950) and Cronquist (1980) were used for nomenclature and identification of Poaceae and Asteraceae, respectively.

Composite soil samples were collected from each of the 16 0.04 ha quadrats by coring the surface layer (A horizon) at approximately 1 m intervals along the quadrat's midline. Samples were air-dried, thoroughly mixed, and passed through a 2 mm wire mesh sieve. Soil chemical analyses were performed by the Soil Testing Section of the N.C. Agronomic Division (Mehlich II Acid Extractant technique (0.2N NH₄Cl-0.2N HOAc-0.015N NH₄F-0.012N HCl at pH 2.5, Mehlich 1978); wet oxidation for organic matter). A ceramic pressure plate apparatus (Richards 1947) was used for the determination of percentage water (dry mass basis) retained at tensions of -33 and -1500 kPa.

VEGETATION CHARACTERIZATIONS. The complete species lists for the 0.04 ha quadrats in each sample (consisting of 11 quadrats on serpentine, 5 quadrats on mica gneiss) were used to compute mean (per quadrat) species richness statistics; these were further subdivided into tree, shrub, and herb categories. Species richness was also expressed on a quadrat subsample basis (10 m² or 0.001 ha).

The number of prevalent species in each sample was defined as mean 0.04 ha species richness values for trees, shrubs, and herbs rounded up to the nearest integer (Curtis 1959). Prevalent species are those most frequently encountered in the sample representing a vegetation type. Constancy, the percentage of quadrats in a sample in which a species occurs, was computed for all species. Species were assigned to prevalence lists in order of descending constancy; average cover was used as the tie-breaking criterion when necessary.

All species were placed into life-form categories that follow the Raunkiaer system (cf. Mueller-Dombois and Ellenberg 1974) and geographic-areal categories that were designated after consideration of distinct

physiographic, climatic, and floristic areas within the North American continent. Species' covers in each category were summed over the quadrats in the serpentine and the mica gneiss samples and these values were then expressed as percentages of total cover within each sample.

Results. SITE CHARACTERIZATIONS. The elevations of both study sites can be considered moderate for the southern Appalachians. Slopes were moderate to steep with a maximum of 21 degrees for the serpentine area and 24 degrees for mica gneiss. Aspect of both study sites was west to southwest (Table 1A). Total cover of undergrowth vegetation (0–2 m) was less than 50% in both samples (Table 1A); the relatively low covers determined for the open serpentine site were probably the result of the early sampling date and the exclusion of non-living materials.

Significant differences between the two study sites were observed with respect to water retention differences, cation exchange capacity, percentage base saturation, extractable calcium and magnesium,

calcium–magnesium ratio, and pH (Table 1B). Water retention difference in soil derived from gneissic parent material was estimated at almost 2.5 times that of the serpentine soil. The higher percentage base saturation and lower calcium–magnesium ratio on serpentine are primarily due to the higher level of magnesium in the soil. This level of magnesium is consistent with that reported for serpentine sites throughout the world (Proctor and Woodell 1975); our calcium–magnesium ratio is at the low end of the range of reported values. Reaction of the serpentine soil is circumneutral, whereas that of the mica gneiss soil is acidic and thus more typical of southern Appalachian mountain soils (Lee 1955).

VEGETATION CHARACTERIZATIONS. Various classification systems have been used to name vegetation units (cf. Mueller-Dombois and Ellenberg 1974). The concepts that probably come closest to representing the vegetation types described here are the consociation discussed by DuRietz (1921), and the community cover class proposed by Radford (1980). Vegetation type names used below follow the latter author

Table 1. Site and substrate characteristics of serpentine and mica gneiss sites. Significance levels of Wilcoxon Rank Sum Test (null hypothesis: $\mu_1 = \mu_2$) are indicated by asterisks (*, significant at 0.01 level; **, significant at 0.002 level; n.s., not significant).

Sample Characteristics	Serpentine (N = 11)	Mica Gneiss (N = 5)
A. Site characteristics (mean; \pm one standard deviation in parentheses)		
Elevation (m)	1015 (\pm 16)	1088 (\pm 22)**
Slope (degrees)	16.3 (\pm 3.1)	21.6 (\pm 1.9)**
Compass direction (degrees)	260 (\pm 14.0)	255 (\pm 12.2) n.s.
Undergrowth (0–2 m) vegetation cover (%)		
Trees	4.72 (\pm 4.54)	6.33 (\pm 7.86) n.s.
Shrubs	12.11 (\pm 9.45)	7.78 (\pm 8.35) n.s.
Herbs	26.71 (\pm 12.33)	33.39 (\pm 37.15) n.s.
All	43.53 (\pm 12.34)	47.50 (\pm 30.36) n.s.
B. Soil physical and chemical properties (mean; \pm one standard deviation in parentheses)		
Average depth surface horizon (cm)	5.6 (\pm 3.8)	5.2 (\pm 2.9) n.s.
% water at –33 kPa, dry mass basis†	27.58 (\pm 3.47)	38.88 (\pm 7.03)*
% water at –1500 kPa, dry mass basis†	20.65 (\pm 3.02)	22.41 (\pm 8.06) n.s.
Water retention difference (based on % water at –33 kPa and –1500 kPa)†	6.93 (\pm 1.75)	16.47 (\pm 1.75)**
Cation exchange capacity (meq/100 g)	17.73 (\pm 3.24)	7.72 (\pm 1.14)**
% base saturation	89.6 (\pm 4.1)	21.2 (\pm 5.7)**
Calcium (meq/100 g)	1.33 (\pm 0.43)	0.84 (\pm 0.38)**
Magnesium (meq/100 g)	14.37 (\pm 2.66)	0.52 (\pm 0.11)**
Ca:Mg	0.09 (\pm 0.03)	1.55 (\pm 0.44)**
pH	6.1 (\pm 0.3)	4.7 (\pm 0.3)**
% organic matter	5.2 (\pm 1.2)	6.1 (\pm 1.9) n.s.

†N = 10 for serpentine sample set.



Fig. 2. The pine-savanna on the Buck Creek olivine-serpentine outcrop.

in that the common generic name of the canopy dominant(s) is combined with the general habitat feature.

Pine-savanna on serpentine: An open canopy of *Pinus rigida* (pitch pine) accompanied by occasional hardwoods dominates the steep west-facing slope of the Buck Creek barren (Fig. 2). Trees are stunted and a two-phase pattern is created in the undergrowth by patches of cespitose grasses that alternate with clumps of tall shrubs. An average of 36 species per 0.04 ha quadrat was observed for the pine-savanna (Table 2). The small number of species occurring in the canopy of the pine-savanna is striking, as is the overwhelming importance of *Pinus rigida* (Table 3), which averages 83 percent of total tree importance value in a quadrat. There is no well developed subcanopy stratum in this vegetation type, although saplings of *P. rigida*, *Acer rubrum* (red maple), and *Quercus alba* (white oak), and mature individuals of *Sassafras albidum* (sassafras) and *Amelanchier arborea* (serviceberry) are present. Total basal area of living trees is 20.6 m²/ha.

Quantitative data (mean cover and constancy) are presented in Table 4 for the prevalent undergrowth species of the serpentine sample. Most tree species occurring in the undergrowth on serpentine are highly constant, although their cover (in terms of seedlings, low branches, or trunk area in the undergrowth sample) is low. Characteristic (i.e., highly constant) and important shrubs of the undergrowth are *Viburnum cassinoides*, *Vaccinium stamineum*, and *Physocarpus opulifolius*.

Several herbaceous species are conspicuous dominants of the undergrowth along

Table 2. Species richness of serpentine and mica gneiss sites (mean number of species; \pm one standard deviation in parentheses).

Growth-forms	Serpentine (N = 11)	Mica Gneiss (N = 5)
Species/0.001 ha		
All	27.9 (\pm 2.8)	27.6 (\pm 14.0)
Species/0.04 ha		
Trees	6.4 (\pm 1.9)	12.2 (\pm 1.6)
Shrubs	7.1 (\pm 1.0)	5.8 (\pm 2.3)
Herbs	22.6 (\pm 4.0)	24.6 (\pm 16.2)
All	36.1 (\pm 5.3)	42.6 (\pm 16.6)

Table 3. Species representation in the canopy of serpentine and mica gneiss sites (mean importance value; percentage constancy in parentheses).

Species	Serpentine (N = 11)	Mica Gneiss (N = 5)
<i>Pinus rigida</i>	83.3 (100)	
<i>Tsuga canadensis</i>	6.1 (64)	1.4 (40)
<i>Quercus alba</i>	4.9 (45)	13.9 (100)
<i>Acer rubrum</i>	3.1 (55)	19.4 (100)
<i>Sassafras albidum</i>	1.3 (18)	
<i>Oxydendrum arboreum</i>	0.9 (18)	6.4 (60)
<i>Betula lutea</i>	0.3 (9)	
<i>Amelanchier arborea</i>		3.3 (60)
<i>Quercus rubra</i>		31.8 (100)
<i>Quercus coccinea</i>		6.8 (60)
<i>Robinia pseudo-acacia</i>		4.4 (40)
<i>Quercus prinus</i>		3.5 (40)
<i>Carya glabra</i>		3.1 (60)
<i>Nyssa sylvatica</i>		2.2 (40)
<i>Ilex ambigua</i>		2.0 (20)

with the above shrubs. Three perennial forbs and two perennial grasses having cover values ranging from 2% to nearly 7% are *Senecio plattensis*, *Hexastylis arifolia* var. *ruthii*, *Thalictrum macrostylum*, *Andropogon scoparius*, and *A. gerardii*. These are also present in every sample quadrat. Another perennial grass, *Poa languida*, is also a characteristic species of the pine-savanna; its cover is low because of its slight stature.

There are, among both the prevalent species listed in Table 4 and additional unlisted species, a large number of forbs and graminoids that occur with low frequency in the pine-savanna, but nevertheless are good indicators for this vegetation type. These species do not occur in the oak-mixed hardwood type, are uncommon in the southeastern United States, and are restricted to particular microhabitats on the serpentine. These include, in more open, grassy areas, *Agropyron trachycaulum*, *Castilleja coccinea*, and the extremely cespitose *Sporobolus heterolepis*; in seeps, *Parnassia grandifolia* and *Sanguisorba canadensis*; and in shaded, moist sites under *Tsuga canadensis* (hemlock) or tall shrubs, *Polygala paucifolia*.

Oak-mixed hardwood type on mica gneiss: Sample quadrats on mica gneiss differ from each other primarily in the composition and structure of their undergrowths. All but one consist of a closed canopy of *Quercus rubra* (red oak) mixed with varying densi-

Table 4. Species representation (prevalent species only) in the undergrowth of serpentine and mica gneiss sites (mean cover; percentage constancy in parentheses).

Species	Serpentine (N = 11)	Mica Gneiss (N = 5)
TREES (seedlings, saplings)		
<i>Sassafras albidum</i>	1.01 (100)	0.03 (40)
<i>Acer rubrum</i>	0.85 (100)	0.82 (100)
<i>Pinus rigida</i>	0.19 (100)	
<i>Tsuga canadensis</i>	2.0 (91)	0.02 (80)
<i>Amelanchier arborea</i>	0.14 (91)	0.43 (100)
<i>Quercus alba</i>	0.11 (54)	0.27 (100)
<i>Magnolia acuminata</i>	0.41 (18)	
<i>Quercus rubra</i>		0.84 (100)
<i>Castanea dentata</i>		0.56 (100)
<i>Cornus florida</i>		2.20 (80)
<i>Carya glabra</i>		0.04 (80)
<i>Quercus coccinea</i>		0.0 (60)
<i>Hamamelis virginiana</i>		0.49 (40)
<i>Nyssa sylvatica</i>		0.02 (40)
<i>Betula lutea</i>		0.0 (40)
SHRUBS		
<i>Viburnum cassinoides</i>	4.92 (100)	
<i>Vaccinium stamineum</i>	1.78 (100)	0.20 (80)
<i>Physocarpus opulifolius</i>	1.38 (91)	
<i>Smilax glauca</i>	0.59 (91)	0.18 (60)
<i>Kalmia latifolia</i>	1.76 (82)	1.18 (60)
<i>Vaccinium constablei</i>	0.72 (82)	
<i>Smilax rotundifolia</i>	0.44 (54)	
<i>Rhododendron maximum</i>	0.01 (27)	
<i>R. calendulaceum</i>		0.02 (80)
<i>Vaccinium vacillans</i>		1.86 (60)
<i>Smilax rotundifolia</i> var. <i>quadrangularis</i>		0.36 (60)
HERBS		
<i>Senecio plattensis</i>	6.94 (100)	
<i>Andropogon scoparius</i>	4.25 (100)	
<i>A. gerardii</i>	3.19 (100)	
<i>Hexastylis arifolia</i> var. <i>ruthii</i>	2.92 (100)	
<i>Thalictrum macrostylum</i>	2.14 (100)	
<i>Poa languida</i>	0.19 (100)	
<i>Carex</i> sp. #1	0.42 (91)	
<i>Agropyron trachycaulum</i>	0.79 (82)	
<i>Phlox carolina</i>	0.46 (82)	
<i>Danthonia spicata</i>	0.34 (82)	0.50 (60)
<i>Prunella vulgaris</i>	0.18 (82)	
<i>Oenothera tetragona</i>	0.10 (82)	
<i>Polygala paucifolia</i>	0.67 (73)	
<i>Houstonia serpyllifolia</i>	0.54 (73)	
<i>Castilleja coccinea</i>	0.04 (73)	
<i>Carex</i> sp. #2	0.62 (64)	
<i>Sporobolus heterolepis</i>	0.43 (64)	
<i>Panicum dichotomum</i>	0.11 (64)	0.30 (40)
<i>Sisyrinchium mucronatum</i>	0.0 (64)	
<i>Deschampsia caespitosa</i> var. <i>glauca</i>	0.24 (55)	
<i>Aster undulatus</i>	0.05 (55)	0.20 (60)
<i>Thaspium trifoliatum</i>	0.03 (55)	0.07 (60)
<i>Aster</i> sp. #1	0.57 (46)	
<i>Chimaphila maculata</i>		0.06 (100)
<i>Carex</i> sp. #3		0.56 (80)
<i>Uvularia pudica</i>		0.40 (80)
<i>Solidago curtisii</i>		0.69 (60)
<i>Lysimachia quadrifolia</i>		0.65 (60)
<i>Panicum boscii</i>		0.36 (60)
<i>Luzula acuminata</i>		0.35 (60)
<i>Prenanthes</i> sp.		0.30 (60)
<i>Solidago</i> sp.		0.28 (60)

Table 4. (continued)

Species	Serpentine (N = 11)	Mica Gneiss (N = 5)
<i>Potentilla canadensis</i>		0.26 (60)
<i>Melampyrum lineare</i>		0.22 (60)
<i>Pedicularis canadensis</i>		0.20 (60)
Aster sp. #2		0.18 (60)
Unidentifiable taxon		0.09 (60)
<i>Viola</i> sp.		0.09 (60)
Poaceae sp.		0.06 (60)
<i>Scutellaria elliptica</i>		0.04 (60)
<i>Smilacena racemosa</i>		0.04 (60)
<i>Goodyera pubescens</i>		0.00 (60)
<i>Thelypteris noveboracensis</i>		24.80 (40)
Aster sp. #3		0.62 (40)

ties of other hardwoods (Mansberg 1981). Differences in undergrowth composition among sample quadrats in this type are reflected by coefficients of variation for herb species richness, which reach 66% in the mica gneiss sample set while not exceeding 18% in the serpentine sample set. Total species richness is slightly higher in the oak-mixed hardwood type because a greater number of canopy species occur there than on serpentine (Table 2). No single hardwood species reaches an importance value of 50% but *Q. rubra* clearly exceeds other species, with *Acer rubrum* and *Q. alba* following. The remaining species range from 1.4% to nearly 7% of total importance and are moderately constant (Table 3). *Castanea dentata* (American chestnut) and *Cornus florida* (flowering dogwood) are highly constant in the undergrowth and thus can be considered characteristic species of the type (Table 4). American chestnut can be assumed to have been an important species here earlier in the century. At least one recognizable large dead stem of *Castanea* occurred in every quadrat on mica gneiss. Total basal area of living trees is 29.8 m²/ha.

Overall shrub cover is low in our sample (Table 1A) though in two quadrats a dense stratum of *Kalmia latifolia* excluded most other shrubs and herbs. The high cover of the fern *Thelypteris noveboracensis* (Table 4) is due to its dominance in two of the five quadrats. *Chimaphila maculata* is the only prevalent undergrowth herb that occurs with 100% constancy. It is rare in the pine-savanna and is thus a differential species for the oak-mixed hardwood type. An un-

identified *Carex* sp. (also not observed in the pine-savanna) and the liliaceous *Uvularia pudica* occur in four out of five quadrats.

COMPARISONS OF LIFE-FORMS AND GEOGRAPHIC AFFINITIES. In terms of number of species, hemicryptophytes, followed by phanerophytes, are the most common life-forms in the pine-savanna (Table 5). In the oak-mixed hardwood type, hemicryptophytic and phanerophytic species are equally common. Hemicryptophytes are somewhat less abundant in the flora on mica gneiss than in that on serpentine. Chamaephytes are better represented in the serpentine flora primarily because of the presence of *Hexastylis arifolia* var. *ruthii* and *Gaultheria procumbens*, non-woody, evergreen perennial forbs of low stature. Therophytes, namely scapose annuals, are barely present in the pine-savanna type but account for 5% of the total species list of the oak-mixed hardwood type.

The vascular plant species of the two study areas have generally similar patterns of geographic distribution (Table 6). Of

Table 5. Life-form representation in serpentine and mica gneiss sites (percent total species list).

Life-forms	Serpentine (N = 11)	Mica Gneiss (N = 5)
Phanerophytes	31.6	33.7
Chamaephytes	6.3	2.1
Hemicryptophytes	41.8	32.6
Geophytes	7.6	12.6
Therophytes	1.3	5.3
Lianas	3.8	3.2
Other	7.6	10.5

Table 6. Geographic-areal representation in serpentine and mica gneiss sites (percent total species list; number of species in parentheses).

Geographic Area	Serpentine (N = 11)	Mica Gneiss (N = 5)
1. Throughout No. Amer.	6.3 (5)	3.2 (3)
2. Throughout E. No. Amer.	19.0 (15)	18.9 (18)
3. E. No. Amer. & Ozarks	8.9 (7)	7.4 (7)
4. E. No. Amer. & Gr. Plains	7.6 (7)	10.5 (10)
5. E. No. Amer., Gr. Plains, & Ozarks	5.1 (4)	5.3 (5)
6. Southeastern States	10.1 (8)	9.5 (9)
7. So. Appalachians	5.1 (4)	9.5 (9)
8. Restricted in/endemic to So. Appalachians	1.3 (1)	2.1 (2)
9. Appalachians & Ozarks	1.3 (1)	2.1 (2)
10. NE No. Amer. to So. Appalachians	10.1 (8)	9.5 (9)
11. NE No. Amer. to So. Appalachians & Gr. Plains	1.3 (1)	1.1 (1)
12. Across No. States, to So. Appalachians	3.8 (3)	2.1 (2)
13. Disjunct	6.3 (5)	0.0 (0)
14. Other	12.7 (10)	19.0 (18)
Total number of species in sample	79	95

particular interest is the relatively weak representation, on serpentine, of species having a generally southern Appalachian distribution. Although the mica gneiss sample contains a few more species that are found both on the Great Plains and in eastern North America, the serpentine sample contains a noteworthy disjunct element representing northern and midwestern prairie regions.

Discussion. Numerous studies have described a compositional gradient for intermediate elevations in the southern Appalachians (Braun 1950, Whittaker 1956, Cooper and Hardin 1971, Wentworth 1980): mesophytic forests of coves, gorges, and lower slopes; oak-mixed hardwood forests of upper slopes; and pine forests of steep south- and west-facing slopes and ridges. These major vegetation types occupy a complex environmental gradient, which in its broadest sense is characterized by increasing soil and air temperatures and decreasing moisture availability for plants. The pine-dominated types that have been described (e.g., Whittaker 1956, Racine 1966) resemble the Buck Creek pine-savanna in structure, although details of their composition (especially for undergrowth components) vary considerably. Nevertheless, the physiognomy, preponderance of evergreen and shrub or graminoid growth-forms, xeric microclimate, and frequent occurrence on shallow, rocky, nutrient-poor

soils (Cooper and Hardin 1971) of these pine-dominated types suggest that most occupy sites distinguished by stressful environmental conditions.

Our determination of lower water retention difference and calcium-magnesium ratio in the serpentine soils (Table 1B) supports the supposition that the pine-savanna vegetation of our study area experiences a more stressful environment than does the oak-mixed hardwood type. However, Miller (1977) showed little difference in plant extractable water between serpentine and adjacent schist-derived soils. Certain community attributes provide further, albeit indirect, evidence that conditions on the serpentine site may be stressful. For example, total species richness and canopy basal area are both lower on serpentine. The interpretation of these measures, particularly richness, must be made with caution. Whittaker (1960) and others have noted that species richness does not always increase with decreasing environmental stress, and recent studies indicate that total forest diversity actually declines as a result of canopy closing, which itself occurs with increasing nutrient availability and moisture (Auclair and Goff 1971). Of interest in this regard is the fact that shrub and herb richness indices were similar in our two study areas, whereas the canopy of the mica gneiss site was somewhat more diverse.

It is common in eastern deciduous forests for phanerophytes and hemicrypto-

phytes to share floristic importance (Whittaker 1960), as we observed for both the pine-savanna on serpentine and the oak-mixed hardwood vegetation type on gneiss. Increases in floristic importance of hemipterophytes and chamaephytes on the Buck Creek serpentine relative to mica gneiss, as well as a slight decrease in importance of phanerophytes, are suggestive of trends observed by Whittaker (1960) for serpentine contrasted to gabbro and diorite in the Siskiyou Mountains of Oregon (see also Kruckeberg 1969a). Slight decreases in number of phanerophytes and larger increases in hemicryptophytes have also been observed along gradients of decreasing moisture (cf. Proctor and Woodell 1975, Table II). The above observations support the widely asserted hypothesis that environmental stress is at least partly responsible for the peculiarities of serpentine flora and communities.

Serpentine vegetation in several regions, notably in the northwestern United States, illustrates the effect of incomplete canopy closure on community diversity and structure. The type of patchy, or two-phase, vegetation pattern so striking at Buck Creek has been repeatedly observed: examples are scattered conifers over scattered and stunted sclerophyllous shrubs interspersed with grassland on xeric serpentine in the Siskiyou Mountains of Oregon (Whittaker 1960), chaparral and grassland on serpentine in the coast ranges of southern California (Woodell, Mooney, and Lewis, unpublished; cited in Proctor and Woodell 1975), and scattered pines above dense hemicryptophytes and shrubs in the Wenatchee Mountains of Washington (Kruckeberg 1969a, Del Moral 1972, 1974). An important consequence of the development of such a pattern is that the resulting patterns of light, of root occupation, and of levels of competitive intensity generate relatively high levels of habitat heterogeneity (Del Moral 1972). On the Buck Creek serpentine there may also be a high level of habitat heterogeneity generated by veins of differentially weathering minerals within the olivine matrix. Although our data do not appear to support Del Moral's prediction that greater total species richness will occur in this type of system (relative to a closed-canopy one) it may be that these soils are

sufficiently droughty or nutrient-deficient to counterbalance the heterogeneity effect of the vegetation pattern.

Some floristic features of the Buck Creek serpentine vegetation are consistent with those observed on serpentine elsewhere, whereas other features appear not to be. Disjunct species occurrences, as found in 6% of the Buck Creek flora, have been observed on serpentine (Rune 1953, Duvigneaud 1966). For example, the main range of *Senecio plattensis* includes the prairies and plains states of central North America; the species also occurs at disjunct stations in eastern prairie relicts (Uttal 1982). *Sporobolus heterolepis*, another important herbaceous species at Buck Creek, is also disjunct from its main range. *Agropyron trachycaulum*, *Deschampsia caespitosa* var. *glauca*, and *Muhlenbergia glomerata* occur here at the periphery of their ranges.

Ecotypic differentiation is also typically observed on serpentine (Kruckeberg 1954, 1967, Proctor 1971, Ernst 1972); this trend is represented at Buck Creek by the presence of morphological variants and undescribed taxa: a stoloniferous form of *Hexastylis*, tentatively called *H. arifolia* var. *ruthii* Blomquist, a hybrid *Aster* (J. Semple, pers. comm.), an unusually small form of *Thalictrum macrostylum*, and a low stoloniferous form of *Rhododendron viscosum* (A. E. Radford, pers. comm.).

The high percentage cover of perennial grasses on the Buck Creek serpentine (about 22% in early summer, slightly higher in late fall) supports the observation that grasses possess a remarkable ability to occupy serpentine sites (Whittaker 1960). In experimental studies (Nixon and McMillan 1964), three grasses, *Andropogon scoparius*, *Panicum virgatum*, and *Sorghastrum nutans*—all taxa occurring at Buck Creek—displayed wide tolerance to a series of edaphic conditions that included a serpentine soil, suggesting that some species can occupy these sites without ecotypic differentiation.

The absence, at Buck Creek, of taxa easily considered endemic is puzzling. Serpentine endemism is frequently observed and has been attributed to both tolerance of and requirements for magnesium and/or heavy metals (Madhok and Walker 1969). There is, however, extreme variability in chemical composition among serpentines.

Johnston and Proctor (1979) have, in fact, described vegetation of intermediate serpentine-effect growing on soils having only slightly lowered calcium-magnesium ratios and relatively higher than usual (for serpentine) phosphorus and potassium levels. Preliminary studies of available metal ions in the plants and soil at Buck Creek suggest that this would be a worthwhile area of research at this site (Wickland and Mansberg 1981). Further examination of the Buck Creek flora also may result in the discovery of new plant taxa, as the presence of morphological variants suggests.

The pine-savanna of the Buck Creek olive-serpentine outcrop resembles in its physiognomy, structure, and, to some extent, its species composition other "barrens" of the eastern United States. The vegetation of serpentine barrens of Lancaster County, Pennsylvania, has been characterized as consisting of scattered oaks (*Quercus marilandica*, blackjack oak, and *Q. stellata*, post oak), pines (*Pinus virginiana*, virginia pine, and *P. rigida*), *Juniperus virginiana* (red cedar), and red maple, with dense undergrowth of ericaceous shrubs, *Smilax*, and mixed grasses and forbs (Miller 1977). Braun (1950) described the cedar glades of Tennessee and Kentucky as consisting of widely scattered *Juniperus virginiana* and an herbaceous stratum containing high proportions of prairie species (cf. also Quarterman 1950a,b). Braun (1950) also noted a belt of barrens, characterized by tall grasses and little woody vegetation, extending from the Ohio River southwest across Kentucky almost to the Tennessee border, and "relict prairies" along belts of limestone in the Knobs Border area of northern Kentucky and southern Ohio (Braun 1928). The natural vegetation of the Black Belt of central Alabama (Gulf Coastal Plain) probably consisted of prairie and savanna: examination of 19th century survey notes has led several researchers to conclude that presettlement vegetation included both unforested and low-density forested acreage over alkaline clays associated with Late Cretaceous chalk (Jones and Patton 1966, Rankin and Davis 1971). Braun (1950) noted that present day remnants of these communities consisted principally of "species of the interior."

These and other areas of similar physiognomy and floristic composition have

been described (e.g., Pennell 1910, De Selm *et al.* 1969, Wherry 1963) in the eastern United States. Most occur on substrates that would be considered "unusual" or "extreme" in the regional context. As a group, these eastern North American "barrens" are worthy of further study. Comparisons of their flora and vegetation, coupled with experimental study of species' responses to unusual substrate conditions and disturbance, could yield insight into the common factors responsible for their persistence as "islands" in the deciduous forest region. Such research may also aid our understanding of the origin of the barrens when interpreted in light of the increasing body of knowledge of holocene climatic and vegetational changes.

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