Jerry L. Burgess, Steven Lev, Christopher M. Swan, and Katalin Szlavecz "Geologic and Edaphic Controls on a Serpentine Forest Community," Northeastern Naturalist 16(sp5), 366-384, (1 June 2009). https://doi.org/10.1656/045.016.0527

Geologic and Edaphic Controls on a Serpentine Forest Community

Authors: Burgess, Jerry L., Lev, Steven, Swan, Christopher M., and Szlavecz, Katalin

Source: Northeastern Naturalist, 16(sp5) : 366-384

Published By: Eagle Hill Institute

URL: https://doi.org/10.1656/045.016.0527

Soil and Biota of Serpentine: A World View
2009 *Northeastern Naturalist* 16(Special Issue 5):366–384

Geologic and Edaphic Controls on a Serpentine Forest Community

Jerry L. Burgess[1,*], Steven Lev[2], Christopher M. Swan[3], and Katalin Szlavecz[1]

Abstract - This study examined woody vegetation, edaphic factors, bedrock geochemistry, petrography, and outcrop structure to evaluate some of the community-structuring factors in an ultramafic terrain of Maryland. Analyzing the dynamic nature of combined geological and ecological processes can detect correlative relationships between factors that are typically considered as independent such as tectonically driven bedrock fracturing and ecological community interaction. This study provides evidence for structural variation in fracture density of bedrock as a partial control on tree species distribution in an ultramafic woodland/forest ecosystem. Increases in the number of bedrock fractures correlates negatively with plot-level volumetric soil moisture. Additionally, the degree of serpentinization of the ultramafic parent material results in compositional variation in Ca, Mg, and Ni of parent materials and soils. The combination of these factors provides a significant level of control on the distribution of xeric tree species.

Introduction

Plant community structure and diversity is controlled by many factors. Among the many factors that work in concert with biotic interactions (competition, predation, etc.) are the abiotic mechanisms that shape species diversity and distributions. Spatial and temporal heterogeneity in the physical environment also plays a key role in structuring community composition. One such mechanism that influences plant diversity is the fundamental structure and geochemistry of the parent materials–the underlying geodiversity. The overall patterns of vascular plant diversity on the landscape are a function of the biodiversity and geodiversity (Mutke and Barthlott 2005). As geodiversity increases, the number of niche dimensions afforded for organismal distribution also increases (Silvertown 2004). Geodiversity has many components, but with respect to plant community compositional control, one geological factor that is often overlooked is the importance of the structure of the parent rock to plant community composition. In this case, geological structure refers to the macroscopic features shown by rocks. Such features

[1]Department of Earth and Planetary Sciences, Johns Hopkins University, 301 Olin Hall, 3400 North Charles Street, Baltimore, MD 21218. [2]Department of Physics, Astronomy, and Geosciences, Towson University, 8000 York Road, Towson, MD 21252-0001. [3]Department of Geography and Environmental Systems, University of Maryland, 211 Sondheim Hall, 1000 Hilltop Circle, Baltimore, MD 21250. [*]Corresponding author - jerry.burgess@jhu.edu.

are jointing, foliation, cleavage, shear fabrics, fractures, faults, and other fissures. These features provide preferred pathways for agents of weathering such as water or root structures. Other structural features such as shear zones are generally accompanied by grain-size reduction via dynamic recrystallization in the host rock, and accordingly, these differences in parent-material grain size will also affect soil genesis, creating spatial heterogeneity that is fundamental to the dynamics of ecosystems (Levin 1992).

The relationship between geodiversity and forest woody species distribution remains obtuse in many ecosystems. Areas with serpentinized rocks are model habitats for geoecological studies as they are considered extreme environments with plants having special adaptations or where the rock may serve as refugia for many species (Kruckberg 2002). The tight coupling between rock, soil, and flora evident in these areas provides a unique opportunity to explore relationships between geodiversity and biodiversity. In addition, the temporal component of heterogeneity supplemented by anthropogenic disturbances plays an equally important role in determining tree species distribution creating patch mosaics in forest communities (Denslow and Hartshorn 1994). Semi-natural grassland and savannah ecosystems, such as serpentine barrens and associated woodlands, are of considerable interest for their number of endemic species, rare and threatened species, biodiversity, and landscape value. These habitats have become reduced and fragmented throughout Eastern North America due to changes in management, grazing, and the absence of frequent and widespread fires formerly promoted by Amerindians (Marye 1955a, b, c, Tyndall and Hull 1999). The subsequent extirpation of Amerindians, a lack of livestock grazing, and selective clearing has allowed the once expansive xerophytic grasslands and savannahs to become forested; however, remnants of these grasslands are still present (Tyndall 2005, Tyndall and Hull 1999). It is these successional forested regions that are of interest to this work.

Unusual species assemblages are typically equated with the eastern serpentine barrens, but serpentine savannas, woodlands, and forests may also contain regionally unique communities (Brush et al. 1980, Latham 1993). Typically, these local assemblages are equated to edaphic physical and chemical properties such as shallow soil depth and low water-holding capacity. Chemical attributes which are characteristic of serpentine soils worldwide include: elevated levels of heavy metals such as Cr, Ni, and Co that are toxic to many plants; near-neutral pH values; and Ca:Mg ratios <1 (Alexander et al. 2007; Rajakaruna et al. in press; Roberts and Proctor 1992).

The influence of parent rock material on soil formation and flora has long been evident to ecologists. However, small-scale investigations of such phenomena are rarely available. Local variation in geologic substrate and derived soils within an ultramafic lithotype may act as abiotic templates that correspond to associated tree-community compositions and successional trajectories. In this paper, we investigate edaphic properties derived from ultramafic parent materials in relation to xeric tree species abundance. The

results are discussed in terms of the factors controlling xeric species abundance. Specifically, this study investigates the following question: How is woody plant community composition affected by the spatial distribution of structural and chemical discontinuities across a single ultramafic lithotype?

Materials and Methods

Field area

The Pilot Serpentine Barrens (PSB) is located approximately 1 km east of the town of Pilot, in the Piedmont of western Cecil County, MD. The barrens lie within the Conowingo Dam Susquehanna River watershed as part of the Upper Western Shore basin and extend to the Pennsylvania state line. Mean annual temperature is 12.2 ºC with 122.1 cm precipitation (MSCO 2008). Bedrock consists of a northeast-trending group of undifferentiated serpentinite and other mafic-ultramafic bodies that may be an extension of the Baltimore Mafic Complex and that were tectonically emplaced into the metasediments of the Wissahickon Formation (Crowley 1976, Hanan 1980).

Natural resource and mining reports combined with historical aerial photographs spanning 1937 to 2007, indicate some portions of the PSB and surrounding serpentinite were mined for albite (Na feldspar) or building stone in the mid–late 1800s, and there was selective cutting of oaks for charcoal production. However, in the 20th century, there is only limited evidence of farming on these typically nutrient-poor soils. Nearly all of the forested area was extensively logged by clear-cutting during the 1920s and early 1930s. Since that time, the forested areas have remained virtually intact, with most of the forested area today held by private landowners.

Ecology

Serpentine outcrops in the Mid-Atlantic region are characterized by prairie or savanna grassland if maintained by periodic disturbance such as fire. In the absence of fire, the prairies vary from of patch mosaics of prairie-like openings and pine scrub or greenbrier thickets to mixed pine-deciduous woodlands to oak-dominated forests in areas of deeper soils. The deeper soils on serpentine can support vegetation similar to that supported by soils derived from silica-rich parent materials (Brush et al. 1980, Dearden 1979, Shreve 1910). The PSB is a federally endangered barren community protecting rare and endangered wildflower species such as *Talinum teretifolium* Pursh (Fameflower), *Aster depauperatus* Fern (Serpentine Aster), and *Sporobolus heterolepis* Gray (Prairie Dropseed), among other species.

Of the serpentinite-dominated rocks of the Mid-Atlantic States, afforestation of nearly all of the serpentine barrens has occurred since the mid-twentieth century (Anderson et al. 1999, Latham 1993). The major threat to this ecosystem is the invasion of woody plants, primarily *Juniperus* and *Pinus* species (Tyndall 2005). In Eastern North America, the broadly termed Conowingo Barrens of Pennsylvania and Maryland have received

considerable attention. Of the original 21,000 ha of serpentinite lands, only 1100 ha have persisted (Kruckeberg 2004). On a few extant barrens, efforts to restore the habitats have been undertaken. In a study from the Conowingo Barrens of Pennsylvania, Barton and Wallenstein (1997) reported that *Pinus virginiana* Mill. (Virginia Pine) does not, at the stand level, change soil chemical imbalances characteristic of serpentine soils, but cautioned that the pine's positive influence on soil depth alone could promote further succession towards forests typical of non-serpentine sites in the region. Though these studies document the influence of pine on serpentine soils, the PSB are also heavily encroached upon by *Juniperus virginiana* L. (Eastern Red Cedar). However, mixed deciduous woodlands and forests cover much of the PSB area. The forests of the PSB include xeric woodlands of open stands of Virginia Pine intermingled with *Quercus marilandica* Meunch. (Blackjack Oak) and *Quercus stellata* Wang. (Post Oak). Mesophytic forests are composed of these oaks and others such as *Quercus rubra* L. (Red Oak), *Q. alba* L. (White Oak), *Q. montana* Willd (Chestnut Oak), and *Q. velutina* Lam (Black Oak) along with numerous other species, most notably *Carya* spp. (hickory), *Prunus* spp. (cherry), *Fagus grandifolia* Ehrh (American Beech), *Acer rubrum* L. (Red Maple), *Sassafras albidum* Nutt (Sassafras), *Betula lenta* L. (Sweet Birch), and *Robinia pseudoacacia* L. (Black Locust). Based on observational data, such as diameter at breast height, and historical records (Shreve 1910), the forests are undergoing successional change towards maple and beech domination. On exposed rock surfaces, common serpentinophiles are saplings of Blackjack Oak, *Cerastium arvense* L. var. *villosum* (Darl.) (Serpentine Chickweed), and *Symphyotrichum depauperatum* Fern (Serpentine Aster).

The majority of PSB soils are Chrome Series soils that are typical of the other Maryland serpentine areas (shallow with sandy textures). PSB soils are mostly chrome silt loams and chrome clay loams, with lesser amounts from the Neshaminy Series silt and clay loams (USDA 1973). The soils are mostly alfisols, classified as fine-silty or fine-loamy, mostly serpentinic, mesic Typic Hapludalfs or Lithic Hapludalfs, with loess added, which has given them properties atypical of serpentine soils (Rabenhorst et al. 1982).

Geology

There are a number of fault-bounded, tectonically emplaced, and variably metamorphosed ultramafic bodies in the Maryland Piedmont. The Conowingo Barrens and their southernmost expression, the PSB, are the southern extension of the State-Line mafic complex, which underlies part of the Maryland and Pennsylvania Piedmont. In turn, the State-Line mafic complex is the northern-most segment of the Baltimore Mafic Complex (BMC). The BMC is a large exposure of mafic and ultramafic rocks that includes Soldier's Delight, but not all of the complex need have the same tectonostratigraphic interpretation. The northern part of the BMC is bounded to the northwest by the Peters Creek - Westminster terrain (Gates et al. 1999, Muller et al. 1989). This boundary is interpreted to be a thrust fault that was later reactivated as a

dextral strike-slip fault (Gates 1992, Higgins and Conant 1990). Ultramafic components of the BMC contain a basal unit of serpentinized peridotite with relict websterite and dunite kernels with an overlying massive and layered gabbronorite that contains minor silica unsaturated peraluminous to aplitic igneous bodies. The PSB portion also displays an upper mafic component that varies from gabbro to quartz gabbro to diorite. The unit is approximately 3 km thick and is tectonically placed against rocks of the Wissahickon formation that is in the Glenarm series of early Paleozoic metasedimentary rocks (Hanan and Sinha 1989, Higgins and Conant 1990). The Glenarm series rests unconformably on Proterozoic basement of Baltimore gneiss (Hanan and Sinha 1989). Work by Shaw and Wasserburg (1984) and Hanan and Sinha (1989) provide compelling evidence that the State-Line, Conowingo Barrens portion of the BMC intruded continental crust at approximately 490 Ma. Other ultramafic bodies in the area (i.e., Soldier's Delight) are petrologically distinct, and these units likely represent an ophiolitic island arc complex that was obducted onto Laurentia during the closure of the Iapetus at the time of the Taconic orogeny, approximately 455 Ma (Muller et al. 1989). In a detailed study of the State-Line Complex of Pennsylvania, Gates (1992) documented a series of NE-trending dextral transcurrent shear zones of 0.2–1.4 km width creating well-foliated L-S tectonites across the serpentinite. The shear zones contain lenticular pods of weakly deformed serpentinite between the anastomosing mylonitic bands. These pods range in size from several millimeters to several hundred meters.

Sampling and measurement

Edaphic factors contributing to forest woody species community structure were investigated using 21 randomly stratified plots (25 x 50 m) with similar aspect (when possible) and elevation (>90 m) oriented along the perceived environmental gradient (Fig. 1). No plots were overlapping. At all plots, associated rock, soil, and floristic woody species canopy and understory were surveyed. Geologic data such as rock type, cleavage, foliation, kinematic indicators, mylonitic fabrics, faults, shear zones, and late fractures/joints were measured. A fracture/joint inventory was conducted by defining a representative region and measuring all structures and their spatial orientations in that region. Measurements were taken perpendicular to each set over 100 cm. Fracture density is calculated as the total number of fractures or joints per 1 m^3.

Tree species occurrence, diameter at breast height, vegetation cover, and substrate characteristics (percent soil, litter, rock) were assessed. Soil samples were collected from each site using a push probe or soil auger to establish soil depth. Soil-moisture measurements were made using a ThetaProbe® soil-moisture sensor. Composite soils for analysis were collected 1 m in from each corner, at 25 m from the end, and at the center of each plot. Litter was brushed aside and samples were taken at 0–5 cm and 5–15 cm depth, referred to as "surface" and "deep," respectively Soil characteristics measured included soil depth, pH, soil organic matter content, major

and trace element analysis, C:N ratio, soil moisture, and textural analysis. Moist-soil color was determined in the field using Munsell color charts. Samples were combined, mixed, and split to give two samples of 200–400 g that were lightly crushed, sieved to 2 mm, and sampled for textural analysis (sieving followed by measurment with a hydrometer). A moist-soil subset was taken for pH analysis. Soil pH was measured with a 20-g to 20-ml soil/water slurry using a glass electrode. The remainder was oven dried at 30 °C and powdered using an agate ball mill. A powdered subset was subsequently used for X-ray fluorescence (XRF) and C:N analyses. Total N and C were measured with an automated Perkin-Elmer 2400 Series II CHN analyzer. Soil organic matter content was estimated as loss on ignition (LOI) at 550 °C for 3 hours. Total P, Na, K, Ca, Mg, Mn, Fe, Cr, Ni, Si, and Al were measured by X-ray fluorescence using a Bruker AXS S4 Explorer wavelength-dispersive X-ray fluorescence spectrometer following the procedures outlined in Potts (1987). All samples analyzed by XRF were quantified using a matrix-matched set of USGS- and NIST-certified soil standards. At least one duplicate, one replicate, and one certified reference sample (SRM 2709, San Joachin Soil) was run with every 10 samples analyzed to monitor for external and internal reproducibility.

Values reported are typically means with the associated standard error. To assess the consistency of the data and to identify the most strongly

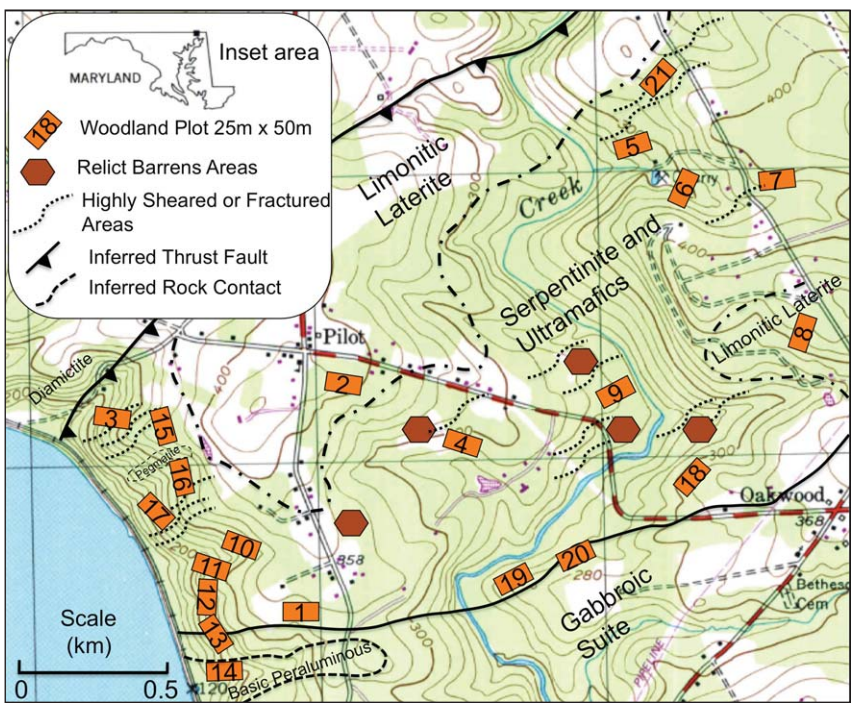

Figure 1. Map showing study location along the Susquehanna River of Maryland. Note that plot sizes are not to scale.

discriminating variables, a principal component analysis (PCA) of the rock and soil variables from the plots was performed. There were six variables in the rock PCA: fracture density, Ca:Mg ratio, and P, Cr, Ni, and Al concentrations. For the soils PCA, the following variables were assessed, for each of the two depths: soil depth, texture (gravel, silt, and clay), C:N, organic matter, pH, Ca:Mg ratio, and P, Cr, Ni, and Al concentrations.

Results

Mapped area

The major geologic boundaries, features, and contacts were mapped during this study (Fig. 1). Though mapped in greater detail, the boundaries of the serpentinite are consistent with previous mapping work of Higgins and Conant (1986). Areas where the serpentinite was highly altered to a limonitic laterite were recognized as a yellow-brown "honeycomb" outcrop or float (Fig. 1). Using an approach similar to that of Gates (1992) in the Pennsylvania State-Line mafic complex, we characterize the PSB site structurally as a series of shear zones that anastomose around lenticular pods of less-sheared, though still faulted and fractured, serpentinized peridotites. Measured fracture densities vary from four fractures per m^3 in the less sheared pods to 80 factures per m^3 in the relict barrens areas (Table 1). Sheared, folded, and fractured talcose serpentinite were apparent underlying areas predominantly composed of upland oaks (Fig. 2). Structural differences in terms of fracture density that are typically encountered in the more-sheared and-fractured bedrock (Fig. 3) and the less-fractured lenticular pods with pyroxenite (Fig. 4) were also apparent. Chemically, the bedrock is typical of other ultramafic rocks with SiO_2 around 40 percent by weight and high MgO, Cr, and Ni concentrations (Table 1). Corresponding P, Ca, and Ca:Mg ratio values are very low. The limonitic chalcedony or honeycomb lithology has similar trace-metal concentrations (high Cr and Ni), but is nearly 80% SiO_2. Ni concentrations are higher for the more sheared and (or) serpentinized rocks.

Petrography

In areas that are highly sheared, such as the vicinity of the northwestern fault contact and the relict barrens areas, the outcrop is a steatite or talcose

Table 1. Major and trace elemental data for plot-level bedrock, separated by the level of shearing and fractures and by mineralogy for the limonitic parent materials. FD = fractive density.

Rock properties	Mean all plots	Mean of sheared and highly fractured plots (FD >20/m^3)	Mean of lenticular pods of low fracture density (FD < 20/m^3)	Mean of limonitic laterites
Si (%)	39.04 ± 3.07	33.56 ± 0.93	37.01 ± 1.22	76.31 ± 2.09
Al (%)	0.55 ± 0.28	0.02 ± 0.02	1.53 ± 0.40	0.00 ± 0.00
P (%)	0.00 ± 0.01	0.00 ± 0.01	0.00 ± 0.00	0.02 ± 0.00
Cr (ppm)	2215.37 ± 111.95	2256.68 ± 122.40	2229.80 ± 109.25	1937.64 ± 89.20
Ni (ppm)	1650.81 ± 209.73	2343.86 ± 133.13	762.48 ± 105.88	948.20 ± 39.28
Ca: Mg	0.12 ± 0.05	0.02 ± 0.01	0.30 ± 0.07	0.00 ± 0.00

Figure 2. Large-scale fold with fracturing. Associated trees include the dominate Blackjack Oak with lesser numbers of Eastern Red Cedar and minor regresentation of Sassafras.

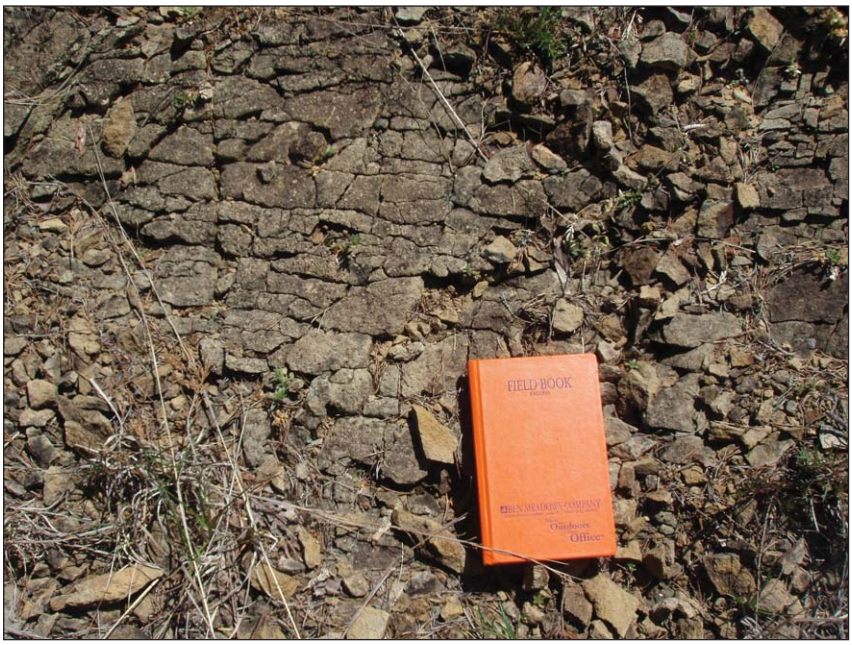

Figure 3. High fracture density serpentinite associated with barrens areas.

serpentinite with little evidence of original mineralogy. In thin section, these rocks are fine-grained with strong foliations defined by talc, lizardite, and chrysotile in a felted-mesh pattern typically cut by late serpentine veins. Serpentinized rocks at the southeastern contact with the gabbro are also talcose, with minor chlorite. Other minerals include minor magnesite and opaque minerals such as magnetite and/or chromite. Relict igneous minerals, though lacking in the highly sheared rocks, are visible in the less-sheared lenticular pods and kernels. These massive rocks come in two end-member varieties. The first is a completely serpentinized rock with a felted-mesh pattern of interlocking grains of interpenetrating serpentine, possibly antigorite, with magnetite and minor chromite, talc, or brucite. The other massive rock is a dense, partially serpentinized, often pseudomorphic rock, with abundant relict minerals of olivine, orthopyroxene, clinopyroxene, and amphibole in various proportions indicating igneous protoliths of websterite, wehrlite, and pyroxenite.

Forest characteristics

The forest canopy was mostly deciduous trees of irregular height. The understory included very dense greenbrier to more open, sapling-dominated areas. In all plots, dense *Smilax* spp. (greenbrier) was restricted to the more heavily serpentinized areas, with more open understory found on the limonitic lateritic soils or massive peridotites. A total of 33 tree species was observed across the 21 plots, with species richness ranging from 5 to 19. Table 2 details the dominant species in each plot and the

Figure 4. Low fracture density partially serpentinized peridotite from a lenticular pod. Dominant canopy species are White and Red Oak along with American Beech.

associated geology. Diversity values using the Q-statistic of Kempton and Taylor (1976), which is less sensitive to the commonest species in the sample, range from 1 to 7.7 for the plots.

Soils data are presented in Table 3. Soil depths varied from 8 cm to greater than 40, cm with variable texture and soil color across the sites. Soil colors ranged from dark-brown (7.5YR 3/2) to grey (7.5YR 6/1) in the upper 1–3 cm of the soil profile to yellow-browns (10YR 5/6) and red-browns (2.5YR 4/4) with depth. The redder (2.5YR Hues) soils are located in conjunction with the peridotites, and the reddest (2.5YR 4/6) soils with the limonitic chalcedony. The talcose serpentinites yield more yellow (10YR Hues) varieties. All soils, with the exception of plots 14 and 20, are texturally gravel-dominated. Upon laboratory analysis and thin-sectioning, it was shown that plots 14 and 20 are hosted by a mafic-ultramafic parent that is not part of the serpentinized sequence and hence is excluded from further analysis. The ultramafic rocks contain around 30% gravel by mass, but the limonitic soils contain a smaller percentage of gravel and a larger component of sand. Mg concentrations are high and corresponding Ca:Mg ratios low (<0.7) across all sites. The Ca:Mg ratio is a measure of serpentine cation imbalance. Soil organic matter content is consistently below 4% across all sites. C and N analysis of the soils yielded low N concentrations and C:N ratios between 16 and 22, with the higher values on the more fertile limonitic

Table 2. Plot-level (25 m x 50 m) data detailing the dominant geologic rock type, the tree species that comprise the majority of the forest canopy, and biodiversity measures.

Plot #	Geology	Forest canopy	Species richness	Q-statistic	Percent abundance xeric species
Plot 1	Massive serpentinite	Hickory-oak	14	4.74	6.24
Plot 2	Limonitic laterite	Cherry-maple-oak-Tulip Poplar	11	5.01	0.00
Plot 3	Talcose serpentinite	Sassafras-oak	12	5.00	12.11
Plot 4	Serpentinite	Oak	7	1.67	83.09
Plot 5	Serpentinite	Eastern Red Cedar-maple	9	3.42	34.07
Plot 6	Peridotite	Oak-gum-beech	13	3.02	5.40
Plot 7	Serpentinite	Eastern Red Cedar-oak-pine	11	3.08	66.03
Plot 8	Limonitic laterite	Beech-oak	5	0.99	0.00
Plot 9	Serpentinite	Beech-Eastern Red Cedar	15	5.41	36.20
Plot 10	Pyroxenite	Maple-oak-cherry	12	4.35	1.80
Plot 11	Pyroxenite	Maple-hickory-oak	19	7.74	1.65
Plot 12	Pyroxenite	Beech-oak-maple	19	5.65	1.30
Plot 13	Massive serpentinite	Maple-oak-hickory-ailanthus	19	6.14	0.00
Plot 14	Leuco-ultramafic	Maple-beech-gum-Tulip Poplar	12	3.42	0.00
Plot 15	Talcose serpentinite	Sassafras-oak-maple	16	6.14	21.40
Plot 16	Serpentinite	Oak-sassafras-maple	13	5.99	16.50
Plot 17	Serpentinite	Sassafras-oak	12	3.37	38.47
Plot 18	Mass	Maple-hickory-oak	16	7.21	25.00
Plot 19	Talc serpentine schist	Beech-birch-oak-aspen	13	6.37	0.00
Plot 20	Gabbro	Tulip Poplar-walnut-hickory	16	6.83	2.10
Plot 21	Serpentinite	Oak-maple-Sassafras	18	5.14	41.10

soils. Cr concentrations are enriched in the laterites compared with the other host lithologies. This finding is likely due to resistance of Cr-oxides to weathering and suggests that these phases are not likely sources for Cr in soil solutions and plants of serpentine soils (Oze et al. 2004). The pH of the soils is typically low to slightly acid (c. 4–6), leading to a low cation exchange capacity (McFee et al 1977).

Since many of the data are related covariates, a PCA was used to reveal the internal structure of the data. For the rock-related PCA (Fig. 5), both axes account for 68% of the variation. Fracture density and Ni correlate positively

Table 3. Soil data partitioned by rock parent material. Soils are separated into shallow (0–5 cm below ground surface) and deep (5–15 cm below ground surface) soils.

Soil properties	Serpentinite and steatite parent materials (n = 12)	Partially serpentinized websterite, wehrlite, and pyroxenite parent materials (n = 5)	Limonitic chalcedony parent material (n = 2)
SOM (LOI)			
Shallow	2.56 ± 0.42	1.55 ± 0.21	2.64 ± 0.10
Deep	1.23 ± 0.35	1.11 ± .025	1.67 ± 0.26
C:N			
Shallow	19.73 ± 3.49	19.12 ± 2.54	21.91 ± 3.74
Deep	16.41 ± 2.93	17.18 ± 0.42	18.54 (1 Plot)
pH			
Shallow	4.99 ± 0.38	5.48 ± 0.29	4.61 ± 0.28
Deep	5.27 ± 0.31	5.11 ± 0.15	4.70 ± 0.20
Gravel %			
Shallow	30.18 ± 7.55	31.10 ± 1.12	7.85 ± 6.35
Deep	37.47 ± 9.72	28.50 ± 1.44	0.80 (1 Plot)
Cr (ppm)			
Shallow	2526.00 ± 883.37	1891.74 ± 748.92	4904.60 ± 1855.19
Deep	2092.87 ± 648.13	1912.82 ± 745.95	4841.84 ± 2212.33
Ni (ppm)			
Shallow	1055.18 ± 346.47	453.46 ± 187.42	999.68 ± 276.53
Deep	1182.28 ± 371.19	434.03 ± 196.87	1107.76 ± 402.59
P (%)			
Shallow	0.05 ± 0.01	0.03 ± 0.01	0.07 ± 0.00
Deep	0.04 ± 0.01	0.02 ± 0.01	0.06 ± 0.01
K (%)			
Shallow	0.32 ± 0.19	0.51 ± 0.19	0.53 ± 0.22
Deep	0.33 ± 0.21	0.70 ± 0.15	0.54 ± 0.26
Ca (%)			
Shallow	0.69 ± 0.65	1.57 ± 0.28	0.08 ± 0.04
Deep	0.69 ± 0.74	1.83 ± 0.60	0.04 ± 0.02
Mg (%)			
Shallow	4.95 ± 1.64	3.94 ± 1.00	0.54 ± 0.03
Deep	5.92 ± 2.07	4.17 ± 0.99	0.56 ± 0.04
Ca:Mg (total)			
Shallow	0.25 ± 0.30	0.46 ± 0.06	0.14 ± 0.06
Deep	0.20 ± 0.24	0.49 ± 0.13	0.07 ± 0.04
Al (%)			
Shallow	1.97 ± 0.69	1.93 ± 0.39	2.81 ± 0.22
Deep	2.29 ± 0.92	1.92 ± 0.48	2.98 ± 0.26

with component one, and the Ca:Mg and Al content correlate negatively. Component two has most of the variation accounted for by fracture density and Ca:Mg. For the soil-related PCA, the first three components explained only 67% of the variance (Fig. 6). Ca:Mg, soil moisture, and Al accounted for the bulk of the eigenvector totals for principal component one, while SOM, C, and

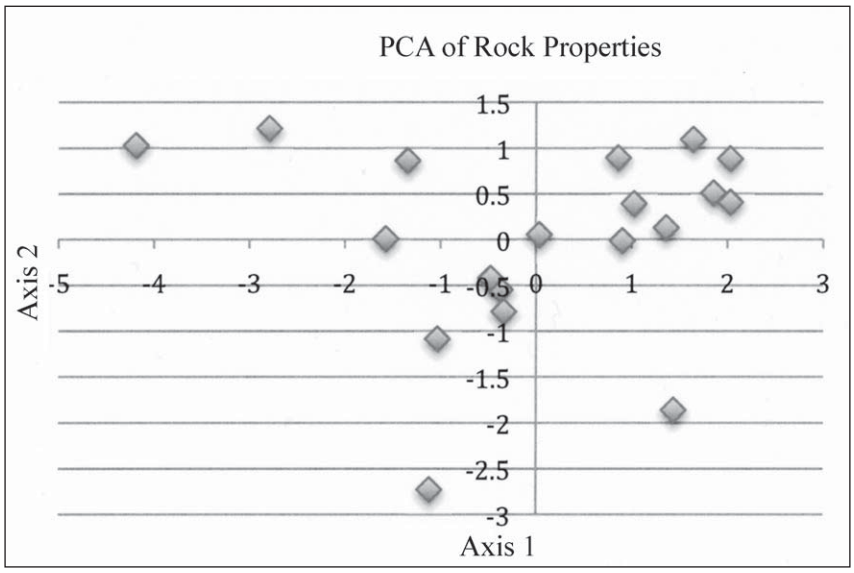

Figure 5. Principal component analysis of initial rock variables.

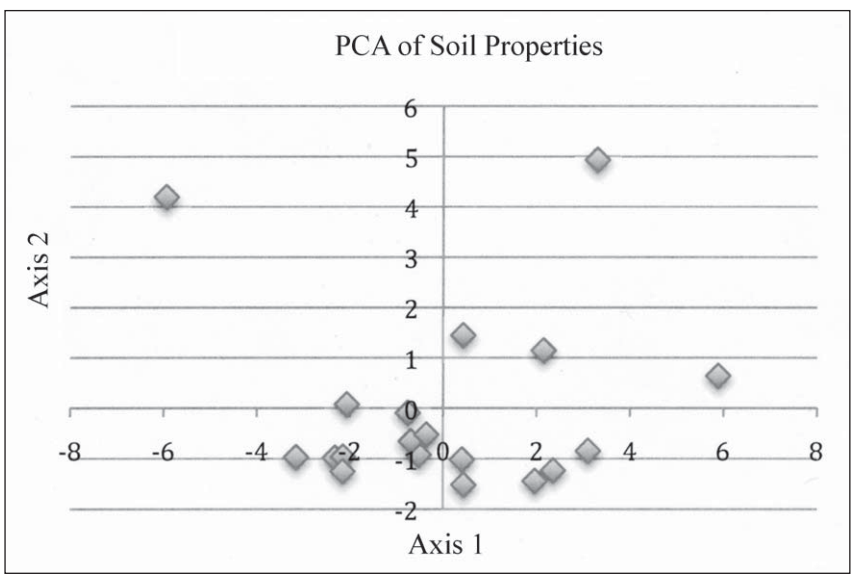

Figure 6. Principal component analysis of initial soil variables.

C:N comprise the majority of the discriminatory power of principal component two. Plots of fracture density versus percent xeric tree species (Fig. 7) and

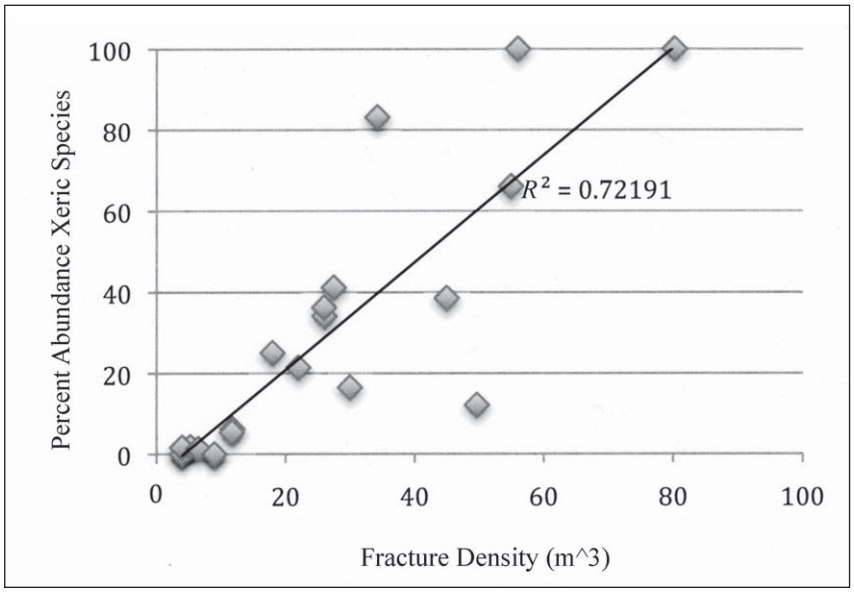

Figure 7. Fracture density verses the xeric tolerant woody species. Graph details the percent abundance of typical barrens/savanna and woodland xeric species (Blackjack Oak, Post Oak, Virginia Pine, Eastern Red Cedar) at each ultramafic plot and the corresponding fracture density of the bedrock.

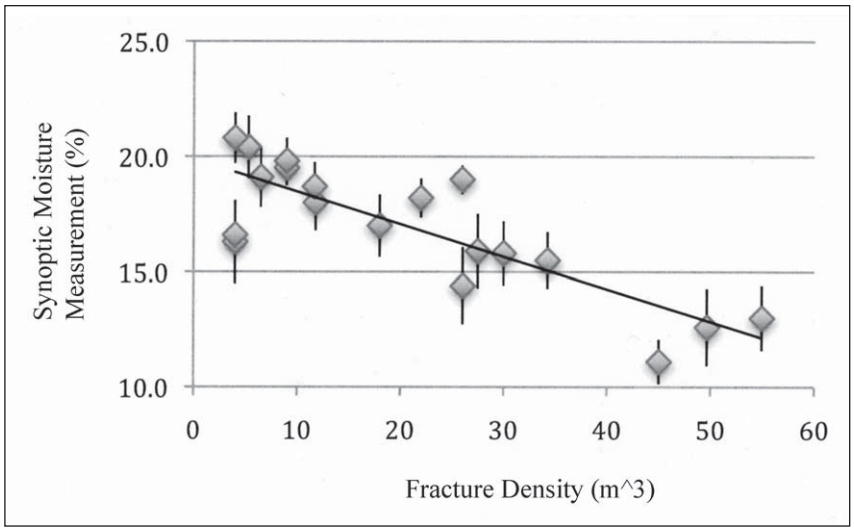

Figure 8. Plot of fracture density versus synoptic volumetric moisture content of all ultramafic plots. Data points are the mean and standard error of a minimum of twelve plot-level data points per quadrat.

versus synoptic volumetric moisture content (Fig. 8) display predominately linear trends, with xeric tree species having a positive correlation and moisture content a negative correlation with respect to fracture density.

Discussion

The dominance of certain tree species such as the oaks, hickories, Eastern Red Cedar, Red Maple, and American Beech with the associated rock formations and their derived soils is strikingly shown by Table 2. Oaks such as Blackjack, Post, and Chestnut Oak are commonly found in serpentine areas of the Mid-Atlantic. Prior to the cessation of fire by the Amerindians, many of these woodlands and forests were likely savanna or barrens areas. Further, between 70–100 years ago, the serpentinized areas of the PSB were extensively logged, though not farmed. This anthropogenic disturbance provides the canvas whereon the flora competes for scant resources such as moisture and nutrients. Edaphic factors and disturbance play an important role in the unusual vegetation properties of these xeric oak forests and woodlands. Geochemical data are consistent with other serpentinites containing elevated Cr, Ni, V, and Mg with low Ca, Na, Al, and K.

Concentrations of potentially toxic metals such as Ni, Cr, and Co are usually considered as one of the main causes of the vegetation dynamics of ultramafic soils. However, in this study, the highest Cr values reside in the limonitic laterites. Limonitic laterites often support typical Maryland Piedmont tree species such as *Liriodendron tulipifera* L. (Tulip Poplar). These soils (low in gravel content compared to the ultramafics) are also suitable to be farmed in the PSB area. Proctor and Nagy (1992) and Roberts and Proctor (1992) note that the role of metals in causing the infertility of ultramafic soils are pH dependent and should be reconsidered with respect to hydrological and nutritional stresses. Plant elemental stresses are broadly similar across the landscape. However, outcrops with sheared and mylonitic fabrics tend to have greater fracture densities and slightly higher Ca:Mg ratios (Tables 1, 3).

Upland oaks are known for their strategies and adaptations that promote tolerance of drought and nutrient-poor soils. There are 60 species of oak in North America, with Blackjack and Post Oak being the two most common associates in dry, fire-prevalent, and nutrient-poor sites (Abrams 1992). On xeric, serpentine soils of Maryland, Virginia Pine and Eastern Red Cedar are also common. The upland xeric oaks seen at the PSB possess a suite of ecophysiological adaptations for these conditions, but not for competing in a closed-forest understory dominated by shade-tolerant species such as American Beech. A number of the plots contain shade-tolerant species such as the American Beech and Red Maple (Table 2). DBH measurements (J.L. Burgess, unpubl. data) as a proxy for tentative age suggest that these forests are undergoing continual transformation and in the absence of fire may be on a trajectory towards typical Maryland piedmont flora in the future, when only the most xeric and extreme Ca:Mg microsites will retain the serpentine

character. The positive correlation of xeric, edaphic specialists as a function of fracture density suggests higher dominance of xeric species with more fracturing (Fig. 7). The presumed effect of the fracturing (a composite of tectonic shearing and late jointing) is to create preferred pathways for water drainage. The availability of soil water was once thought to be the main factor limiting plant diversity and growth on the serpentine soils (Hughes et al. 2001, Rajakaruna et al. 2003). However, Hull and Wood (1984) measured summer soil water and oak tree xylem potentials and concluded that the availability of water does not appear to be the factor allowing Blackjack and Post Oaks to replace White and Black Oaks in serpentine soils of Soldier's Delight, MD. Accordingly, the consensus has shifted toward the Ca:Mg ratio as a major factor controlling which plants will grow on serpentine soils (E.B. Alexander, unpubl. data; Brady et al. 2005). To test if there is any control of moisture content with increasing fractures, a synoptic record of soil moisture was measured at all plots and indicated a significant negative relationship between soil moisture and bedrock fracturing (Spearman Rank Correlation $R_s = -0.76$; Fig. 8).

These results suggest that, at least in part, the distribution and abundance of woody species and the persistence of remnant "barrens" areas may be controlled by the fracture density, associated soil texture, and soil moisture. Lutz and Chandler (1946) were two of the first forest ecologists to state that the differentiation effects of parent material are enhanced on immature soils that are likely to be chemically unbalanced or deficient, especially when soils are derived from a single geological formation. In a more modern treatment, Roberts (1980) explores these same physio-chemical properties of mature and immature soils as a function of parent material in Western Newfoundland. Since most of the forest soils in this region are shallow, poorly sorted, immature, and derived from the same ultramafic parent material, the geologic controls on tree distribution may be more important than in many other habitats. For example, the Ca:Mg ratio of all the ultramafics is low (mean of 0.12 ± 0.05), but the less sheared, less serpentinized peridotites have a significantly higher Ca:Mg ratio of 0.30 ± 0.07 (t-test: $P = 0.005$). This same composition is displayed in the soils derived from these parent materials (Table 3). Thus, the increase in shearing or mylonitization of the parent rock correlates with a lack of relict minerals such as olivine and clinopyroxene. The absence of clinopyroxene (a Ca-bearing phase) and the subsequent replacement by serpentine minerals in the more-sheared rocks is associated with the lowest Ca:Mg ratios and the lowest moisture contents. Consequently, the more-xeric forest tree species are more abundant in these areas.

Additionally, of the small, relict grasslands that occur at the PSB, none of these barrens occur on the lenticular pods of peridotite. The decrease in Ca due to serpentinization of ultramafics has been observed in many serpentinized peridotites (Coleman 1963; Puga et al. 1999; Roberts and Proctor 1992; Roberts and Rodenkirchen 1997; Rodenkirchen and Roberts 1993a, b; Shervais et al. 2005) and is attributed to the breakdown of

clinopyroxene during serpentinization by fluid infiltration. Such mobilization may be accompanied by fracturing, faulting, and shearing, and hence in the Conowingo Barrens, there is a direct relationship between: structural features, Ca:Mg ratios, soil moisture, and ultimately floristic community structure. Bulk rock and soil geochemistry are also important in those areas where limonitic chalcedony occur. These "honey-comb" lithologies, though Cr rich, do not contain abundant serpentinites or pyroxenites and do not host remnant grasslands areas, or the xeric oaks, and historically are among the first soils to be farmed.

Conclusion

Petrologic and structural diversity supports different plant communities based on soils evolved from ultramafic materials. There are many confounding factors and feedbacks in operation at the Pilot Serpentine Barrens and the wider Conowingo Barrens. The integration of geologic, edaphic, and biologic factors suggest that fracture density, the result of shearing during orogenesis, and subsequent terrain uplift of the Baltimore Mafic Complex, are exerting some level of control on forest tree community composition. This tectonic influence has resulted in ultramafic lithologies and derived soils with varying Ca:Mg ratios as well as different outcrop fracture densities that, in some part, influence soil moisture content. Ultimately the combination of these factors results in landscapes that host a higher proportion of xeric woody species in areas of more-sheared and fully serpentinized ultramafics. Plots with communities that more closely resemble those on adjacent non-ultramafic sites have lower fracture density, higher Ca, higher moisture, and lower Ni content.

Areas of highest bedrock fracturing at the PSB survive as relict barrens, while other bedrock variations may result in soil trajectories towards savanna or wooded forest communities. Such heterogeneous geology may explain why some barrens appear resistant to woody plant invasion.

Acknowledgments

The authors would kindly like to thank Dr. Richard Back for his aid in obtaining the C:N data and The Nature Conservancy and the Girl Scouts of America for permission to use their sites. Further, we would like to acknowledge thoughtful reviews by B. Roberts, E. Hellquist, and E.F. Stoddard.

Literature Cited

Abrams, M.D. 1992. Fire and the development of oak forests. Bioscience 42(5):346–53.

Alexander, E.B., R.G. Coleman, T. Keeler-Wolfe, and S.P. Harrison. 2007. Serpentine Geoecology of Western North America. Oxford University Press, New York, NY, USA.

Anderson, R.C., J.S. Fralish, and J.M. Baskin. 1999. Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cambridge University Press, New York, NY, USA.

Barton, A.M., and M.D. Wallenstein. 1997. Effects of invasion of *Pinus virginiana* on soil properties in serpentine barrens in southeastern Pennsylvania. Journal of the Torrey Botanical Society 124(4):297–305.

Brady, K.U., A.R. Kruckeberg, and H.D. Bradshaw, Jr. 2005. Evolutionary ecology of plant adaptation to serpentine soils. Annual Review of Ecology, Evolution, and Systematics 36:243–266.

Brush, G.S., C. Lenk, and J. Smith. 1980. The natural forests of Maryland: An explanation of the vegetation map of Maryland. Ecological Monographs 50(1):77–92.

Coleman, R.G. 1963. Serpentinites, rodingites, and tectonic inclusions in alpine-type mountain chains. Geological Society of America, Special Paper 73, Boulder, CO, USA.

Crowley, W.P. 1976. The geology of the crystalline rocks near Baltimore and its bearing on the evolution of the eastern Maryland piedmont. Maryland Geological Survey Report of Investigations 27, Baltimore, MD, USA.

Dearden, P. 1979. Some factors influencing the composition and location of plant communities on a serpentine bedrock in western Newfoundland. Journal of Biogeography 6(1):93–104.

Denslow, J.S., and G.S. Hartshorn. 1994. Tree-fall gap environments and forest dynamic processes. Pp. 120–127, *In* L.A. McDade, K.S. Bawa, H.A. Hespenheide, and G.S. Hartshorn (Eds.). La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago, IL, USA.

Gates, A.E. 1992. Domainal failure of serpentinite in shear zones, State-Line mafic complex, Pennsylvania, USA. Journal of Structural Geology 14(1):19–28.

Gates, A.E., P.D. Muller, and M.A. Kroll. 1999. Alleghanian transpressional orogenic float in the Baltimore terrane, central Appalachian Piedmont. Pp. 125–139, *In* D.W. Valentino and A.E. Gates (Eds.). The Mid-Atlantic Piedmont: Tectonic Missing Link of the Appalachians. Geological Society of America Special Paper, No. 330.

Hanan, B.B. 1980. The petrology and geochemistry of the Baltimore mafic complex, Maryland. Ph.D. Dissertation. Virginia Polytechnic Institute and State University, Blacksburg, VA, USA .

Hanan, B.B., and A.K. Sinha. 1989. Petrology and tectonic affinity of the Baltimore mafic complex, Maryland. Geological Society of America, Special Paper 231:1–18.

Higgins, M.W., and L.B. Conant. 1986. Geologic map of Cecil County: Baltimore, Maryland. Scale 1:62,500. Maryland Geological Survey. Baltimore, MD, USA.

Higgins, M.W., and L.B. Conant. 1990. The Geology of Cecil County, Maryland. Volume 37. Maryland Geological Survey. Baltimore, MD, USA.

Hughes, R., K. Bachmann, N. Smirnoff, and M.R. Macnair. 2001. The role of drought tolerance in serpentine tolerance in the *Mimulus guttatus* Fisher ex DC. complex. South African Journal of Science 97:581–586.

Hull, J.C., and S.G. Wood. 1984. Water relations of oak species on and adjacent to a Maryland serpentine soil. American Midland Naturalist 112(2):224–34.

Kempton, R.A., and L.R. Taylor. 1976. The Q-statistic and the diversity of floras. Nature 262:818–820.

Kruckeberg, A. 2002. Geology and Plant Life: The Effects of Landforms and Rock Types on Plants. University of Washington Press. Seattle, WA, USA.

Kruckeberg, A. 2004. The status of conservation of serpentinite sites in North America. International Geology Review 46(9):857–60.

Latham, R.E. 1993. The serpentine barrens of temperate eastern North America: Critical issues in the management of rare species and communities. Bartonia 57(supplement):61–74.

Levin, S.A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. Ecology 73(6):1943–67.

Lutz, H.J., and R.F. Chandler. 1946. Forest Soils. John Wiley and Sons, New York, NY, USA.

Marye, W.B. 1955a. The great Maryland barrens. Maryland Historical Magazine 50:11–23.

Marye, W.B. 1955b. The great Maryland barrens: II. Maryland Historical Magazine 50:120–42.

Marye, W.B. 1955c. The great Maryland barrens: III. Maryland Historical Magazine 50:234–53.

McFee, W.W., J.M. Kelly, and R.H. Beck. 1977. Acid precipitation effects on soil pH and base saturation of exchange sites. Water, Air, and Soil Pollution 7(3):401–8.

Muller, P.D., Candela, P.A. and A.G. Wylie. 1989. Liberty Complex: Polygenetic Melange in the Central Maryland Piedmont. Pp. 113–135, *In* J.W. Horton and N. Rast (Eds.). Melanges and Olistostrome of the US Appalachian. Geological Society of America Special Paper 228. Boulder, CO, USA.

Maryland State Climatologist Office (MSCO). 2008. Department of Atmospheric and Oceanic Science [database online]. University of Maryland, College Park, MD, 2008. Available online at http://www.atmos.umd.edu/~climate/conowingodam.html. Accessed July 12, 2008.

Mutke, J., and W. Barthlott. 2005. Patterns of vascular plant diversity at continental to global scales. Biologiske Skrifter 55:521–37.

Oze, C., S. Fendorf, D.K. Bird, and R.G. Coleman. 2004. Chromium geochemistry in serpentinized ultramafic rocks and serpentine soils from the franciscan complex of California. American Journal of Science 304(1):67–101.

Potts, P.J. 1987. A Handbook of Silicate Rock Analysis. Chapman and Hall, New York, NY, USA.

Proctor, J., and L. Nagy. 1992. Ultramafic rocks and their vegetation: an overview. Pp. 469–494, *In* A.J.M. Baker, J. Proctor, and R.D. Reeves (Eds.). The Vegetation of Ultramafic (Serpentine) Soils. Intercept Ltd., Andover, Hampshire, UK.

Puga, E., J.M. Nieto, A. Díaz de Federico, J.L. Bodinier, and L. Morten. 1999. Petrology and metamorphic evolution of ultramafic rocks and dolerite dykes of the betic ophiolitic association (mulhacén complex, SE Spain): Evidence of alpine subduction following an ocean-floor metasomatic process. Lithos 49(1–4) (10):23–56.

Rabenhorst, M.C., J.E. Foss, and D.S. Fanning. 1982. Genesis of Maryland soils formed from serpentinite. Journal of the Soil Science Society of America 46:607–16.

Rajakaruna, N., G.E. Bradfield, B.A. Bohm, and J. Whitton. 2003. Adaptive differentiation in response to water stress by edaphic races of *Lasthenia californica* (Asteraceae). International Journal of Plant Science 164(3):371–376.

Rajakaruna, N., T.B. Harris, and E.B. Alexander. In press. Serpentine geoecology of eastern North America: A review. Rhodora.

Roberts, B.A. 1980. Some chemical and physical properties of serpentine soils from western Newfoundland. Canadian Journal of Soil Science 60:231–240.

Roberts, B.A. 1992. The serpentinized areas of Newfoundland, Canada: A brief review of their soils and vegetation. Pp. 53–66, *In* A.J.M. Baker, R.D. Reeves, and J. Proctor (Eds.).The Vegetation of Ultramafic (Serpentine) Soils. Proceedings of the First International Conference on Serpentine Ecology. Intercept Ltd., Andover, Hampshire, UK. 509 pp.

Roberts, B.A. and J. Proctor (Eds). 1992. The Ecology of Areas with Serpentinized Rocks. A World View. Kluwer Academic Publishers, Dordrecht, The Netherlands. 427 pp.

Roberts, B.A., and K.W. Deering 1995. Chemical properties of soil leachate measured with porous cup lysimeters from two sites with serpentinized rocks, Newfoundland, Canada. Paper presented at the Second International Conference on Serpentine Ecology, Noumea, New Caledonia, July 31–August 5, 1995. Abstract published. P. 42, *In* T. Jaffré, R. Reeves, and T. Becquer (Eds.). Proceedings of The Second International Conference on Serpentine Ecology. Centre Orstom de Noumea, BP A5, 98848 Noumea Cedax. Nouvelle-Caledonie.

Roberts, B.A., and H. Rodenkirchen. 1997. Soil and plant nutrition on a serpentinized ridge in South Germany. Pp. 211–212, *In* T. Jaffré, R. Reeves, and T. Becquer (Eds.). Proceedings of The Second International Conference on Serpentine Ecology. Centre Orstom de Noumea, BP A5, 98848 Noumea Cedax. Nouvelle-Caledonie.

Rodenkirchen, H., and B.A. Roberts 1993a. Soils and plant nutrition on a serpentinized ridge in south Germany. I. Soils. Journal of Plant Nutrition and Soil Science 156:407–410.

Rodenkirchen, H., and B.A. Roberts 1993b. Soils and plant nutrition on a serpentinized ridge in south Germany. II. Foliage macro-nutrient and heavy metal concentrations. Journal of Plant Nutrition and Soil Science 156:411–413.

Shaw, H.F., and G.J. Wasserburg. 1984. Isotopic constraints on the origin of Appalachian mafic complexes. American Journal of Science 284(4–5):319–49.

Shervais, J., Kolesar, P., and K. Andreasen. 2005. A field and chemical study of serpentinization, Stonyford, California: Chemical flux and mass balance. International Geology Review 47(1):1–23.

Shreve, F. 1910. The ecological plant geography of Maryland, midland zone, lower midland district. Pp. 199–219, *In* F. Shreve, M.A. Chrysler, F.H. Blodgett, and F.W. Besley (Eds.). The Plant Life of Maryland. Johns Hopkins University Press. Baltimore, Maryland.

Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology and Evolution 19(11):605–11.

Tyndall, R.W. 2005. Twelve years of herbaceous vegetation change in oak savanna habitat on a Maryland serpentine barren after Virginia Pine removal. Castanea 70(4):287–97.

Tyndall, R.W., and J.C. Hull. 1999. Vegetation, flora, and plant physiological ecology of serpentine barrens of eastern North America. Pp. 67–82, *In* R.C. Anderson, J.S. Fralish, and J.M. Baskin (Eds.). Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cambridge University Press. Cambridge, UK.

United States Department of Agriculture (USDA). 1973. Soil survey - Cecil County, Maryland. US Department of Agriculture, Soil Conservation Service, Washington, DC.