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The Pocono till barrens: shrub savanna persisting on soils favoring forest[1]

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LATHAM, R. E., J. E. THOMPSON, S. A. RILEY AND A. W. WIBIRALSKE (Department of Geology, University of Pennsylvania, Philadelphia, PA 19104-6316). The Pocono till barrens: shrub savanna persisting on soils favoring forest. Bull. Torrey Bot. Club 123: 330–349. 1996.—A previously undescribed shrub savanna community, which we refer to as the Pocono till barrens, occurs mainly on soils weathered from glacial till of Illinoian age on the southern Pocono Plateau of Pennsylvania. Unlike most "barrens" in east-central North America, its soils are not sandy or shallow to bedrock; the same deep, fine-loamy soil series underlie the barrens and nearby northern hardwoods forest. An unusual abundance of rare plant and animal species in and near the barrens has attracted the attention of scientists and biodiversity conservation professionals. In an effort to understand the ecological dynamics of the Pocono till barrens and why the barrens are different from their mostly forested surroundings, we undertook studies of vegetation history, landscape patterns, plant species distributions and water table depth. The Pocono till barrens (1) are old, pre-dating European settlement of the area; (2) have burned frequently and over large areas throughout their recorded history; (3) presently cover more than 22 km^2 adjacent to a belt of xeric ridgetop barrens totaling approximately 18 km^2; (4) have in abundance plants usually found in moist or wet soil conditions living side-by-side with those normally associated with xeric habitats; and (5) include several vegetation types which are distributed on the landscape, in part, in association with a soil moisture gradient. The Pocono till barrens appear to flout the conventional wisdom that barrens vegetation reflects droughty, nutrient-poor soils. Although the Pocono till barrens substantially pre-date European settlement of the area, fire is clearly the key to maintenance of barrens vegetation in this system. We hypothesize that biotic factors are more important than abiotic factors in determining distributions of barrens and forest vegetation on the southern Pocono Plateau.

Key words: barrens, heathlands, Illinoian glacial till, *Kalmia angustifolia*, Pennsylvania, *Pinus rigida, Quercus ilicifolia, Rhododendron canadense, Vaccinium.*

"Barrens" in eastern North America have received a surge of attention recently from botanists and ecologists (e.g., Dirig 1994; Heikens et al. 1994; Tyndall 1994; Vickery et al. 1994; Abrams and Orwig 1995; Bernard and Seischab 1995; Carbyn and Catling 1995; Titus et al. 1995; Dieffenbacher-Krall 1996). Widespread agreement on an all-encompassing definition for barrens vegetation is still lacking (Homoya 1994). In traditional usage in temperate eastern North America, where closed-canopy forests are the norm, the term barrens refers to areas with sparse tree cover (but it does not include wetlands or areas dominated by early successional species following disturbance). Woodlands also may be called barrens if they are dominated by species perceived as indicators of droughty soils, low-nutrient conditions or other stresses, especially *Pinus banksiana* Lamb. (jack pine), *Pinus rigida* Mill. (pitch pine) and *Pinus virginiana* Mill. (scrub pine).

Pennsylvania is endowed with an exceptional abundance and diversity of barrens communities. It has the northernmost examples of Appalachian shale barrens (Platt 1951; Keener 1971), the largest area of temperate eastern North American serpentine barrens (Latham 1993), barrens on sand colluvium (Clarke 1946), numerous sandstone and conglomerate ridgetop barrens, northern Appalachian boulder fields, the sparse vegetation of dunes, sand plains and bluffs along Lake Erie's shore, scattered small limestone and diabase glades (Smith 1991), and at least one spruce bald. Paradoxically, the larg-

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est of the state's barrens ecosystems is also one of the poorest known in the scientific community. The system forms an intermittent belt averaging about 1 km in width along 40 km of the southern Pocono Plateau (part of the Appalachian Plateaus physiographic province) and a small part of the adjoining Ridge and Valley province in northeastern Pennsylvania. *Quercus ilicifolia* Wang., *Kalmia angustifolia* L., *Rhododendron canadense* (L.) Torr., *Vaccinium angustifolium* Ait. and numerous other shrub species dominate these barrens, with *Pinus rigida* scattered throughout and clumped in a few woodland stands. We refer to the area and its vegetation as the Pocono till barrens because till (unsorted glacial drift) dominates the underlying geology.

In the late 1980s, ecologists exploring the Pocono till barrens began recognizing several features of the system that seemed to set it apart as highly distinctive from other barrens in eastern North America. There was an apparent concordance between the barrens and a large expanse of Illinoian-aged glacial till, rare in eastern North America (Crowl and Sevon 1980). The U.S. Department of Agriculture, Soil Conservation Service classified the deep soils underlying the barrens as having fine-loamy, not sandy, textures with high water-holding capacity (Fisher et al. 1962; Lipscomb 1981). Comparing soil survey maps with conditions on the ground revealed that northern hardwood forest is at least as likely as barrens vegetation to inhabit the same soil series and phases. The most often recurring subject in conversations with local informants was wildfire, with frequent claims that the barrens have burned more often and over larger areas than anywhere else in the region.

The scientific literature to date on the Pocono till barrens is limited to reports on methods of replacing scrub oak with merchantable timber stands (Burnham et al. 1947; McQuilkin 1961) and a brief site description in a study of plant bugs of the family Miridae living on barrens host plants (Wheeler 1991). Scientific interest in the Pocono till barrens has mounted with the discovery in the 1980s that the barrens and vicinity contain the greatest concentration of globally rare plant and animal species—i.e., those that are endangered or threatened with extinction—of any terrestrial ecosystem in Pennsylvania (Davis et al. 1991). The area also comprises the state's second-largest concentration of regionally rare species represented by disjunct and edge-of-range populations. The barrens and vicinity are now known to harbor more than 30 regionally rare and 10 globally rare and endangered species of plants and animals, with high expectation of additional discoveries. The Nature Conservancy has named the area as its highest priority in the state for land protection, restoration and management for biodiversity.

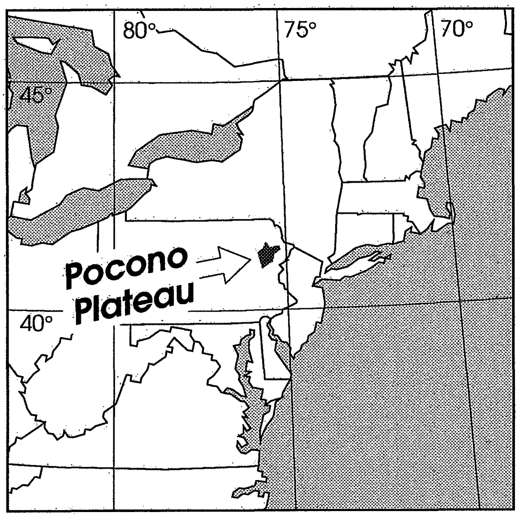

Fig. 1. Location of study area (Pocono Plateau boundary from Berg et al. 1989).

Success in conserving diversity and ecosystem function in this unusual landscape will depend on understanding the ecological dynamics of the Pocono till barrens and why the barrens are different from their surroundings. The first step is to establish how the barrens differ from neighboring vegetation and from other barrens in the region. In this paper we summarize pertinent historical information on the barrens vegetation and describe it at fine and coarse spatial scales. We report on preliminary tests of the assertion that the Pocono till barrens are mesic rather than xeric like most barrens in the region. We conclude by considering to what degree the vegetation's unusual composition may be due to abiotic constraints versus autogenic processes originating with the plants themselves.

STUDY AREA. The Pocono till barrens fringe the southern margin of the Glaciated Pocono Plateau section, Appalachian Plateaus physiographic province, northeastern Pennsylvania (Fig. 1). About 85% of the 1400-km^2 Plateau was ice-covered at the height of the Wisconsinan glaciation (Berg et al. 1989). The glacier left a blanket of pulverized rock across most of this area: ground moraine, outwash and ice-contact

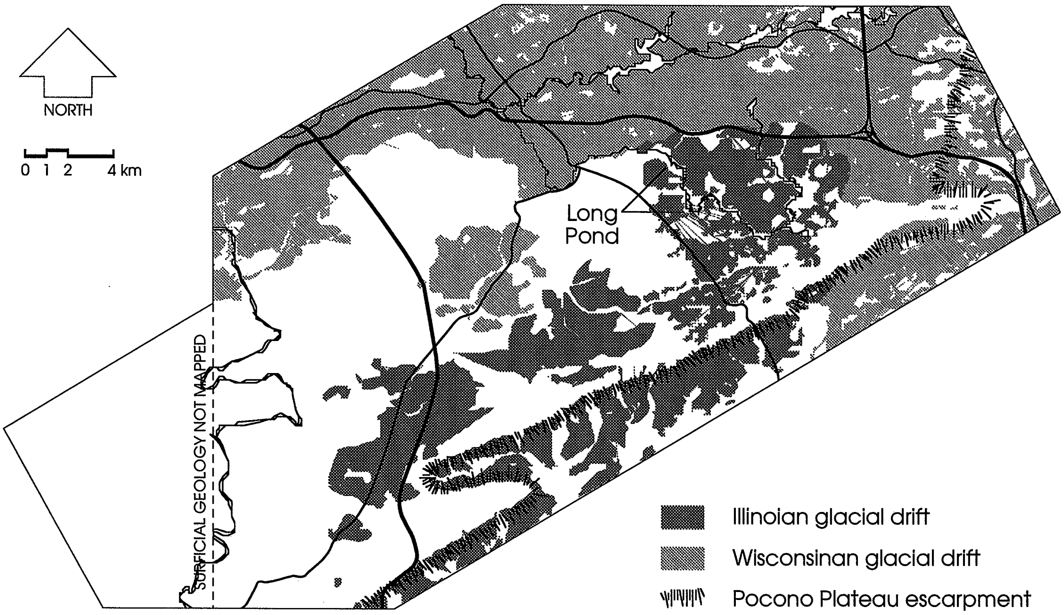

Fig. 2. Southern Pocono Plateau surficial geology (data from Berg, Bucek 1977; Sevon 1975a, 1975b; Crowl and Sevon 1980). The entire mapped area is 793 km².

stratified drift. The ice stopped short of the escarpment defining the Plateau's southern rim. The southern 15% of the Plateau's area, beyond the reach of the Wisconsinan ice, is geologically complex. The Wisconsinan terminal moraine, from which the ice began receding about 15,000 years ago (Crowl 1980), forms the northern boundary. Beneath the surface to the south of this strip lies Devonian sedimentary rock, boulder colluvium shattered under periglacial climatic conditions, alluvium, peat and much deposits, and about 80 km² of glacial drift depos-

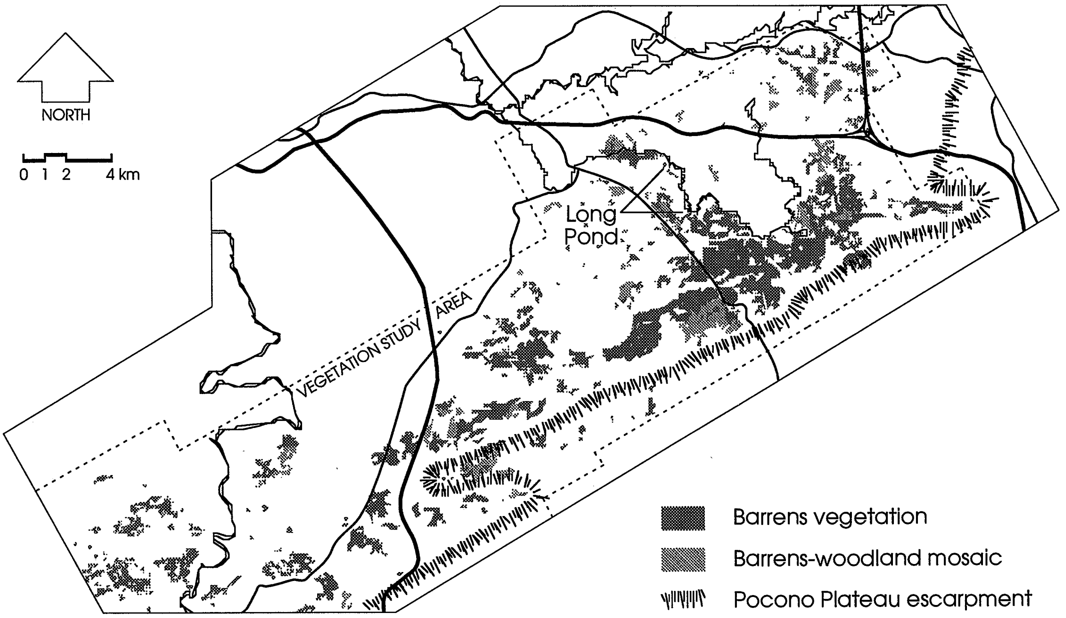

Fig. 3. Southern Pocono Plateau barrens vegetation. The vegetation survey boundary encompasses 406 km².

ited by the much earlier Illinoian glaciation (Berg 1977; Sevon 1975a, 1975b).

The Illinoian till deposits on the southern Pocono Plateau and along the base of the adjacent escarpment comprise the largest remaining deposit of Illinoian glacial till in North America east of western Ohio (see map, Crowl and Sevon 1980). At the southern margin of the Pocono Plateau, Illinoian till remnants occur in two distinct belts (Crowl and Sevon 1980). One lies on top of the nearly flat southern end of the Plateau, parallel and adjacent to the escarpment. The other, just to the south, sheaths the lower slopes of the escarpment (Braun 1989).

The study area centers on the Illinoian till plain on top of the Plateau (75°30′W, 41°03′N), consisting of three adjacent lobes in a 30 × 11-km area (Fig. 2). Mean elevation is approximately 550 m. The Wisconsinan terminal moraine meanders along the northern boundary of the study area, forming a low ridge about 40 m high and 2000 to 2500 m wide. At the escarpment along the study area's southern margin, the elevation drops off 250 to 350 m in a horizontal distance of 1200 to 2000 m.

The Pocono Plateau and nearby Appalachian Mountain ridges rise to elevations intermediate between the low plateaus, valleys and coastal plain to the north, east and south, and the high Appalachian plateaus (Allegheny and Catskill Mountains) to the southwest, west and northeast. Despite its modest elevation, the southern Pocono Plateau claims two climatic superlatives. It coincides with the area of the coolest mean daily maximum temperatures in summer in Pennsylvania (from map based on 1931–1960 data, Dailey 1971). Mean daily maximum, minimum and 24-hour temperatures are 25.2°C, 12.8°C and 19.0°C in July and −1.4°C, −11.7°C and −6.6°C in January at the nearest temperature recording station (1961–1990 data, Owenby and Ezell 1992). Also, Long Pond has 129.2 cm mean annual precipitation, the highest of all 161 climatic data stations in Pennsylvania (1961–1990 data, Owenby and Ezell 1992). Precipitation occurs evenly throughout most of the year, with a dip in December–February (median 8.1 cm) and a peak in May (median 12.9 cm).

The southern Pocono Plateau is at the boundary between the hemlock-white pine-northern hardwoods region northward and the oak-chestnut or Appalachian oak forest region to the west, south and east (Braun 1950; Küchler 1964). Despite its relatively low elevation, the Plateau hosts the greatest concentration of boreal plant species in Pennsylvania (see Rhoads and Klein 1993), probably because of its anomalously cool summers and abundant wetlands. "Island" populations of many vascular plants with mainly boreal and montane ranges occur on the Pocono Plateau. Most are species characteristic of bogs and boreal forests, including *Abies balsamea* (L.) P.Mill., *Amelanchier bartramiana* (Tausch) M. Roemer, *Arceuthobium pusillum* Peck, *Carex lasiocarpa* Ehrh., *Carex oligosperma* Michx., *Carex paupercula* Michx., *Eriophorum vaginatum* L. ssp. *spissum* (Fern.) Hulten, *Gaultheria hispidula* (L.) Muhl. *ex* Bigel., *Glyceria obtusa* (Muhl.) Trin., *Juncus filiformis* L., *Kalmia polifolia* Wang., *Ledum groenlandicum* Oeder, *Lycopodiella inundata* (L.) Holub, *Muhlenbergia uniflora* (Muhl.) Fern., *Myrica gale* L., *Picea mariana* (P.Mill.) BSP, *P. rubens, Smilacina trifolia* (L.) Desf. and *Vaccinium oxycoccos* L. Some of the disjunct populations are common in the till barrens, including *Carex polymorpha, Gentiana linearis, Lycopodium hickeyi, Panicum boreale, Platanthera blephariglottis* and *Rhododendron canadense* (see Appendix for author attributions of barrens species).

VEGETATION HISTORY. Evidence is scant pertaining to prehistoric human influences on the vegetation of the southern Pocono Plateau. The few data gathered so far are consistent with small-scale seasonal utilization of the Plateau from more than 10,000 yr ago to early historic times (Cruse, et al. 1989; Perazio 1991).

The earliest known written mention of the area's vegetation consists of eight words written in 1737 on a sketch map by Benjamin Eastburn on which a 106-km straight line across the southern Pocono Plateau was labeled as running "... through a mountainous barren country abounding with pines ..." (Davis 1876). Passing through in late June 1779 various members of General John Sullivan's military expedition against the Iroquois wrote of "sunken swamps and burning plains," "the ground universally covered with brush by the name of ground oak [*Quercus ilicifolia*]," "the most barren part of the country I ever saw," a "great Swamp, which is interspersed & barren piney Spots throughout very Stony," and land "very poor & barren & I think Such as will never be Inhabited" (Cook 1887).

The first botanist known to visit the area was Frederick Pursh, on 13 and 14 June 1807, when the southern Plateau was still virtually uninhabited and untouched by lumbering. His description of the barrens included the observation that "coming to the barrens in the top [of the Plateau], I soon found ... *Rhodora* [*Rhododendron*] *canadensis* grows here in great plenty" (Beauchamp 1923). Naturalist and traveler Maximilian, Prince of the German kingdom of Wied, wrote on passing through the Pocono barrens on 25 and 26 August 1832 (in translation; Thwaites 1906), "On an elevated plain we were surrounded, as far as the eye could reach, with woods or thickets of low oaks, from which numbers of slender, half-dried, short-branched pines (Pinus rigida) shot up.... in the dry season these woods have often been destroyed by extensive conflagrations .... Even now, clouds of smoke rose at a distance, and announced a fire in this great lonely wilderness.... We crossed a valley, with thickets and scorched pines rising above them .... An old path led us half a league over an eminence; after which we found a valley, where the lake, called Long Pond, is situated ...".

Botanist Thomas C. Porter observed on a visit on 22 to 25 August 1859 "woods, which are here very open & called 'windfalls,' because the majority of the trees are supposed to have been overturned by the storms & the numerous little hillocks found everywhere confirm the supposition. Fire too has no doubt done its part. These 'Windfalls,' or barrens, are very extensive & their vegetation quite uniform" (Porter 1859). The 77 species mentioned by Porter include virtually all that characterize the barrens now, including those that are most abundant (e.g., *Amianthium muscaetoxicum, Gaylussacia resinosa* [*G. baccata*], *Kalmia angustifolia, Pinus rigida, Pyrus arbutifolia* var. *melanocarpa* [*Aronia melanocarpa*], *Quercus ilicifolia, Rhodora Canadensis* [*Rhododendron canadense*], *Vaccinium Pennsylvanicum* [*V. angustifolium*], *Viburnum nudum* [*V. cassinoides*]) and many that are less conspicuous (e.g., *Calamagrostis coarctata* [*C. cinnoides*], *Diplopappus umbellatus* [*Aster umbellatus*], *Gentiana Saponaria* var. *linearis* [*G. linearis*], *Lygodium palmatum, Platanthera blephariglottis, Solidago puberula*).

Agriculture has never occupied more than a small fraction of the land on the Pocono Plateau (Mathews 1886; 1938–1939 aerial photographs, Cartographic Branch, National Archives, Washington, DC). Small-scale timber cutting started around 1820 (Mathews 1886) but most lumbering occurred from the 1870s to about 1900 (Taber 1970). Presumably because of frequent wildfires, most of the hardwood timber was small, used mainly for mine props in the anthracite coal-mining region just southwest of the Plateau (Taber 1970) and for such items as clothespins and shoe-pegs (Mathews 1886). After the marketable timber was depleted, one of the principal economic pursuits on the Plateau was wild blueberry and huckleberry picking.

FIRE HISTORY. Berry pickers enhanced production by setting large-scale, frequent fires (Anonymous 1898; Rowland 1957). An 1897 act authorizing state funding for wildland fire suppression and criminalizing wildland burning in Pennsylvania brought the berry pickers into conflict with the state (Anonymous 1898), culminating in 1942 with the designation of 120 km^2 near Long Pond as a "non-protection area" (Pyle 1942a, 1942b) in an effort to coerce local landowners into putting a stop to the burning (Wirt 1944). A section through a 31-cm-diameter pitch pine cut in 1946 near Long Pond showed 10 major fires in the 120-yr lifetime of the tree, with six occurring in the last 27 yr alone (Burnham, et al. 1947). In the vicinity of this tree, the mean fire frequency increased from one in 23 yr in the 1820s to 1918 to one in 4.5 yr from 1919 to 1946. Single fires of 10 to 20 km^2 were not uncommon on the southern Plateau from when records were first kept, around 1900, until the resumption in the late 1950s of fire suppression by the state, the establishment of local volunteer fire companies, and road and equipment improvements resulting in faster response by fire-fighters (Pa. Bur. Forestry Dist. 19, Stroudsburg, unpubl. data).

The Pocono Plateau and vicinity historically have had the highest forest fire frequency of any area of comparable size in Pennsylvania (Haines et al. 1978). Records show no decrease in fire frequency from the late 1950s to the present but they do show a dramatic decrease in the late 1950s in mean area burned per fire (Pa. Bur. Forestry Dist. 18, Cressona, and Dist. 19, Stroudsburg, unpubl. data). The decrease is due partly to active fire suppression and partly to the steadily increasing fragmentation of natural vegetation by roads, utility lines and other effective firebreaks. The rates of fragmentation and attrition of natural vegetation increased after the completion in the mid-1950s of the first of several limited-access highway connections to large cities and a resulting boom in second-home development.

Methods. LANDSCAPE ANALYSIS. We built a computerized geographic information system

(GIS) depicting a 793-km^2 area in and around the Pocono till barrens, using a workstation version of the computer program ARC/INFO (version 5.0.1, 1990, Environmental Systems Research Inst., Inc., Redlands, CA). Digitized data layers include bedrock and surficial geology (Berg et al. 1977; Sevon 1975a, 1975b; Crowl and Sevon 1980), topography and surface hydrology (U.S. Geological Survey 7.5′ quadrangle maps), and—in a 406-km^2 subset of the study area—current vegetation patterns (see Figs. 2 and 3). Vegetation was mapped by interpreting 1:12,000-scale false-color infrared aerial photographs taken in May and June 1992 and ground-truthing. Cover types were classified using a hierarchical system modified from Reschke (1990) and Smith (1991).

The GIS is vector-based, i.e., the data layers are planes tiled with polygons (mapping units). A practical lower limit on mapping unit size for the vegetation data layer was set at approximately 0.06 ha. Where mosaics of smaller patches occur, polygons were given two, or occasionally three, vegetation type designations. Mosaic mapping units presented a problem in estimating areas covered by individual vegetation types. Our solution was to estimate the average proportions of the area occupied by constituent vegetation types, among all polygons of each multiple-type class. Then we allocated the corresponding fractions of the polygons' areas to the individual vegetation types.

We compared the distribution of vegetation types among categories of geological parent material by constructing a summary table. Comparisons between current vegetation and parent material distributions are considered to be valid, because surficial geology was mapped using landforms and natural and artificial rock exposures as indicators, not vegetation (W. D. Sevon, Pennsylvania Topographic and Geologic Survey, pers. comm.). Although our GIS included detailed information from soil surveys, we did not compare vegetation patterns with soil attributes because soil mapping methodology relies heavily on extrapolation from plant cover types interpreted from aerial photographs. Thus, our vegetation map and the Soil Conservation Service's soil survey maps are not truly independent data layers.

VEGETATION CENSUS. Vegetation census plots were established in 87 locations at six sites (mean intersite distance 6.8 km), in shrub-dominated barrens and nearby forests on Illinoian and Wisconsinan glacial till. Three sites had both barrens and forest plots; three had only forest. Since our focus was the shrub-dominated barrens types, *Pinus rigida* woodlands were not sampled. Shrub barrens appeared to be dominated by either *Quercus ilicifolia, Rhododendron canadense,* or a mixture of mostly ericaceous shrubs other than *R. canadense,* so quotas were used to insure roughly equal numbers of samples from these three subjective categories (i.e., after 20 sampling locations in one subjective category were established, additional randomly chosen locations were rejected if they appeared to belong in that category). The breakdown of samples by geological and vegetation classes is 15 on Illinoian till and 12 on Wisconsinan till in forest, and 48 and 12 in barrens.

Census plots were randomly located on x, y-coordinate grids at each site, and marked by steel reinforcing bar stakes with numbered aluminum tags to facilitate long-term measurements of successional trends and to monitor the results of planned controlled experiments. Four 1 × 1 m quadrats were staked 3 m from each plot center at the cardinal compass points. Percent cover of each plant species was censused subjectively in three strata (<1 m, 1 to 2 m, >2 m). A species' percent cover in a plot was estimated as the mean, across the four quadrats, of the largest value among the three strata at each quadrat.

While these plot sizes are rather small for measuring canopy cover of tree species, percent values obtained from the plots for all species occurring in non-trivial abundance were not statistically different from those obtained on larger plots concentric to subsets of those used in this study ($N = 87$), using point-contact ($N = 19$) and basal area ($N = 65$) methods (unpubl. data).

Our census included 116 "species," which were species of vascular plants, species or genera of mosses, and general morphological types of lichens. Census data were classified using the two-way indicator species analysis (TWINSPAN) routine of the computer program CANOCO (Microcomputer Power, Ithaca, NY). All subsequent analyses involved comparisons among the vegetation categories resulting from the TWINSPAN classification. All statistical analyses also were checked using the original subjective vegetation categories; *P* values in every case fell on the same side of 0.05 as in the analyses using the TWINSPAN-defined categories and, in most cases where differences were significant, the TWINSPAN vegetation types yielded lower probabilities of Type I error.

Table 1. Area (km²) of the southern Pocono Plateau study area categorized by vegetation class and geological parent material. Cultural cover types (32.1 km²) are included in the "Total" column; artificial fill (0.7 km²) and open water (7.4 km²) are omitted.

Parent material	Total	(%)	Upland forest	(%)	Barrens	(%)	Wetlands	(%)
Bedrock (including colluvium)	179.4	(45)	150.2	(50)	17.9	(43)	1.7	(7)
Illinoian drift	115.7	(29)	76.3	(26)	19.8	(47)	3.5	(15)
Wisconsinan drift	74.4	(19)	57.9	(19)	2.4	(6)	8.3	(35)
Stream and swamp deposits	28.2	(9)	15.9	(5)	1.4	(3)	10.0	(43)
Total	397.7	(100)	300.3	(100)	41.5	(100)	23.5	(100)

Three of the six vegetation types were sampled on both Illinoian and Wisconsinan glacial till: beech-northern hardwoods forest, mixed deciduous forest and heath barrens. Using MANOVA, we compared mean cover within each vegetation type between the two kinds of glacial till, of species with greater than 5% overall mean cover. It should be pointed out that each site had only one kind of till; the site effect is confounded with the till-type effect, and results must be interpreted with caution.

We ordinated census data using the detrended correspondence analysis (DCA) routines of the computer program CANOCO, comparing distributions of vegetation types in ordination space. We performed DCA with two data sets, one including all 116 species and the other with only the 55 species having greater than 10% overall frequency among samples. Plots of the first two DCA sample score axes showed essentially the same pattern in both analyses. We present the DCA of the 55-species data set because the more abundant species are likely to be more important ecologically and because the plot of species scores may be interpreted more readily if uncluttered by rare species.

We compared vegetation types in two measures of species diversity: species richness (number of species) and Simpson's index of dominance:

$$D = \sum \left(\frac{n_i(n_i - 1)}{N(N - 1)} \right)$$

where n_i is the abundance of the ith species and N is the total abundance of all species (Magurran 1988). The significance of differences between vegetation types was tested using analysis of variance (ANOVA) and the T′-method (Tukey's HSD test) for multiple comparisons (Sokal and Rohlf 1995). Simpson's index was reciprocal-transformed to improve homogeneity of variances and avert correlation between means and variances. For vegetation types that occurred on both Illinoian and Wisconsinan glacial drift, we compared mean cover on the two drift types of species with greater than 5% overall mean cover using multiple analysis of variance (MANOVA).

WATER TABLE STUDY. Wells were installed at 60 of the vegetation sampling plots in 1992–1993 in order to conduct a long-term study of seasonal high water tables. Wells were encased using 1-m lengths of 4 cm inside-diameter PVC pipe with 7 mm-diameter holes dispersed at about one per 12 cm². Wells were placed in the holes left after sampling soil organic horizons and 80 cm of mineral soils. Thus, most wells extend 80 cm deeper than the bottom of the humus layer. Some wells are shallower due to rocky soils. Water table depths were measured approximately monthly, except in winter, from August 1993 to September 1994. The significance of differences between vegetation types as defined by TWINSPAN was tested in two ways. The proportion of measurements in which a high water table was present was compared by ANOVA followed by the T′-method. The depth to the water table was compared by repeated-measures multivariate analysis of variance (RMANOVA) followed by the T′-method. In all cases in which the well was dry the water table was assumed for the RMANOVA to be 1 cm deeper than the bottom of the well.

Results. LANDSCAPE PATTERNS. The barrens of the southern Pocono Plateau cover approximately 41.5 km² (10% of the vegetation study area) in a few large and many small fragments (Fig. 3; Table 1). Of the total area in barrens vegetation, 21.7 km² (52%) are the till barrens, overlying Illinoian ground moraine (19.3 km²), Wisconsinan terminal moraine (1.9 km²) and Wisconsinan stratified drift (0.50 km²). Barrens overlying alluvium (1.4 km²) closely resemble the till barrens, with high proportions of typically wetland-dwelling plants (Table 2). The re-

Table 2. Wetland plant species commonly found in the mesic barrens on the southern Pocono Plateau. Data are from plot censuses and field records. The wetland indicator status (Reed 1988) represents the estimated probability of occurrence in wetlands under natural conditions: OBL, >99%; FACW, 67 to 99%; +, higher end of frequency range; −, lower end of frequency range. The designations represent consensus among a large number of botanists and ecologists with extensive field experience, reviewed by regional panels to insure reproducibility and defensibility (Reed 1988). Also included here are moss species that live mainly or exclusively in wet habitats, according to Crum and Anderson (1981).

Aster umbellatus	FACW
Bartonia virginica	FACW
Calamagrostis canadensis	FACW+
Calamagrostis cinnoides	OBL
Carex stricta	OBL
Chamaedaphne calyculata	OBL
Coptis trifolia	FACW
Eleocharis tenuis	FACW+
Gentiana linearis	OBL
Juncus filiformis	FACW
Larix laricina	FACW
Lygodium palmatum	FACW
Lyonia ligustrina	FACW
Nyssa sylvatica	FACW+
Osmunda cinnamomea	FACW
Platanthera blephariglottis	OBL
Polytrichum commune	
Rhododendron canadense	FACW
Rubus hispidus	FACW
Sphagnum capillifolium	
Sphagnum magellanicum	
Sphagnum palustre	
Spiraea latifolia	FACW+
Spiraea tomentosa	FACW
Vaccinium corymbosum	FACW−
Viburnum cassinoides	FACW

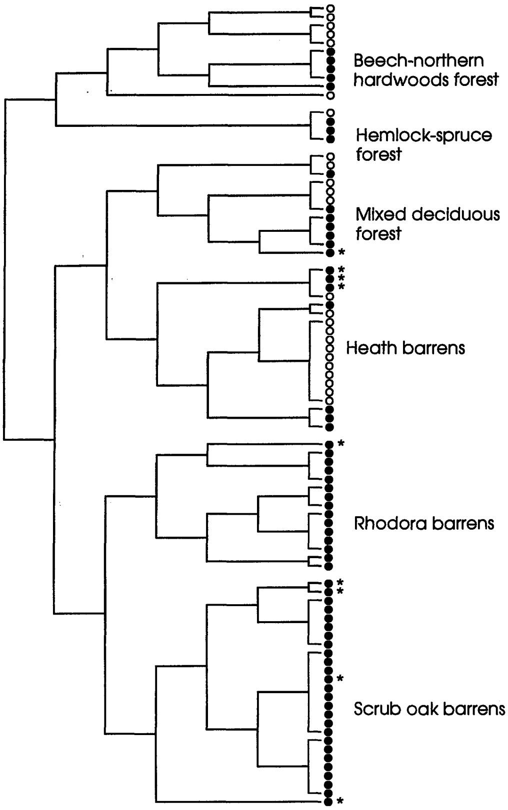

Fig. 4. TWINSPAN dendrogram of 87 vegetation samples. Samples are underlain by Wisconsinan till (open circles) or Illinoian till (filled circles). Asterisks denote samples subjectively considered as belonging to a different category prior to the analysis: the two flanking the heath barrens group had been identified as heath barrens; the remainder had been classified as rhodora barrens except for the lowest sample on the dendrogram, which had been identified as forest.

mainder is mainly xeric scrub oak barrens overlying Devonian sandstones and conglomerates of the Catskill Formation and colluvium derived from the same material (17.9 km^2), with few or no plants usually associated with wetlands. The breakdown of Pocono barrens vegetation types in the study area is scrub oak barrens, 37.7 km^2 (55% of this area overlies glacial drift or alluvium); heath barrens, 3.28 km^2 (71%); upland pitch pine woodlands, 3.14 km^2 (64%); and rhodora barrens, 0.67 km^2 (87%).

Although the barrens occur disproportionately on Illinoian glacial till (Table 1) they occupy only 23% of the area underlain by this parent material (Fig. 2). The rest of the Illinoian till is covered by the region's prevailing upland forest types (57%), cropland and high-density residential development (16%), and wetland vegetation (4%).

VEGETATION. In Pocono till barrens samples, we recorded 91 vascular plant species in 34 families and 11 moss species in seven families (Appendix). Of these, 64 species occurred on at least 5% of the census plots (see Appendix superscripts). Plants usually found in wetland habitats (Table 2) make up a substantial proportion of the till barrens flora.

TWINSPAN grouped samples at the third level of division into six categories (Fig. 4). Three of the categories, representing 60 samples, correspond closely to the three shrub-dominated barrens types identified subjectively prior to data collection; the other three, with 27 samples, are forest types (described in Table 3). Some samples were subjectively considered as belonging to a different category prior to the analysis (asterisks in Fig. 4). Species composition in most

Table 3. Species with mean cover greater than 5% in community types defined by TWINSPAN. Values are mean percent cover ± SE (standard error of the mean). Vegetation types are: F, beech–northern hardwoods forest; T, hemlock-spruce forest; A, mixed deciduous forest; K, heath barrens; R, rhodora barrens; Q, scrub oak barrens.

	Forest types			Barrens types		
	F	T	A	K	R	Q
Acer rubrum	28 ± 11.3	70 ± 21.8	53 ± 7.5	—	9 ± 2.7	8 ± 2.5
Amelanchier arborea, A. laevis	14 ± 9.9	—	15 ± 3.3	7 ± 3.0	—	—
Aronia melanocarpa	—	—	—	17 ± 4.4	—	—
Betula populifolia	—	—	6 ± 3.8	—	—	—
Dennstaedtia punctilobula	10 ± 3.8	—	—	—	—	—
Fagus grandifolia	62 ± 11.0	6 ± 6.3	—	—	—	—
Gaultheria procumbens	—	—	—	12 ± 3.2	9 ± 3.3	13 ± 2.6
Gaylussacia baccata	—	—	—	—	—	16 ± 4.2
Kalmia angustifolia	—	—	7 ± 3.9	31 ± 5.5	13 ± 3.9	10 ± 1.8
Picea rubens	—	21 ± 5.9	—	—	—	—
Pinus rigida	—	—	—	—	29 ± 5.5	10 ± 2.7
Polytrichum commune	—	—	5 ± 4.0	—	10 ± 2.6	—
Prunus serotina	10 ± 7.9	—	5 ± 2.7	—	—	—
Pteridium aquilinum	—	—	—	—	8 ± 1.9	17 ± 3.6
Quercus coccinea	—	—	5 ± 2.8	—	—	—
Quercus ilicifolia	—	—	—	—	—	33 ± 3.2
Rhododendron canadense	—	—	—	8 ± 4.4	56 ± 7.0	23 ± 5.4
Rhododendron maximum	—	7 ± 4.8	—	—	—	—
Sphagnum spp.	—	—	—	7 ± 3.4	—	—
Thelypteris noveboracensis	14 ± 5.8	—	—	—	—	—
Tsuga canadensis	—	27 ± 17.3	—	—	—	—
Vaccinium angustifolium	—	—	6 ± 3.6	32 ± 5.0	20 ± 4.9	13 ± 2.6
Viburnum cassinoides	—	—	—	7 ± 3.1	—	—

of these anomalous samples departs markedly from other samples in the same TWINSPAN-defined group. For example, the rhodora barrens sample closest to heath barrens in the TWINSPAN analysis has no rhodora (*Rhododendron canadense*). One sample (bottom of Fig. 4) was in the only oak forest stand we sampled; TWINSPAN lumped it with the group of samples most similar in species composition—the scrub oak barrens. The anomalies apparently had little effect on statistical comparisons (see Methods).

Comparing the plots of sample scores and species scores (Figs. 5 and 6) gives clues to the nature of the first and second-axis gradients and highlights the species that best define each vegetation type. The first axis (eigenvalue 0.81) represents a forest-barrens continuum. The lowest scoring forest samples are in northern hardwoods dominated by *Fagus grandifolia* Ehrh., which did not occur in any barrens samples. The forest sample with a first-axis score nearly as high as the barrens samples is dominated by *Sassafras albidum, Betula populifolia, Quercus alba* and *Acer rubrum,* all of which occur in the barrens, and its understory consists mainly of the common barrens shrubs *Gaylussacia baccata, Viburnum cassinoides* and *Quercus ilicifolia.* The barrens sample with the lowest first-axis score has a high cover of *Acer rubrum.*

The second axis (eigenvalue 0.39) to some extent reflects a moisture gradient. Several of the wetland species (Table 2) cluster near the top of the plot of species scores and the wet hemlock-spruce forest and rhodora barrens samples cluster near the top of the plot of sample scores. It is not clear that the driest sites and most drought-tolerant species cluster at the bottom, however. Second and higher-order axes in DCA are prone to "noise" introduced by detrending (Wartenberg et al. 1987) and should be interpreted with caution.

The effect of vegetation type was significant in ANOVA of both measures of species diversity (Table 4a and 4b). In pairwise comparisons of the six vegetation types using the T′-test (Fig. 7), beech-northern hardwoods forest ranks significantly lower in species richness (mean 13.9 species/plot) and higher in Simpson's index of dominance (mean 0.50) than mixed deciduous forest (26.8, 0.26) and the three barrens types (heath 19.3, 0.23; rhodora 25.3, 0.20; scrub oak 21.0, 0.20). Numbers of species in mixed deciduous forest and rhodora barrens are significantly higher than in heath barrens; mixed deciduous

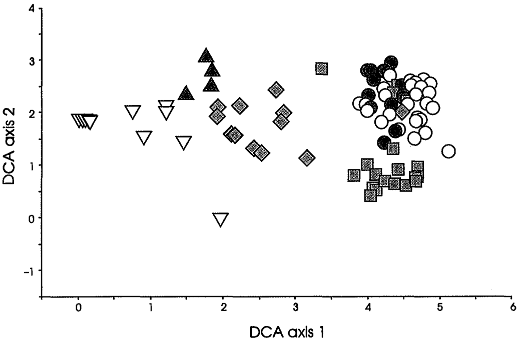

Fig. 5. Ordination of 87 vegetation sample DCA scores. Only the 55 species with >10% overall frequency among samples were included in this analysis. Symbols denote vegetation types classified by TWINSPAN: ▽, beech-northern hardwoods forest; △, hemlock-spruce forest; ◇, mixed deciduous forest; □, heath barrens; ●, rhodora barrens; ○, scrub oak barrens.

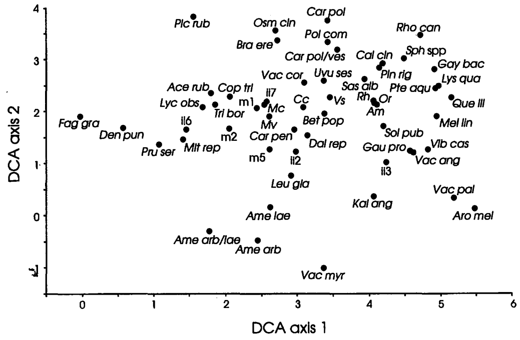

Fig. 6. Ordination of 55 species with >10% overall frequency. Species around the periphery of the DCA plot are most useful for discriminating among vegetation types. Labels consist of abbreviations for most plant names and arbitrary morphological type designations for lichens and some mosses. Two species abbreviations separated by a slash indicate a pair of similar congeners which, in some cases, could not be reliably distinguished in the field. Abbreviations are Ace rub, *Acer rubrum*; Am, *Amianthium muscaetoxicum*; Ame arb, *Amelanchier arborea*; Ame lae, *Amelanchier laevis*; Aro mel, *Aronia melanocarpa*; Bet pop, *Betula populifolia*; Bra ere, *Brachyelytrum erectum*; Cal cin, *Calamagrostis cinnoides*; Car pen, *Carex pensylvanica*; Car pol, *Carex polymorpha*; Car ves, *Carex vestita*; Cc, *Cornus canadensis*; Cop tri, *Coptis trifolia*; Dal rep, *Dalibarda repens*; Den pun, *Dennstaedtia punctilobula*; Fag gra, *Fagus grandifolia*; Gau pro, *Gaultheria procumbens*; Gay bac, *Gaylussacia baccata*; Kal ang, *Kalmia angustifolia*; Leu gla, *Leucobryum glaucum*; li2, li3, li6, li7, lichens; Lyc obs, *Lycopodium obscurum*; Lys qua, *Lysimachia quadrifolia*; m1, m2, m5, mosses; Mc, *Maianthemum canadense*; Mel lin, *Melampyrum lineare*; Mit rep, *Mitchella repens*; Mv, *Medeola virginiana*; Or, *Oryzopsis racemosa*; Osm cin, *Osmunda cinnamomea*; Pic rub, *Picea rubens*; Pin rig, *Pinus rigida*; Pol com, *Polytrichum commune*; Pru ser, *Prunus serotina*; Pte aqu, *Pteridium aquilinum*; Que ili, *Quercus ilicifolia*; Rh, *Rubus hispidus*; Rho can, *Rhododendron canadense*; Sas alb, *Sassifras albidum*; Sol pub, *Solidago puberula*; Sph spp, *Sphagnum* spp.; Tri bor, *Trientalis borealis*; Uvu ses, *Uvularia sessilifolia*; Vac ang, *Vaccinium angustifolum*; Vac cor, *Vaccinium corymbosum*; Vac myr, *Vaccinium myrtilloides*; Vac pal, *Vaccinium pallidum*; Vib cas, *Viburnum cassinoides*; Vs, *Vaccinium stamineum.*

forest is also higher in species richness than scrub oak barrens.

Beech-northern hardwoods forest samples differ significantly in mean cover between tills (Wilks' λ = 0.052, Rao's $R_{(6,4)}$ = 12.1, P = 0.015). Univariate tests show that the differences are due to *Acer rubrum* (mean cover on Illinoian and Wisconsinan till, respectively, 60.2% and 2.0%, $F_{(1,9)}$ = 17.0, P = 0.003) and *Thelypteris noveboracensis* (L.) Nieuwl. (means 29.6% and 0.9%, $F_{(1,9)}$ = 14.2, P = 0.004). Heath barrens samples also differ significantly in mean cover between tills (Wilks' λ = 0.276, Rao's $R_{(8,10)}$ = 3.3, P = 0.042), with the differences due to *Aronia melanocarpa* (mean cover on Illinoian and Wisconsinan till, respectively, 2.8% and 26.0%, $F_{(1,17)}$ = 9.8, P = 0.006), *Gaultheria procumbens* (means 2.3% and 17.9%, $F_{(1,17)}$ = 7.5, P = 0.014) and *Rhododendron canadense* (means 21.8% and 0%, $F_{(1,17)}$ = 7.9, P = 0.012). Mixed deciduous forest samples do not differ significantly between Illinoian and Wisconsinan till (Rao's $R_{(8,3)}$ = 2.9, P > 0.05).

WATER TABLE. The proportion of measurements in which a high water table was present and the depth to the high water table did not vary significantly between forest and barrens samples (Table 4c and 4d) but did differ significantly among the six more specific vegetation types (Table 4e and 4f). The RMANOVA of depth to the high water table is highly conservative, since, when a well was dry, the unknown level of the water table was assumed for the analysis to be just 1 cm deeper than the bottom of the well. Readers should interpret the results with the caveat in mind that site and vegetation type are partially confounded. Multiple comparisons following both analyses had several results in common (Fig. 8): beech-northern hardwoods forest and scrub oak barrens had a high water table significantly less frequently and, at several measurements, they had a significantly lower water table than hemlock-spruce forest, rhodora barrens and heath barrens. Mixed deciduous forest had a high water table significantly less fre-

Table 4. Analysis of variance results.

	SS	df	MS	*F*	*P*
(a) Species richness in census plots among six vegetation types.					
Vegetation type	1273.2	5	254.6	14.1	0.000
Error	1462.1	81	18.1		
(b) Species dominance (Simpson's index) in census plots among six vegetation types. Simpson's index was reciprocal-transformed to meet the assumptions of ANOVA.					
Vegetation type	0.973	5	0.1947	13.6	0.000
Error	1.156	81	0.0143		
(c) Proportions of measurements in which a water table less than 1 m deep was present, between forest and barrens.					
Forest/barrens	0.147	1	0.1475	1.1	0.289
Error	7.218	56	0.1289		
(d) Proportions of measurements in which a water table less than 1 m deep was present, among six vegetation types defined by TWINSPAN.					
Vegetation type	2.493	5	0.4985	5.3	0.001
Error	4.873	52	0.0937		

	df_{effect}	MS_{effect}	df_{error}	MS_{error}	*F*	*P*
(e) Repeated-measures ANOVA comparing minimum depths to high water table between forest and barrens.						
Forest/barrens	1	461.7	56	3920.2	0.1	0.733
Time	7	4911.2	392	209.8	23.4	0.000
Interaction	7	155.8	392	209.8	0.7	0.636
(f) Repeated-measures ANOVA comparing minimum depths to high water table among six vegetation types defined by TWINSPAN.						
Vegetation type	5	9394.7	52	3327.3	2.8	0.025
Time	7	5888.8	364	178.1	33.1	0.000
Interaction	35	529.1	364	178.1	3.0	0.000

quently and often a lower water table than hemlock-spruce forest, a less frequent high water table than rhodora barrens, and often a higher water table than scrub oak barrens. Hemlock-spruce forest, at several measurements, had a significantly higher water table than heath barrens and rhodora barrens.

Discussion. Conventional wisdom holds that barrens vegetation in climatic zones with abundant year-round precipitation indicates unusual soil conditions, principally droughtiness and low nutrients (e.g., Platt 1951; Walker 1954; Reich and Hinckley 1980; Homoya 1994). Several lines of evidence point to the Pocono till barrens as an exception. On glacial drift deposits of the southern Pocono Plateau, shrub-savanna vegetation does not correlate with xeric conditions. Analyses of well data showed no significant difference between barrens and forest vegetation in the occurrence of a high water table less than 1 m from the surface. In the summer, forest and barrens had a similar range of wetter and drier sites. By remote sensing and ground-truthing, nearly 4 km^2 of the Pocono shrub savanna were delineated as rhodora barrens and heath barrens, much of which has a *Sphagnum* ground layer and abundant wetland vascular plant species. The rhodora barrens and portions of the heath barrens meet the criteria for classification as wetlands, but they are distinct from nearby dwarf shrub swamps in species composition and in always lying adjacent to upland (but usually mesic) shrub barrens (Thompson 1995). In these barrens hydrophytes predominate but they live side-by-side with shrub species with small, thickened, lignin-hardened leaves that commonly live in xeric habitats. The scrub oak barrens overlying Illinoian glacial till also have plants characteristic of wet or mesic habitats interspersed with xerophytes.

We measured the water table during years of relatively ordinary precipitation. Thus we could not rule out that barrens vegetation might indicate sites that are subject to more severe drying than nearby forested sites only during drought years. However, this seems to us unlikely based on the prevalence of wetland species in the till barrens, the frequent occurrence of barrens downslope from forests, and evidence of the same wide range of water table depths in the barrens as in the forest. The hypothesis that the

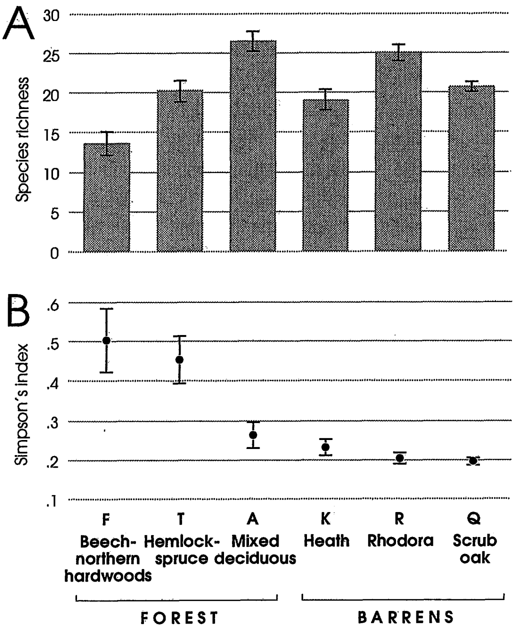

Fig. 7. Diversity by vegetation type. A—Species richness and B—Simpson's index (species dominance) by vegetation type. Error bars indicate ±1 standard error of the mean. Significantly different pairs of means (T′-method, $\alpha = 0.05$) are, for species richness, FA, FK, FR, FQ, AK, AQ, KR and, for Simpson's index, FA, FK, FR, FQ.

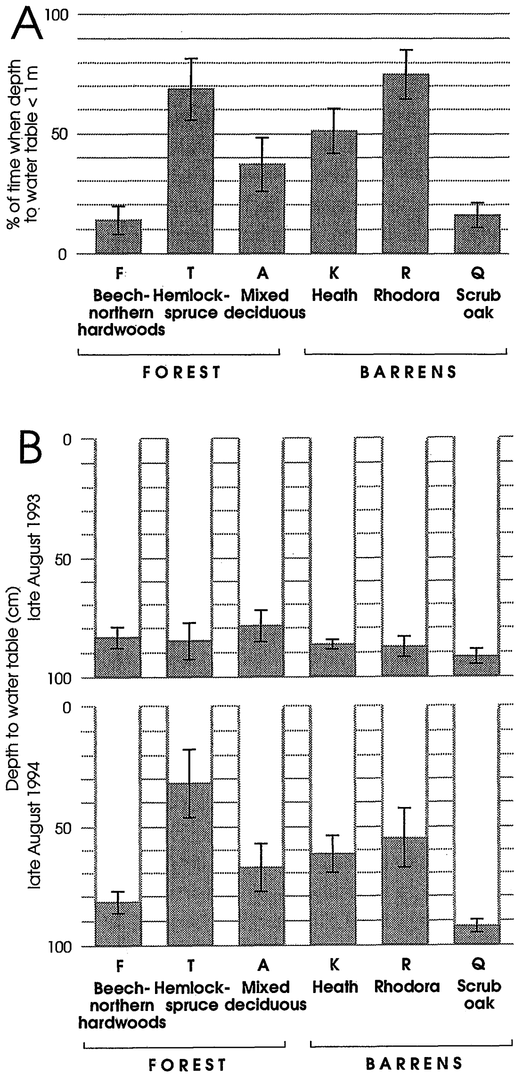

Fig. 8. Depth of water table by vegetation type. A—Percentage of eight measurements over 14 months in which a high water table was present, by vegetation type. Significantly different pairs of means (T′-method, $\alpha = 0.05$) are FT, FK, FR, TA, TQ, AR, KQ, RQ. B—Mean high water table depth in late August 1993 and late August 1994, by vegetation type. Means are significantly different only on the second graph (T′-method, $\alpha = 0.05$): FT, FK, FR, TA, TK, TR, TQ, AQ, KQ, RQ. The numbers of wells in each vegetation type are 10(F), 4(T), 11(A), 17(K), 5(R) and 11(Q). Error bars indicate ±1 standard error of the mean.

till barrens soils are no drier during a drought than forest soils on till can be tested only during a drought year.

Although the Pocono till barrens occur disproportionately on Illinoian glacial till, they occupy only 28% of the area underlain by this substratum that has not been cleared for human use. Furthermore, 18% of the barrens overlying unconsolidated materials (glacial drift and alluvium) do not occupy Illinoian till. We have not yet identified any topographic factor, such as slope and aspect, or other vegetation-independent predictor, such as soil depth or drainage class, distinguishing the area covered by barrens vegetation from the area covered by the region's prevailing forest types. Clearly, parent material provides at best only a partial explanation for the distinctiveness of the barrens vegetation.

Plant traits linked with drought tolerance are found abundantly in the Pocono till barrens, as is the case in certain other reliably moist habitats worldwide (e.g., Jackson 1968; Gimingham 1972; Damman 1975; Kellman 1979; Streng and Harcombe 1982; Meades 1983; Read 1984; Ash 1988; Unwin 1989; Weetman et al. 1990; Geldenhuys 1994). Grime (1977) offered a resolution to the apparent paradox of vegetation resembling that of arid regions living on moist soils in a humid climate by proposing a generalized stress toleration syndrome. Plants resembling xerophytes are common in situations where soils are inherently low in some essential mineral nutrient or even where water is superabundant, causing oxygen deficit in the rooting zone and other stresses. So far no such inherent soil quality has been found that might explain the presence of the mesic barrens on the Pocono Plateau. Here and in other mesic barrens, the key may lie in the broad overlap between tolerance of soil-based stresses and tolerance of fire. What may have arisen as adaptations to soil factors may function in some habitats as "pyric" adaptations (Jones 1971; Chapin 1991; Chapin et al. 1993; Christensen 1993).

POSSIBLE ORIGIN OF THE POCONO TILL BARRENS FLORA. *Age of the Barrens.* Two lines of circumstantial evidence suggest that the barrens are more than a few hundred years old. One is the presence of a large concentration of rare species and disjunct populations. The other consists of accounts written before the European settlement of the Plateau remarking on the barrens' prominence.

No one has yet investigated fossil pollen stratigraphy in the vicinity of the barrens. However, a palynological study has been completed at a flat, shrub-dominated portion of the Shawangunk Mountains, New York (McIntosh 1959), the ecosystem floristically most similar to the Pocono till barrens (M. Anderson, The Nature Conservancy, Conservation Science Department, Eastern Region, pers. comm.). A 9000-yr chronology at Shawangunk Spruce Swamp places the origin of the nearby barrens at approximately 2000 yr ago, marked by charcoal peaks, abrupt expansion of Ericaceae and *Viburnum* (presumably *V. cassinoides*), more gradual expansion of *Pinus rigida* and *Betula populifolia,* with charcoal and barrens species' pollen values remaining high to the present (Laing 1994).

Origin of the Disturbance Regime. The southern Pocono Plateau is the only place in Pennsylvania documented as having had large expanses of scrub oak prior to European settlement (Cook 1887). Scrub oak's local beachhead was most likely on the shallow, sandy soils along the sandstone ridge defining the Pocono Plateau escarpment, where the benefits of its adaptations to the habitat's harsh stresses—drought, low-nutrient conditions and frequent fire—outweigh the presumed costs of maintaining these traits, such as an inherently slow aboveground growth rate (Bloom et al. 1985). The high flammability of scrub oak and associated ericaceous shrubs may have allowed the area affected by frequent fire to advance gradually farther from the Plateau's rim into areas with moist soils. Lightning may have ignited some fires, but humans were a more likely source. Radiocarbon dates verify human occupation more than 10,000 yr ago within 18 km of the southern Plateau (McNett 1986). Native Americans were managing vegetation by burning in late prehistoric and early historic times in many parts of eastern North America (Day 1953; Myers and Peroni 1983; Patterson and Sassaman 1988; Denevan 1992). Several pollen stratigraphy studies at barrens in eastern North America show a relatively abrupt accession of charcoal and barrens species' pollen (Lewis 1976; Laing 1994), consistent with the cultural spread of the use of fire to improve hunting or to foster food-producing wild plants such as blueberries.

MAINTENANCE OF THE POCONO TILL BARRENS FLORA. *The Role of Topography.* The apparent relationship between Illinoian glacial till and the barrens vegetation may not be causal. The barrens and the large Illinoian till deposits both may be on the southern Pocono Plateau in part because the site is so flat. Between the terminal moraine and the escarpment is a series of large, nearly flat areas including the largest in the northeastern quarter of Pennsylvania (based on areas devoid of 30-m contour lines on the U.S. Geological Survey's 1:250,000-scale topographic maps)—an area approximately 12 × 7 km surrounding Long Pond. The low gradient would have resulted in low rates of erosion, preserving the older till. The flat areas and the adjoining summit of the steep, southward-facing escarpment provide conditions that are especially conducive to the spread of fire. Spot fires on the escarpment face are likely to spread quickly upslope. Persistent winds blowing uninterrupted across the plains at the top are likely to fan ignition points into wildfires covering large areas. This model is consistent with the virtual absence of barrens on the north side of Tunkhannock Creek and its broad wetland corridor (a barrier to the spread of fire), despite the prevalence of Illinoian till there (Figs. 2 and 3). The largest barrens area north of the Tunkhannock is adjacent to a reach flowing through a narrow ravine, without the broad, virtually fire-immune wetland corridor which is characteristic of most of the stream's length.

Are Plants Driving the Maintenance of Alternative Vegetation States? Biotic factors may be more important than abiotic factors in sustaining the dichotomy in vegetation on the southern Pocono Plateau. Successional pathways may diverge autogenically, driven by positive feedbacks between plants and their abiotic environment (Vitousek 1982; DeAngelis et al. 1986; Roberts 1987; Perry et al. 1989; Hobbie 1992; Wilson and Agnew 1992). Members of some of the dominant plant species in both barrens and forest may be altering soil organic matter dynamics, nitrogen cycling, wildfire and microclimate in ways that favor the persistence of the incumbent species and inhibit invasion by members of the alternative assemblage. Thus, the different dominant species in each vegetation category may regulate the factors that in turn determine species composition.

Nitrogen availability sometimes increases immediately after a fire, but it decreases with repeated fires due to a shift toward dominance by fire-tolerant plant species (Vitousek 1982; Ojima et al. 1994). Such plants have a generalized stress-tolerance syndrome including high nitrogen-use efficiency and low foliar nitrogen concentrations. Sclerophylly (having thickened, tannin-rich, lignin-hardened foliage resistant to water loss) gives rise to recalcitrant (decay-resistant) litter with high carbon:nitrogen and lignin:nitrogen ratios and slow rates of nitrogen release. By thus restricting nitrogen availability, stress-tolerant plants where they are abundant can inhibit invasion by taller, faster-growing species which tend to have lower maximum nitrogen-use efficiencies. As a separate issue from fire tolerance, some stress-adaptive traits coincidentally confer higher flammability, for example, volatile, oily or resinous anti-herbivore secondary compounds and sclerophylly, which induces slow litter decomposition rates resulting in high fuel loads (Rundel 1981). (The common shrubs of the southern Pocono Plateau barrens are so flammable that local firefighters and other residents call one or more species "kerosene bush.") Given a reliable ignition source (e.g., humans), sites with greater proportions of plants with such traits will have larger, more frequent and more intense fires. A positive feedback may result: each incremental change decreases the success of competitors (nitrogen-demanding, fire-sensitive species) and increases the likelihood that the stress tolerators will persist and spread, which in turn increases the magnitude of the change, and so on. Thus, the decrease in nitrogen availability with repeated fires may be sustained autogenically (Vitousek 1982; Ojima et al. 1994).

The existence of heath barrens and rhodora barrens as vegetation types distinct from the prevailing scrub oak barrens may be due, in part, to the "frost-pocket" phenomenon (Hough 1945; Clarke 1946; Schlegel and Butch 1980). In these shrub-dominated depressions, invasion by forest trees is inhibited even in the absence of fire. A frost pocket starts with wildfire or lumbering removing the tree canopy. Heat absorbed by the ground during the day is re-emitted at night as infrared radiation, which escapes into space unless it is reflected back by tree canopies or clouds. With only a shrub cover, radiative cooling at the ground surface is unimpeded on clear nights. Swales and saddles—often so subtle that they are imperceptible without a topographic map—act as conduits for cool air drainage. The result is unseasonable frost, which occurs in June, July and August during most years in Pocono barrens frost pockets (D. Miller, Pa. Bur. Forestry Dist. 19, Stroudsburg, unpubl. data). Tree seedlings, scrub oak and other nonericaceous shrubs are killed or stunted, either by freezing, increased susceptibility to insect herbivory (Aizen and Patterson 1993), soil changes induced by ericaceous shrubs and associated mycorrhizal fungi (Read 1984; Leake 1992), or a combination of these processes. Our observations over several years indicate that *Kalmia angustifolia, Rhododendron canadense* and the low *Vaccinium* spp. are resistant, and *Quercus ilicifolia* and the seedlings of *Acer rubrum* and most other hardwoods are susceptible. A 4-ha heath barren near Long Pond with low, tundra-like vegetation has persisted for over 40 years without fire or other disturbance (1938–1939 aerial photographs; D. Miller, Pa. Bur. Forestry Dist. 19, Stroudsburg, pers. comm.).

The rhodora barrens may owe their existence partly to frost pockets but their position on the wetter parts of the landscape and their highest rank in species diversity among the barrens types leads us to conjecture that they may also be an ecotone between scrub oak barrens and swamp forest, with species from both communities. Similarly, mixed deciduous forest is highest in species diversity of all six vegetation types we studied most likely because it is a successional community with species from both barrens and forests, where forest trees, mainly *Acer rubrum,* are invading barrens in the prolonged absence of fire.

A common feature of the mesic barrens is an abrupt transition along the perimeter of a barrens patch to fully developed forest vegetation. Autogenic processes originating with the plants themselves provide a more plausible explanation for the sharp boundaries than abiotic constraints such as soil moisture gradients, which should generally result in more gradual transitions (Wilson and Agnew 1992).

CONCLUSIONS. Plants growing in fire-prone habitats often closely resemble or are the same species as plants living in drought-prone, oligotrophic or waterlogged habitats. Because many stress-tolerance traits or their byproducts also happen to enhance flammability, fire-prone vegetation on mesic or wet sites may violate the assumed direct relationship between moisture availability and fire activity, in which fire frequency peaks in moderately dry environments and declines steadily across increasingly wet (or dry) habitats (e.g., Huston 1994).

Research is currently underway to test underlying assumptions and some predictions arising from the following scenario. Scrub oak may be the principal fire carrier in the Pocono till barrens system, chiefly responsible for the persistence of the other fire-maintained populations. Scrub oak and other fire-tolerant (but highly flammable) shrubs may have established a foothold along the Pocono Plateau's rim where sandy soils weathered from sandstones and conglomerates are kept shallow by wind and erosion. Such ridgetop barrens may be prone to lightning fires and during droughts fires would have spread away from the escarpment across the top of the Plateau and into vegetation growing on the finer, wetter soils of the Illinoian till plains and Wisconsinan terminal moraine. Severe burns during droughts would have killed forest trees, allowing fire-tolerant barrens shrubs to spread. Once established, the mesic barrens may be self-sustaining, owing to feedbacks between the dominant shrub species and fire, soil nutrient availability, and microclimate.

Implications for Conservation. "Alternative stable state" models such as the one we propose here hold that certain perturbations can shift a given site from one relatively stable species composition to another (Sutherland 1990). The mesic barrens have been shrinking over the last 40 to 60 years. Heath, scrub and savanna landscapes—harboring many rare and endangered species—appear to be shifting to a woodland landscape dominated by common species. We hypothesize that the mesic barrens' decline is a state transition in progress, resulting mainly from fire suppression.

The southern Pocono Plateau has 4150 ha of extant barrens, of which 2310 ha overlie till and alluvium and appear mesic to wet based on species composition. The North Fork Mountain, West Virginia, barrens total less than 100 ha, a small fraction of which is mesic barrens (Harmon 1981). The area of the Shawangunk Mountain, New York, barrens is approximately 2850 ha, of which an estimated 16 ha are mesic or wet (unpubl. GIS data). Thus, the Pocono till barrens probably comprise more than 90% of the known global extent of a rare vegetation type apparently endemic to moist montane sites in eastern North America.

The mesic to wet barrens vegetation, often dominated by *Rhododendron canadense,* is the foundation and framework of a globally rare natural community. It has the highest plant species richness among the local barrens types and it includes the highest density of the globally rare plant *Carex polymorpha,* whose Pocono Plateau population is one of the largest in the entire species' range (Rawinski and Sneddon 1991). To the degree that protection and management for biodiversity are based on the ranking of vegetation types, the mesic barrens are worthy of the highest level of priority. However, the mesic barrens may well depend on the proximity of more xeric barrens as a vector of wildfire and of wetlands as a source of species. Because of the probable interdependence among vegetation patch types and the large cluster of rare species inhabiting both the barrens and nearby wetlands, an integrated, landscape-scale approach must guide conservation efforts at this important site.

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Appendix: List of plant species found in the Pocono till barrens. Listed species were found at more than one site or they are widespread in at least one site. Plants seen only on trails or other artificially disturbed areas are excluded. Superscripts preceding plant names indicate frequency on the 60 barrens census plots: ^{1}, ≥75%; ^{2}, 50–74%; ^{3}, 25–49%, ^{4}, 5–24%; no superscript, <5% or found elsewhere besides census plots. Voucher specimens are in the herbarium of the Morris Arboretum, University of Pennsylvania, for species marked with an asterisk. Species were identified by Roger Latham and Ann Rhoads (vascular plants) and Christine Manville (mosses). Nomenclature follows Rhoads and Klein (1993) for vascular plants, with synonyms from Gleason and Cronquist (1991) where the two sources differ, and Anderson, Crum and Buck (1990) for mosses.

Vascular Plants

ACERACEAE

^{2} *Acer rubrum* L.

AQUIFOLIACEAE

Ilex montana (Torr. & A.Gray) A.Gray*

ARALIACEAE

Aralia hispida Vent.*
^{4} *Aralia nudicaulis* L.
^{4} *Panax trifolius* L.

ASTERACEAE

^{4} *Aster umbellatus* P.Mill.
Erechtites hieraciifolia (L.) Raf. *ex* DC.
^{4} *Prenanthes trifoliolata* (Cass.) Fern.*
^{3} *Solidago puberula* Nutt.*

BETULACEAE

^{3} *Betula populifolia* Marshall

CAPRIFOLIACEAE

^{1} *Viburnum cassinoides* L. (syn. *V. nudum* L. var. *cassinoides* [L.] Torr. & A.Gray)

CORNACEAE

^{4} *Cornus canadensis* L.

CYPERACEAE

^{1} *Carex pensylvanica* Lam.
^{3} *Carex polymorpha* Muhl.*
Carex stricta Lam.*
^{4} *Carex vestita* Willd.*
Eleocharis tenuis (Willd.) Schultes

DENNSTAEDTIACEAE

Dennstaedtia punctilobula (Michx.) T.Moore
^{1} *Pteridium aquilinum* (L.) Kuhn

ERICACEAE

Chamaedaphne calyculata (L.) Moench.
^{4} *Epigaea repens* L.
^{1} *Gaultheria procumbens* L.
^{3} *Gaylussacia baccata* (Wang.) K.Koch
Gaylussacia frondosa (L.) Torr. & A.Gray *ex* Torr.
^{1} *Kalmia angustifolia* L.
Lyonia ligustrina (L.) DC.
^{2} *Rhododendron canadense* (L.) Torr.*
^{1} *Vaccinium angustifolium* Ait.
^{4} *Vaccinium corymbosum* L.
^{4} *Vaccinium myrtilloides* Michx.
^{3} *Vaccinium pallidum* Ait.
^{4} *Vaccinium stamineum* L.

FAGACEAE

Quercus alba L.
Quercus coccinea Muenchh.
^{2} *Quercus ilicifolia* Wang.
Quercus palustris Muenchh.

GENTIANACEAE

Bartonia virginica (L.) BSP*
^{4} *Gentiana linearis* Froel.*

HAMAMELACEAE

Hamamelis virginiana L.

JUNCACEAE

Juncus filiformis L.*

LAURACEAE

^{3} *Sassafras albidum* (Nutt.) Nees

LILIACEAE

^{3} *Amianthium muscaetoxicum* (Walt.) A.Gray
Lilium philadelphicum L.
^{3} *Maianthemum canadense* Desf.
^{4} *Medeola virginiana* L.
Trillium undulatum Willd.
^{3} *Uvularia sessilifolia* L.

LYCOPODIACEAE

Diphasiastrum digitatum (A.Braun) Holub (syn. *Lycopodium digitatum* Dillen.)
^{3} *Lycopodium hickeyi* W.Wagner, Beitel & R.C.Moran* (syn. *L. obscurum* L. var. *isophyllum* Hickey)
Lycopodium obscurum L.

LYGODIACEAE

Lygodium palmatum (Bernh.) Swartz*

MONOTROPACEAE

^{4} *Monotropa uniflora* L.

MYRICACEAE

^{4} *Comptonia peregrina* (L.) Coult.

NYSSACEAE

Nyssa sylvatica Marshall

ORCHIDACEAE

^{4} *Cypripedium acaule* Ait.
Platanthera blephariglottis (Willd.) Lindl. (syn. *Habenaria blephariglottis* [Willd.] Hook.)

OSMUNDACEAE

^{4} *Osmunda cinnamomea* L.
^{4} *Osmunda claytoniana* L.

PINACEAE

Larix laricina (DuRoi) K.Koch
^{4} *Picea rubens* Sarg.
^{2} *Pinus rigida* P.Mill.
^{4} *Pinus strobus* L.
Tsuga canadensis (L.) Carr.

POACEAE

^{4} *Brachyelytrum erectum* (Schreb.) Beauv.
Calamagrostis canadensis (Michx.) Beauv.
^{4} *Calamagrostis cinnoides* (Muhl.) Bart.

Appendix (Continued).

[4] *Danthonia spicata* (L.) Beauv. *ex* Roemer & Schultes
[1] *Oryzopsis racemosa* (Smith) Ricker *ex* A.S.Hitchc.*
Panicum boreale Nash*
Panicum meridionale Ashe (syn. *P. leucothrix* Nash)

POLYGALACEAE
Polygala paucifolia Willd.

PRIMULACEAE
[3] *Lysimachia quadrifolia* Sims
[3] *Trientalis borealis* Raf.

RANUNCULACEAE
[4] *Coptis trifolia* (L.) Salisb.

ROSACEAE
[4] *Amelanchier arborea* (Michx.f.) Fern.*
[4] *Amelanchier laevis* Wieg.*
[4] *Amelanchier sanguinea* (Pursh) DC.
[4] *Amelanchier stolonifera* Wieg. (syn. *A. spicata* [Lam.] K.Koch)
[1] *Aronia melanocarpa* (Michx.) Ell.
[4] *Dalibarda repens* L.
Prunus serotina Ehrh.
Prunus pensylvanica L.f.
[1] *Rubus hispidus* L. *sensu lato**
Spiraea latifolia (Ait.) Borkh. (syn. S. *alba* DuRoi var. *Latifolia* [Ait.] Dippel.)
Spiraea tomentosa L.

RUBIACEAE
[4] *Mitchella repens L.*

SALICACEAE
Populus tremuloides Michx.
Salix humilis Marshall*

SANTALACEAE
Comandra umbellata (L.) Nutt.

SCROPHULARIACEAE
[3] *Melampyrum lineare* Desr.

SMILACACEAE
Smilax herbacea L.
Smilax rotundifolia L.

Mosses

AULACOMNIACEAE
[4] *Aulacomnium androgynum* (Hedw.) Schwaegr.

BRYACEAE
Pohlia cf. nutans (Hedw.) Lindb.

DICRANACEAE
[4] *Dicranum montanum* Hedw.
[4] *Dicranum scoparium* Hedw.

HYPNACEAE
Callicladium haldanianum (Grev.) Crum
[4] *Hypnum imponens* Hedw.

LEUCOBRYACEAE
[3] *Leucobryum glaucum* (Hedw.) Ångstr. *ex* Fries

POLYTRICHACEAE
[2] *Polytrichum commune* Hedw.

SPHAGNACEAE
[4] *Sphagnum capillifolium* (Ehrh.) Hedw. var. *capillifolium*
[4] *Sphagnum magellanicum* (Ehrh.) Hedw.
[4] *Sphagnum palustre* L.