

Classification and Successional Changes of Mixed-Oak Forests at the Mohn Mill Area, Pennsylvania

WARREN G. ABRAHAMSON^{1*} and ADAM C. GOHN²

¹Department of Biology and

²Program in Environmental Studies, Bucknell University,
Lewisburg, Pennsylvania 17837

ABSTRACT

A vegetation study was conducted within central Pennsylvania's Ridge and Valley Province at the Mohn Mill natural area, an area that harbors the federally endangered northeastern bulrush, *Scirpus ancistrochaetus*. A non-metric multidimensional scaling ordination identified two gradients of species replacement distinguished by differences in forest canopy species and groundcover. Basal-diameter histograms for red maple (*Acer rubrum*), eastern hemlock (*Tsuga canadensis*), and witch hazel (*Hamamelis virginiana*) showed distributions indicative of populations recruiting new individuals, whereas basal-diameter distributions for white oak (*Quercus alba*), chestnut oak (*Q. montana*), and red/black oak (*Q. rubra/Q. velutina*) indicate declining populations with limited recruitment. Consequently, as current populations of overstory oaks age and ultimately die, they will be replaced by red maple and eastern hemlock. This transition has major implications for herbaceous plants, including the persistence of the northeastern bulrush, given that ground-level light levels will decrease due to the denser canopies of red maple and eastern hemlock recruits.

INTRODUCTION

A growing body of literature indicates that many mixed-oak forest communities of eastern North America are currently undergoing dramatic compositional shifts (see Abrams 1992 for a review). The main beneficiaries of oak succession have been shade-tolerant species, particularly maples (*Acer*) (Abrams 1998). This oak-to-maple transition has been widely reported throughout the East, including the New England (Lorimer 1984), Mid-Atlantic (Russell 1980), Piedmont (Christensen 1977, McDonald et al. 2002), Appalachian (Abrams et al. 1995, Tift and Fajvan 1999), and Great Lakes regions (Host et al. 1987, Nowacki et al. 1990).

In the Ridge and Valley Province of central Pennsylvania, understories of oak-dominated forests frequently are composed primarily of red maple (*Acer rubrum* L.), striped maple (*A. pensylvanicum* L.), and black birch (*Betula lenta* L.) on xeric ridges and red maple and black cherry (*Prunus serotina* Ehrh.) in mesic valleys (Nowacki and Abrams 1992). Prior to European settlement, these forests consisted of oaks, chestnut [*Castanea dentata* (Marsh) Borkh.], hickories (*Carya*), and pines (*Pinus*), and were apparently maintained by recurrent surface burning (Abrams and Ruffner 1995, Abrams et al. 1995). During the exploitation era of European settlement (1780–1900), Ridge and Valley forests experienced frequent disturbance due to logging (especially charcoal production for iron furnaces) and associated fires (Abrams and Nowacki 1992). Chestnut blight (*Endothia parasitica*) swept through this region in the early 1900s (Illick 1921) eliminating chestnut and allowing red and chestnut oak (*Q. rubra* L. and *Q. montana* Willd., respectively) to expand (Hepting 1971, Russell 1987, Abrams and Ruffner 1995). Fire-suppression efforts soon followed (1920s and onward), largely eliminating fire from these pyrogenic forests (Abrams and Nowacki 1992, Abrams et al. 1995). Under the

* email address: abrahmsn@bucknell.edu

current disturbance regime, harvest removal of large, overstory oaks releases shade-tolerant trees in the understory, which accelerates the succession from oak to maple (Abrams and Nowacki 1992, Ruffner and Arabas 2000). The outcome of this disturbance history was an initial increase of fire-adapted oaks followed by the current replacement of oak by fire-sensitive yet shade-tolerant hardwoods, especially red maple (Nowacki and Abrams 1992). Formerly restricted primarily to poorly drained sites, red maple now occurs abundantly in early and late successional settings under a wide variety of edaphic conditions (Abrams 1998).

At the present, oak regeneration in eastern North America is inhibited not only by fire suppression (e.g., Kruger and Reich 1997, Dey and Guyette 2000) but also by over foraging by white-tailed deer (*Odocoileus virginianus*) over the past 80 years (Rooney 1995) and by periodic outbreaks of the introduced gypsy moth (*Lymantria dispar*) (Stalter and Serrao 1983, Abrams 1998). White-tailed deer feed on oak foliage and acorns, and some authors have suggested that deer avoid browsing red and striped maples (Kittredge and Ashton 1995, Crete et al. 2001). Likewise, gypsy moths preferentially feed on oak foliage compared to foliage of red or striped maples (Lechowicz and Jobin 1983, Mauffette et al. 1983). As a result of these combined impacts, oaks are virtually absent from the sapling layer of mixed-oak forests even though oaks dominate forest canopies.

We investigated the possibility of an oak-to-maple compositional shift within the Mohn Mill area of central Pennsylvania's Ridge and Valley Province out of a concern for an endangered herbaceous plant's persistence. The Mohn Mill site is a state-proposed wild plant sanctuary primarily because of the presence of the federally endangered northeastern bulrush (*Scirpus ancistrochaetus* Schuyler). Northeastern bulrush inhabits small vernal ponds that occur within the forest matrix. Lentz and Dunson's (1999) study of central Pennsylvania vernal ponds containing northeastern bulrush reported a mean surface-water area of only 437 m² and a 60% mean canopy coverage. Consequently, the surrounding forest composition and its correlated light attributes are likely important for northeastern bulrush persistence because of its impact on light reaching the pond's surface. Only about 60 populations of this sedge are known to exist across its range from West Virginia to Massachusetts with the majority of known sites located in central Pennsylvania (United States Fish and Wildlife Service 1991, 1993; Lentz 1998). Although the northeastern bulrush occurs in partially shaded ponds, this species performs best when light is less limiting (Lentz 1998, 1999; Lentz and Cipollini 1998, Lentz and Dunson 1999). Shifts from forest overstories dominated by open, generally single-canopied oaks to denser, multi-layered canopies of shade-tolerant species such as red maple would reduce light availability reaching the forest floor and vernal ponds, possibly negatively affecting northeastern bulrush.

As a proposed wild plant sanctuary, the Mohn Mill site is currently protected from logging (A. Griffith, Pennsylvania Department of Conservation and Natural Resources [DCNR], pers. comm.). The site was logged approximately 90 years ago (Kline 1970) and has recently experienced periodic outbreaks of gypsy moths (W. Diggins, Sand Run Lodge, pers. comm.) and considerable browsing by white-tailed deer. The successional trends found elsewhere within the Ridge and Valley Province (e.g., Abrams and Nowacki 1992, Nowacki and Abrams 1992, 1997) coupled with our observations at Mohn Mill led us to hypothesize that the site is experiencing oak replacement by more shade-tolerant maples and, in more mesic areas, eastern hemlock.

Our successional study compared canopy and understory woody species compositions as well as the size-class distributions of woody species within the non-wetland portions of the Mohn Mill site. Our goal was to investigate the possibility of an oak-to-maple compositional shift within the Mohn Mill area. To do so, we analyzed the existing successional patterns and evaluated edaphic (topography and soils) or biotic (e.g., canopy cover) factors that correlated with successional changes.

STUDY SITE AND METHODS

Study Site

The 154-ha Mohn Mill area (41°4'N, 77°8'W) is located on the border of the Bald Eagle and Tiadaghton State Forests as it straddles the boundary of Union and Lycoming Counties at their

intersection with Clinton County. The site experiences a temperate climate with warm, humid summers and moderately cold, humid winters. The region's highest average monthly temperature is in July (23°C) and the lowest is in January (-3°C). Mean annual precipitation for the region is 103 cm and is evenly distributed throughout the year (30-year means, NOAA data for nearby Williamsport, Pennsylvania).

Elevations in the Mohn Mill area range from approximately 420 to 570 m above mean sea level. Topography grades from flat bottomlands through gentle toeslopes to steep side slopes. The sandstone-derived soils are Ultisols (Typic Hapludults, Aeric Fragiaquults, and Aquic Fragiuults) and Inceptisols (Typic Dystrochrepts) having sandy loam to loam textures (Eckenrode 1985, Kohler 1986). The Typic Hapludults are in the Ungers and Clymer series, which are very stony loams of moderate permeability. These stony loams cover the majority of oak-dominated uplands within the site. Aeric Fragiaquults and Aquic Fragiuults comprise streamsides and bottomlands supporting eastern hemlock, and are represented by very stony loams of the Buchanan, Cookport, and Alvira series. These loams have slow permeability because of fragipan (a hard, compact layer that restricts water and root penetration). Typic Dystrochrepts, limited within the site to steep slopes, are extremely stony, sandy loams with rapid permeability of the Dekalb series. Taken together, these soils provide moderate to high site productivity.

The study site has experienced many natural disturbances during recent decades including canopy-damaging winds, ice storms, and wet snow events (authors' pers. obs.). In addition, chestnut blight occurred in the region during the 1910s, eliminating chestnut from forest canopies in this portion of Pennsylvania (see Illick 1921). Gypsy moth outbreaks occurred within the study site from 1979 to 1982 and again during of 1996 (W. Diggins, Sand Run Lodge, pers. comm.). The site was logged over 90 years ago between 1904 and 1912 (Kline 1970) during the period identified as the "clear-cut or hemlock-chemical wood" era (Abrams and Ruffner 1995). There is no evidence of fires in at least 50 years within the area (A. Griffith, DCNR, pers. comm.; authors' pers. obs.).

Sampling

Individual stems of woody plants were recorded systematically throughout the Mohn Mill site from 169 circular plots. Plots, 10 m in diameter, were located every 50 m along 15 transects oriented north to south and spaced 100 m apart. Transects and plot locations were located by pacing with the aid of a topographic map, property boundaries, and a USGS elevation marker (at 487.1 m) present at the site.

Trees ≥ 3 m in height were counted within a 5 m radius of each plot center (plot area = 78.5 m²), while shrubs, specifically blueberries (*Vaccinium* spp.), black huckleberry (*Gaylussacia baccata* (Wang.) K. Koch), and mountain laurel (*Kalmia latifolia* L.), were counted within a 1.5 m radius of the plot's center (plot area = 7.1 m²). In all, 1.33 ha of the 154-ha area was sampled for trees ≥ 3 m in height and 0.12 ha for shrubs. Species identity and basal diameter of each stem were recorded within each plot. Data for red oak and black oak (*Q. velutina* Lam.) were combined, as these two species could not be consistently separated. Stem coring was not performed due to sampling limitations. Although there are limitations in using size distributions to infer past tree recruitment (Lorimer 1985), such data provide considerable insight into the successional states of species (Skowno et al. 1999, Zawadzka and Abrahamson 2003).

All non-vegetation measurements were taken at the center point of each plot. A Suunto® clinometer and a Silva® Type 15 Ranger compass were used to measure slope and aspect, respectively, at each plot. A Robert E. Lemmon spherical densiometer model C was used to estimate the canopy coverage of the overstory trees with one measurement taken in each of the four cardinal directions and averaged for each plot. Soil samples, taken with an auger to a depth of 30 cm, were analyzed by Pennsylvania State University's Agricultural Analytical Services Laboratory for the following characteristics: particle size and texture class, pH, buffer pH, total nitrogen, phosphorus (as P₂O₅), exchangeable cations (hydrogen, potassium, magnesium, calcium), cation exchange capacity (CEC), and percentage saturation of CEC for potassium,

magnesium, and calcium. All vegetation sampling and field measurements were completed between May 19 and July 26, 2002.

Data Analysis

Density (number of stems per ha), dominance (basal area per ha), and frequency (proportion of plots occupied) were calculated for each species (Brower et al. 1990). Relative values for each of these measures were averaged to calculate species importance percentages. Means and standard errors were determined for an array of biotic and abiotic factors and the normality of each was tested using the Kolmogorov-Smirnov statistic, with a Lilliefors significance correction. Variables that lacked normal distributions were transformed using root, arcsine, exponential, and logarithmic transformations in an attempt to generate normal distributions. Canopy coverage and clay content were normalized with \log_{10} -transformations whereas a third-root transformation normalized slope. Other variables could not be normalized. SPSS® Version 11 software was used for all statistical analyses (SPSS Inc., Chicago, Illinois).

Non-parametric multidimensional scaling (NMS) from PC-ORD version 4 was implemented on density data to ordinate the distributions of species and plots as well as to determine if any abiotic factors correlated with the ordination axes (McCune and Mefford 1999, McCune and Grace 2002). Such an ordination reduces data by extracting the strongest correlation structure from the many-dimensional relationship of species abundances across plots and then expresses this correlation structure on a small number of dimensions. Thus, the correlation structure is used to position species along axes based on similarities in occurrence across plots and to position plots by their similarities in species composition and abundance. Environmental and edaphic factors are subsequently correlated with the ordination axes to help interpret any gradients represented by the axes. Non-parametric multidimensional scaling reports species and environmental correlations with axes as both parametric r-values and non-parametric T (tau) values. The non-parametric T values were used for environmental and edaphic variables that were not normalized through transformation.

RESULTS

Species and Size Distributions

Overall, 17 canopy and sub-canopy tree species were sampled, with species ranked in decreasing importance from red maple, white oak, chestnut oak, witch hazel (*Hamamelis virginiana* L.), red/black oak, and eastern hemlock [*Tsuga canadensis* (L.) Carr] (Table 1). All other species together accounted for <10% of relative importance.

The basal-diameter histograms for red maple, white oak, chestnut oak and eastern hemlock showed differing recruitment patterns over time (Figure 1). Those for red maple, eastern hemlock, and witch hazel (histogram not shown because it is similar to those of red maple and eastern hemlock) showed stable size-class distributions in which each species was successfully replacing itself. However, the distributions for white oak, chestnut oak, and red/black oak (histogram not shown because it was similar to the preceding) suggest a pulse of recruitment, likely associated with past disturbance, with little to no recruitment thereafter. Oak saplings and small trees were particularly sparse.

Vegetative Patterns

Non-parametric multidimensional scaling analysis confirmed that each species had a distinct distribution based on their unique positions along the two ordination axes. Axis 1 accounted for 35% of the variation, and axis 2 explained 48% in the original matrix of species and plots. Altogether, the NMS ordination model explained 83% of the variation.

Axis 1 reflected a shrub gradient from mountain laurel (Figure 2, left) to blueberry and huckleberry (right). Axis 2 was correlated with a groundcover gradient from abundant (bottom) to sparse (top). Abundant groundcover was affiliated with blueberry, huckleberry, and mountain laurel occurrence whereas plots with little-to-no groundcover occurred beneath eastern hemlock or striped maple. Blueberry/huckleberry correlated positively with axis 1 and

Table 1. Means and standard errors of density, dominance, frequency, and relative density, dominance, frequency, and relative importance for all sampled tree species (>3 m height) within the Mohn Mill area

Species	Density (stems/ha)	Dominance (m/ha)	Frequency (% of plots)	Relative Density (%)	Relative Dominance (%)	Relative Frequency (%)	Relative Importance (%)
Red maple	403.8 ± 22.7	53.5 ± 3.0	91.7 ± 2.1	45.9 ± 2.1	39.0 ± 2.1	36.9 ± 1.6	40.6 ± 1.8
White oak	74.5 ± 8.5	23.6 ± 2.8	39.6 ± 3.8	10.4 ± 1.3	17.2 ± 2.0	14.1 ± 1.5	13.9 ± 1.5
Chestnut oak	82.9 ± 11.3	27.0 ± 3.6	31.4 ± 3.6	9.9 ± 1.4	16.6 ± 2.1	11.5 ± 1.5	12.6 ± 1.6
Witch hazel	142.4 ± 20.4	5.4 ± 0.7	38.5 ± 3.8	13.2 ± 1.6	4.4 ± 0.7	12.5 ± 1.3	10.0 ± 1.1
Red/black oaks	46.7 ± 6.6	19.2 ± 2.8	27.2 ± 3.4	5.1 ± 0.8	9.9 ± 1.4	8.6 ± 1.1	7.9 ± 1.1
Eastern hemlock	46.7 ± 12.5	9.8 ± 2.8	12.4 ± 2.5	5.2 ± 1.3	4.7 ± 1.2	4.4 ± 1.0	4.8 ± 1.1
Black tupelo	35.4 ± 8.9	5.0 ± 1.3	12.4 ± 2.5	3.6 ± 0.9	3.2 ± 0.8	3.8 ± 0.8	3.5 ± 0.8
White pine	12.8 ± 3.8	2.3 ± 0.7	7.1 ± 2.0	1.7 ± 0.5	1.4 ± 0.5	2.2 ± 0.6	1.8 ± 0.5
Downy juneberry	9.8 ± 3.0	1.0 ± 0.3	7.1 ± 2.0	1.1 ± 0.4	0.9 ± 0.4	1.7 ± 0.5	1.2 ± 0.4
Striped maple	13.6 ± 6.1	1.4 ± 0.7	3.0 ± 1.3	1.4 ± 0.7	0.9 ± 0.5	1.0 ± 0.4	1.1 ± 0.5
Hawthorn	4.5 ± 2.1	0.2 ± 0.1	3.0 ± 1.3	0.8 ± 0.4	0.2 ± 0.1	1.1 ± 0.5	0.7 ± 0.3
Black cherry	1.5 ± 1.1	0.4 ± 0.3	1.2 ± 0.8	0.2 ± 0.2	0.5 ± 0.4	0.4 ± 0.3	0.4 ± 0.3
Sweet birch	1.5 ± 1.1	0.3 ± 0.2	1.2 ± 0.8	0.4 ± 0.3	0.4 ± 0.3	0.4 ± 0.3	0.4 ± 0.3
American basswood	1.5 ± 1.1	0.3 ± 0.2	1.2 ± 0.8	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.2 ± 0.1
Yellow birch	0.8 ± 0.8	0.3 ± 0.3	0.6 ± 0.6	0.1 ± 0.1	0.3 ± 0.2	0.2 ± 0.2	0.2 ± 0.2
White ash	0.8 ± 0.8	0.1 ± 0.1	0.6 ± 0.6	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
Unknown	1.5 ± 1.5	0.2 ± 0.2	0.6 ± 0.6	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
TOTAL	880.7	150.0	278.8	100.0	100.0	100.0	100.0

negatively with axis 2 ($T = 0.534$ and -0.643 , respectively), whereas mountain laurel correlated negatively with both axis 1 and axis 2 ($T = -0.342$ and -0.459 , respectively). Both eastern hemlock and striped maple correlated positively with axis 2 ($T = 0.248$ and 0.230 , respectively).

These correlative patterns coupled with qualitative assessments of species occurrences across plots suggest that vegetation can be grouped into three associations with white oak, eastern hemlock, and striped maple serving as “indicators” for each association (Figure 2). The most common association representing the greatest number of plots has relatively high white-oak density. White, chestnut, red, and black oaks dominate the overstory, whereas the subcanopy is dominated by red maple, witch hazel, black tupelo (*Nyssa sylvatica* Marsh.), and downy serviceberry [*Amelanchier arborea* (Michx.f.) Fern.]. The subcanopy also contains a scattering of hawthorn (*Crataegus*), black cherry, white pine, and eastern hemlock. Groundcover was comprised of dense blueberry and huckleberry or mountain laurel. This association is typically found in areas with gentle slopes or flat terrain.

The second association is characterized by strong presence of eastern hemlock in the canopy and subcanopy, with scattered red and black oaks in the canopy. This association has little groundcover (probably due to intense shading by eastern hemlock) and occurs in more mesic sites, particularly along streams. The third association, with little groundcover, occurs on a relatively steep north-facing slope that is distinguished by canopy chestnut oak and subcanopy striped maple.

Variation in Edaphic and Environmental Measures

Particle-size analyses showed substantial variation in soil texture (Table 2). Soils were classified as loams, sandy loams, sandy clay loams, clay loams, and occasionally clay. All samples were strongly acidic with variable but relatively low levels of N, P, K, Mg, and Ca compared to the agricultural-quality soils found within the region. Slopes averaged 12%, varying from flat bottomlands to gently rolling areas to steep inclines reaching 67% slope (Table 2). The forest canopy also varied considerably from plot to plot. Although overstory canopy

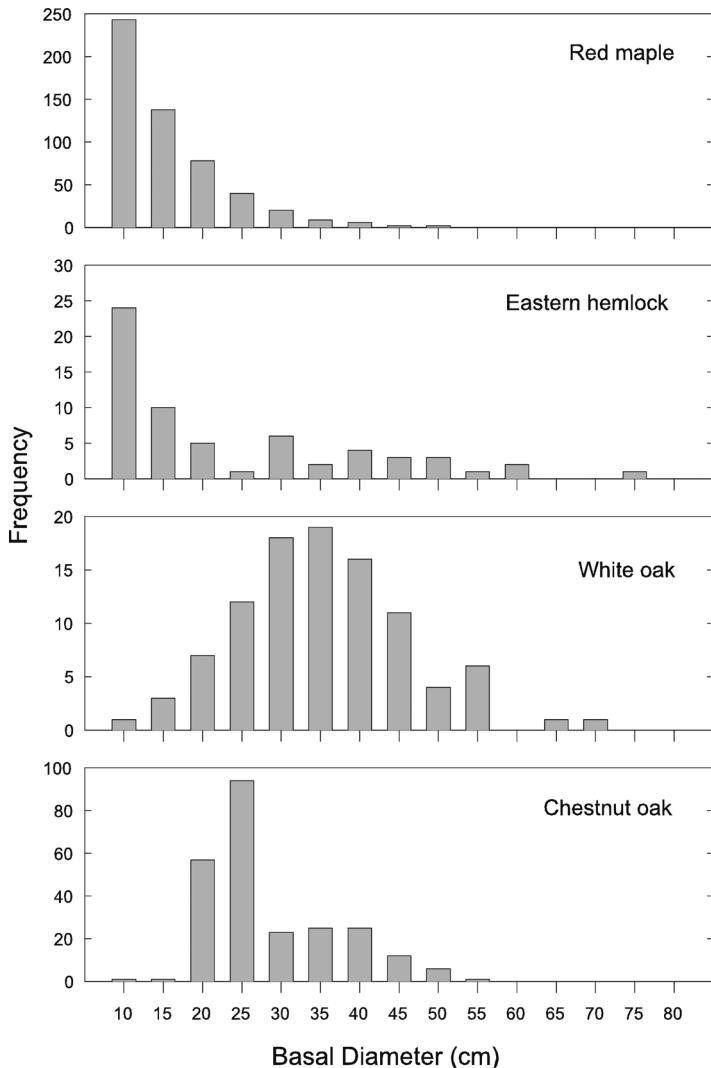


Figure 1. Basal diameter size-class distributions for red maple, eastern hemlock, white oak, and chestnut oak (>3 m in height) sampled at Mohn Mill. Diameters are shown in 5-cm increments except for the first increment, which includes stems ≤ 10 cm. Different scales are used for the vertical axes to adjust for the numbers of stems encountered for each species.

averaged 90% cover (10% open), it varied from 97% cover (only 3% open) in some plots to 72% cover (28% open) in other plots.

In spite of the variation present for abiotic parameters, few correlations were found with the vegetative patterns expressed by the NMS axes. The only strong correlation was between the \log_{10} -transformed canopy cover and NMS axis 2 ($r = 0.445$, Figure 3). This correlation indicates a gradient of increasing canopy cover and decreasing ground level light availability from plots dominated by mixed oaks (bottom) to plots dominated by eastern hemlock or by striped maple (top). Plots with a mixed-oak overstory had multi-layered canopies with sub-canopies of red maple, black tupelo, downy serviceberry, witch hazel, and hawthorn. These plots frequently had dense groundcover of blueberry and huckleberry or of mountain laurel. In contrast, plots dominated by eastern hemlock or by striped maple had little-to-no groundcover.

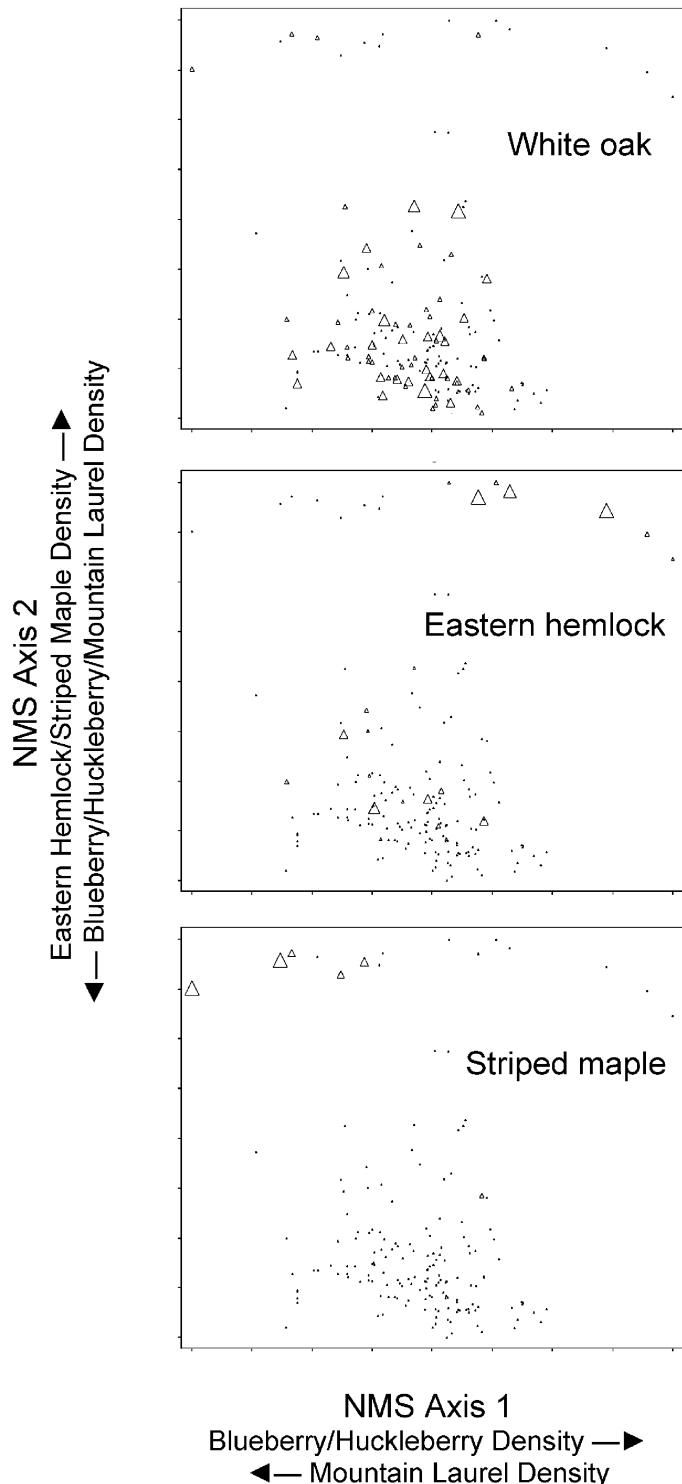


Figure 2. Non-metric multidimensional scaling ordination of plots based on the densities of woody stems >3 m in height sampled at Mohn Mill. Each triangle illustrates the distribution of one of the 169 plots. Larger triangles indicate plots with greater densities of the species indicated.

Table 2. Minimum, maximum, and mean (\pm standard error) for edaphic and environmental factors based on soil samples taken to a depth of 30 cm from the center of each of the 169 plots

Variable	Minimum	Maximum	Mean \pm Standard Error
Sand (%)	15.3	68.1	46.4 \pm 0.6
Silt (%)	14.8	46.0	30.4 \pm 0.4
Clay (%)	13.1	52.4	23.1 \pm 0.4
Organic matter depth (cm)	0.5	5.0	2.4 \pm 0.08
pH	3.7	5.1	4.3 \pm 0.02
Acidity (exchangeable H+) (meq/100 g)	3.9	26.0	12.3 \pm 0.3
Total N (%)	0.04	0.28	0.1 \pm 0.003
P (kg/ha as P ₂ O ₅)	4	1074	75 \pm 8.1
Exchangeable K (meq/100 g)	0.1	1.3	0.1 \pm 0.002
K (% saturation of the CEC)	0.5	2.4	0.9 \pm 0.03
Exchangeable Mg (meq/100 g)	0.1	6.0	0.3 \pm 0.04
Mg (% saturation of the CEC)	1.1	15.0	1.9 \pm 0.1
Exchangeable Ca (meq/100 g)	0.3	4.2	0.6 \pm 0.02
Ca (% saturation of the CEC)	2.2	37.0	4.7 \pm 0.2
Cation Exchange Capacity (CEC, sum of cations) (meq/100 g)	4.7	17.5	12.5 \pm 0.2
Canopy coverage (%)	72.4	96.9	89.8 \pm 0.3
Slope (%)	1	67	12 \pm 0.8

Soil P levels correlated weakly with NMS axis 1 ($T = 0.19$), suggesting that areas of abundant mountain laurel groundcover as well as areas with dense striped maple had lower soil P levels while areas with abundant blueberry and huckleberry cover and areas with eastern hemlock canopies had higher soil P levels.

DISCUSSION

Forest Composition and Succession

Our analyses showed that the woody species at Mohn Mill have distinctive distribution patterns that sorted along two gradients of species replacement. One gradient (Axis 1) reflected a groundcover compositional change from mountain laurel to blueberries and huckleberries. A second gradient (Axis 2) involved the groundcover density change from plots with sparse groundcover (occurring beneath dense canopies of either eastern hemlock or striped maple) to plots with dense groundcover of blueberry and huckleberry or mountain laurel (occurring under a mixed-oak overstory). Canopy cover, a strong correlate of the amount of groundcover-present axis, increased as the overstory changed from mixed oak to eastern hemlock or striped maple. There is likely a feedback loop between canopy cover and groundcover. While canopy cover has obvious impacts on groundcover success, groundcover can also have striking influences on tree regeneration and recruitment (Smith and Vankat 1991, Rooney 1995, George and Bazzaz 1999a, 1999b). It is also possible that some unmeasured variable (e.g., disturbance history, soil moisture) influenced the vegetation patterns observed and would correlate with one or both gradients if such data were available.

Our most fundamental finding was that the woody plants composing the Mohn Mill forest overstory and understory differ markedly, which indicates that the overstory composition is in the process of successional change. Even though oaks dominated the overstory of the Mohn Mill forest, red maple was the predominant tree of the subcanopy and understory strata. The basal-diameter histograms of Mohn Mill trees offer evidence of an ongoing shift from mixed oak to red maple dominance. White oak, chestnut oak, and red/black oak had a scarcity of small-sized individuals, indicating an aging population lacking recruitment. In contrast, red maple and eastern hemlock had many smaller individuals compared to larger ones suggesting expanding populations. These results indicate that as the current populations of oaks age and ultimately

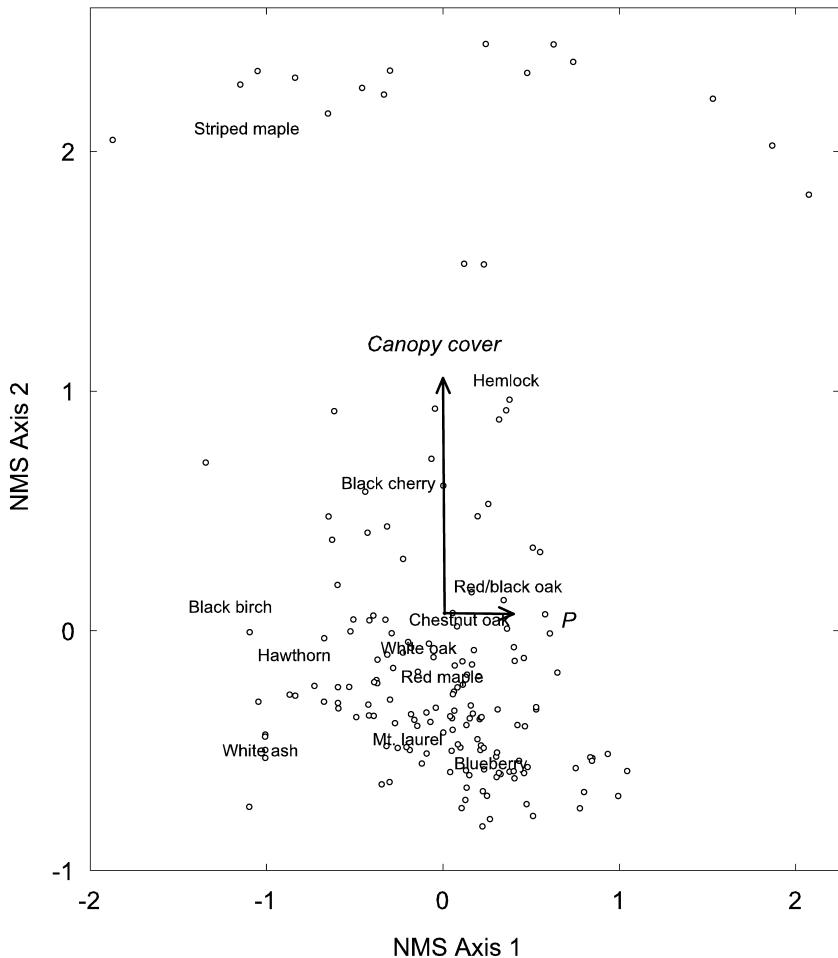


Figure 3. Non-metric multidimensional scaling ordination of species based on the densities of woody stems >3 m in height sampled at Mohn Mill. Circles illustrate the distributions of the 169 plots, text shows the ordination positions of selected woody species, and vectors indicate the direction and strength (scaled at 200%) of the canopy cover and soil phosphorus gradients.

die, they will be replaced by red maple, eastern hemlock, or striped maple based on site conditions. Thus, our expectation that the Mohn Mill forest is undergoing a shift from mixed oak to red maple domination was confirmed, at least on most sites.

There are likely several ancillary factors related to this ongoing succession. It is likely that white-tailed deer are affecting oak regeneration by their consumption of acorns and browsing of seedlings and saplings. Preferential feeding on oaks compared to maples and other shade-tolerant hardwoods can shift the balance of canopy species through differential recruitment (Strole and Anderson 1992, Rooney 1995, Rooney and Dress 1997, Orwig and Abrams 1999). In addition, differential herbivory on oaks by gypsy moth larvae will encourage shade-tolerant species such as red maple that are avoided by these herbivores (Abrams 1998). Episodes of gypsy moth defoliation suppress oak regeneration by encouraging taller or denser groundcover, which in turn enhances the shading of oak seedlings. The recorded gypsy moth outbreaks at Mohn Mill, from 1979 to 1982 and during 1996, caused substantial opening of the mixed-oak canopy. The enhanced light availability at ground level appears to have stimulated increases in blueberry, huckleberries, and mountain laurel (W. Diggins, Sand Run Lodge, pers. comm.), the

shade of which may reduce the regeneration of shade-intolerant species (George and Bazzaz 1999a, 1999b) such as oak (Lorimer et al. 1994).

Mohn Mill's pattern of oak replacement by more shade-tolerant red maple parallels the successional trends found elsewhere within the Ridge and Valley Province (e.g., Abrams and Nowacki 1992, Nowacki and Abrams 1992, 1997) and throughout eastern North America (e.g., Christensen 1977; Lorimer 1984; Abrams 1992, 1998; Lorimer et al. 1994; Goebel and Hix 1996; Tift and Fajvan 1999). The primary factors promoting this replacement of oaks by red maple and other shade-tolerant species in eastern North America likely include the current conditions of minimal fire and logging disturbances (Abrams 1992, 1998; Nowacki and Abrams 1992). After oaks expanded markedly in eastern North America under the regime of increased disturbance (fire and logging) following European settlement (Abrams and Nowacki 1992) and ecological release associated with chestnut blight (Hepting 1971, Russell 1987, Abrams and Ruffner 1995), aggressive fire-suppression measures and changes in logging practices have altered conditions in favor of fire-sensitive, shade-tolerant species.

Successional Impacts on the Federally Endangered Northeastern Bulrush

Our finding an ongoing successional shift from a mixed-oak to red maple canopy at Mohn Mill is not remarkable when taken alone. However, this forest-matrix composition shift has major implications when its impacts on the federally endangered northeastern bulrush are considered. Populations of listed plants like the northeastern bulrush are prone to extirpation because of their occurrence in sensitive habitats. Changes to the forest matrix that surrounds the sensitive vernal-pond habitats of the northeastern bulrush will likely reduce the suitability of these sites for this sedge. Recent field and experimental findings from central Pennsylvania populations of northeastern bulrush, including those at Mohn Mill, indicate that light availability is critical to the plant's performance (Lentz 1998, Lentz and Cipollini 1998, Lentz and Dunson 1999). While northeastern bulrush occurs in ponds with up to 90% canopy cover, it typically grows in the better-lighted ponds with <60% cover. The ongoing shift from open-canopied oaks to the denser and more layered canopies with red maple will reduce the availability of light reaching vernal ponds and thus might threaten the long-term persistence of the shade-intolerant northeastern bulrush. This conclusion is supported by the observation that the vernal ponds at Mohn Mill that contain northeastern bulrush have mixed oak canopies containing many light gaps but this sedge does not occur under the denser canopies of red maple or eastern hemlock (authors' pers. obs.). Consequently, the current low rate of success of oaks in capturing gaps in the Mohn Mill canopy has serious implications for not only northeastern bulrush but also for understory species that require the light regime of a more open-canopied forest.

Management Considerations

Emulating natural disturbance regimes may be the appropriate management for natural area stewardship (Runkle 1991, Engstrom et al. 1999). But ultimately, the fundamental question of natural-area management involves determining what vegetation is desired. In the Ridge and Valley Province of eastern North America, for example, pre-European settlement forests differed markedly from the forests generated by the disturbance regimes during the "clear-cut or hemlock-chemical wood" era (Abrams and Ruffner 1995), which in turn diverged from the forests we see today. Determining which of these communities is most appropriate for Mohn Mill and sites like it or whether Mohn Mill should be managed to benefit northeastern bulrush is a critical question that must be answered before any management plan can be developed. Our findings show that the current management of Mohn Mill is promoting a successional shift from mixed oak to red maple and hemlock, a succession that will threaten the persistence of northeastern bulrush.

If the goal were to maintain a viable northeastern bulrush population within Mohn Mill, then thinning maples to maintain desired light levels in the vicinity of ponds would be advantageous. However, if such management is directed at ponds where northeastern bulrush already occurs, this approach will do little to maintain conditions appropriate for colonization of new vernal ponds. Better tactics could introduce natural disturbances (e.g., prescribed fire) back

onto the site and/or restoration forestry practices (e.g., group selection) to counteract the maple succession and encourage oak regeneration.

While the absences of disturbances such as fire and logging have promoted red maple density and dominance at Mohn Mill, the re-introduction of logging would only accelerate the replacement of oaks by red maple rather than set back the oak-to-maple succession (Abrams and Nowacki 1992). The removal of large, canopy oaks would release red maple saplings and seedlings currently in the understory to grow into the canopy gaps created by oak removal. Red maple is well known for its ability to invade canopy gaps (Sipe and Bazzaz 1994, 1995; Maherli et al. 1997; DeLucia et al. 1998; Tift and Fajvan 1999), and dense maple understories represent a major obstacle to oak seedlings (Lorimer et al. 1994). Similarly, striped maple responds strongly to small canopy gaps (Hibbs and Fischer 1979; Sipe and Bazzaz 1994, 1995) and effectively shades out seedlings of competing species.

Our results suggest that the gap processes operating at Mohn Mill will not sustain an oak canopy since the canopy and sapling compositions differed markedly. If oaks are to continue in the Mohn Mill canopy, the site's gap processes will have to change. For example, larger canopy gaps, of the sizes that tend to result from fires, favor shade-intolerant species such as oaks, whereas the current disturbance regime at Mohn Mill generates small gaps via the periodic death of oaks in the canopy. These small gaps promote replacement of oak by shade-tolerant species such as red maple (Runkle 1982, 1991; Goebel and Hix 1996).

The introduction of fire to stands such as Mohn Mill may be the only practical way to encourage oak regeneration. Lorimer (1985) and others (e.g., Dey and Guyette 2000) have suggested that fire favors oaks over other hardwoods because the thick bark of oaks resists damage but if scarred by fire, oaks have considerable rot resistance. In addition, oaks typically sprout new ramets when top killed and their acorns germinate and survive well on fire-created seedbeds. On the other hand, most other eastern hardwoods are fire sensitive and red maple, in particular, has relatively poor survival relative to oaks following spring fire (Huddle and Pallardy 1999).

ACKNOWLEDGMENTS

We thank Gregory Nowacki, Michael Wise, Paul Schmalzer, Kendra Lentz Cipollini, Duane Griffin, Irene Kralick, and Peter Wilshusen for valuable comments or technical assistance as well as Warren Diggins for providing historical information about the Mohn Mill area. Permission to study the Mohn Mill site was granted by the Pennsylvania Department of Conservation and Natural Resources and we thank District Forester Amy Griffith who was instrumental in handling the permitting process. Bucknell University's Wayne and Margaret Manning Internship in the Botanical Sciences and the David Burpee Chair in Plant Genetics endowment provided financial support.

LITERATURE CITED

- ABRAMS, M.D. 1992. Fire and the development of oak forests. *BioScience* 42:346–353.
- ABRAMS, M.D. 1998. The red maple paradox. *BioScience* 48:355–364.
- ABRAMS, M.D. and C.M. RUFFNER. 1995. Physiographic analysis of witness-tree distribution (1765–1798) and present forest cover through north central Pennsylvania. *Can. J. For. Res.* 25:659–668.
- ABRAMS, M.D. and G.J. NOWACKI. 1992. Historical variation in fire, oak recruitment and post-logging accelerated succession in central Pennsylvania. *Bull. Torrey Bot. Club* 119:19–28.
- ABRAMS, M.D., D.A. ORWIG, and T.E. DEMEO. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine-mixed-oak forest in the southern Appalachians, USA. *J. Ecol.* 83:123–133.
- BROWER, J.E., J.H. ZAR, and C.N. von ENDE. 1990. *Field and laboratory methods for general ecology*, 3rd ed. Wm. C. Brown, Dubuque, Iowa.
- CHRISTENSEN, N.L. 1977. Changes in structure, pattern, and diversity associated with climax forest maturation in Piedmont, North Carolina. *Amer. Midl. Naturalist* 97:176–188.

- CRETE, M., J.P. OUELLET, and L. LESAGE. 2001. Comparative effects on plants of caribou/reindeer, moose and white-tailed deer herbivory. *Arctic* 54:407–508.
- DELUCIA, E.H., T.W. SIPE, J. HERRICK, and H. MAHERALI. 1998. Sapling biomass allocation and growth in the understory of a deciduous hardwood forest. *Amer. J. Bot.* 85:955–963.
- DEY, D.C. and R.P. GUYETTE. 2000. Anthropogenic fire history and red oak forests in south-central Ontario. *For. Chron.* 76:339–347.
- ECKENRODE, J.J. 1985. Soil survey of Union County, Pennsylvania. U.S. Department of Agriculture, Soil Conservation Service, Washington, District of Columbia.
- ENGSTROM, R.T., S. GILBERT, M.L. HUNTER, JR., D. MERRIWETHER, G.J. NOWACKI, and P. SPENCER. 1999. Practical applications of disturbance ecology to natural resource management. p. 313–330. In: Szaro, R.C., N.C. Johnson, W.T. Sexton, and A.J. Malk (eds.). *Ecological stewardship: a common reference for ecosystem management*. volume II. Elsevier Science Ltd., Oxford, United Kingdom.
- GEORGE, L.O. and F.A. BAZZAZ. 1999a. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* 80:833–845.
- GEORGE, L.O. and F.A. BAZZAZ. 1999b. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. *Ecology* 80:846–856.
- GOEBEL, P.C. and D.M. HIX. 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second-growth and old-growth forests. *For. Ecol. Manage.* 84:1–21.
- HEPTING, G.H. 1971. Diseases of forest and shade trees of the United States. USDA Forest Service, Agricultural Handbook No. 386. Washington, District of Columbia.
- HIBBS, D.E. and B.C. FISCHER. 1979. Sexual and vegetative reproduction of striped maple (*Acer pensylvanicum* L.). *Bull. Torrey Bot. Club* 106:222–227.
- HOST, G.E., K.S. PREGITZER, D.W. RAMM, J.B. HART, and D.T. CLELAND. 1987. Landform-mediated differences in successional pathways among upland forest ecosystems in northwestern Lower Michigan. *For. Sci.* 33:445–457.
- HUDDLE, J.A. and S.G. PALLARDY. 1999. Effect of fire on survival and growth of *Acer rubrum* and *Quercus* seedlings. *For. Ecol. Manage.* 118:49–56.
- ILLICK, J.S. 1921. Replacement of the chestnut. *J. For.* 19:105–114.
- KITTREDGE, D.B. and P.M.S. ASHTON. 1995. Impact of deer browsing on regeneration in mixed stands in southern New England. *North. J. Appl. For.* 12:115–120.
- KLINE, B.F.G. 1970. “Wild catting” on the mountain: the William Whitmer & Sons Company and the Whitmer-Steele Company operations in Cambria, Centre, Clearfield, and Union counties, Pennsylvania and Cornwall, Rockbridge county, Virginia. In the Series—Logging railroad era of lumbering in Pennsylvania. Book No. 2. Lycoming Printing Company, Inc. Williamsport, Pennsylvania.
- KOHLER, C.D. 1986. Soil survey of Lycoming County, Pennsylvania. U.S. Department of Agriculture, Soil Conservation Service, Washington, District of Columbia.
- KRUGER, E.L. and P.B. REICH. 1997. Responses of hardwood regeneration to fire in mesic forest openings. III. Whole-plant growth, biomass distribution, and nitrogen and carbohydrate relations. *Can. J. For. Res.* 27:1841–1850.
- LECHOWICZ, M.J. and L. JOBIN. 1983. Estimating the susceptibility of tree species to attack by the gypsy moth, *Lymantria dispar*. *Ecol. Entomol.* 8:171–183.
- LENTZ, K.A. 1998. Ecology of endangered northeastern bulrush, *Scirpus ancistrochaetus* Schuyler. Ph.D. dissertation, The Pennsylvania State University, University Park, Pennsylvania.
- LENTZ, K.A. 1999. Effect of intraspecific competition and nutrient supply on the endangered northeastern bulrush, *Scirpus ancistrochaetus* Schuyler (Cyperaceae). *Amer. Midl. Naturalist* 142:47–54.
- LENTZ, K.A. and D.F. CIPOLLINI. 1998. Effect of light and simulated herbivory on growth of endangered northeastern bulrush, *Scirpus ancistrochaetus* Schuyler. *Plant Ecol.* 139:125–131.
- LENTZ, K.A. and W.A. DUNSON. 1999. Distinguishing characteristics of temporary pond habitat of endangered northeastern bulrush, *Scirpus ancistrochaetus*. *Wetlands* 19:162–167.
- LORIMER, C.G. 1984. Development of the red maple *Acer rubrum* understory in northeastern USA oak forests. *For. Sci.* 30:3–22.
- LORIMER, C.G. 1985. Methodological considerations in the analysis of forest disturbance history. *Can. J. For. Res.* 15:200–213.
- LORIMER, C.G., J.W. CHAPMAN, and W.D. LAMBERT. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* 82:227–237.
- MAHERALI, H., E.H. DELUCIA, and T.W. SIPE. 1997. Hydraulic adjustment of maple seedlings to canopy gap formation. *Oecologia* 112:472–480.
- MAUFFETTE, N., J. LECHOWICZ, and L. JOBIN. 1983. Host preferences of the gypsy moth, *Lymantria Dispar* (L.) in southern Quebec. *Can. J. For. Res.* 13:53–60.

- MCCUNE, B. and J.B. GRACE. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.
- MCCUNE, B. and M.J. MEFFORD. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, Oregon.
- MCDONALD, R.I., R.K. PEET, and D.L. URBAN. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina Piedmont. *Castanea* 67:84–95.
- NOWACKI, G.J. and M.D. ABRAMS. 1992. Community, edaphic and historical analysis of mixed oak forests of the Ridge and Valley Province in central Pennsylvania. *Can. J. For. Res.* 22:790–800.
- NOWACKI, G.J. and M.D. ABRAMS. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol. Monogr.* 67:225–250.
- NOWACKI, G.J., M.D. ABRAMS, and C.G. LORIMER. 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in north-central Wisconsin. *For. Sci.* 36:276–292.
- ORWIG, D.A. and M.D. ABRAMS. 1999. Impacts of early selective logging on the dendroecology of an old-growth, bottomland hemlock-white pine-northern hardwood forest on the Allegheny Plateau. *J. Torrey Bot. Soc.* 126:234–244.
- ROONEY, T.P. 1995. Restoring landscape diversity and old growth to Pennsylvania's northern hardwood forests. *Nat. Areas J.* 15:274–278.
- ROONEY, T.P. and W.J. DRESS. 1997. Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania USA. *Nat. Areas J.* 17:297–305.
- RUFFNER, C.M. and K.B. ARABAS. 2000. Post European impacts on a central Pennsylvania woodlot. *Castanea* 65:9–20.
- RUNKLE, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63:1533–1546.
- RUNKLE, J.R. 1991. Gap dynamics of old-growth eastern forests: management implications. *Nat. Areas J.* 11:19–25.
- RUSSELL, E.W.B. 1980. Vegetational change in northern New Jersey from precolonization to the present: a palynological interpretation. *Bull. Torrey Bot. Club* 107:432–446.
- RUSSELL, E.W.B. 1987. Pre-blight distribution of *Castanea dentata* (Marsh.) Borkh. *Bull. Torrey Bot. Club* 114:183–190.
- SIPE, T.W. and F.A. BAZZAZ. 1994. Gap partitioning among maples (*Acer*) in central New England: shoot architecture and photosynthesis. *Ecology* 75:2318–2332.
- SIPE, T.W. and F.A. BAZZAZ. 1995. Gap partitioning among maples (*Acer*) in central New England: survival and growth. *Ecology* 76:1587–1602.
- SKOWNO, A.L., J.J. MIDGLEY, W.J. BOND, and D. BALFOUR. 1999. Secondary succession in *Acacia nilotica* (L.) savanna in the Hluhluwe Game Reserve, South Africa. *Plant Ecol.* 145:1–9.
- SMITH, L.L. and J.L. VANKAT. 1991. Communities and tree seedling distribution in *Quercus rubra*- and *Prunus serotina*-dominated forests in southwestern Pennsylvania. *Amer. Midl. Naturalist* 126:294–308.
- STALTER, R. and J. SERRAO. 1983. The impact of defoliation by gypsy moths on the oak forest at Greenbrook Sanctuary, New Jersey. *Bull. Torrey Bot. Club* 110:526–529.
- STROLE, T.A. and R.C. ANDERSON. 1992. White-tailed deer browsing species preferences and implications for central Illinois forests. *Nat. Areas J.* 12:139–144.
- TIFT, B.D. and M.A. FAJVAN. 1999. Red maple dynamics in Appalachian hardwood stands in West Virginia. *Can. J. For. Res.* 29:157–165.
- UNITED STATES FISH AND WILDLIFE SERVICE (USFWS). 1991. Endangered and threatened wildlife and plants; determination of endangered status for *Scirpus ancistrochaetus* (northeastern bulrush). *Fed. Regist.* 56:21091–21096.
- UNITED STATES FISH AND WILDLIFE SERVICE (USFWS). 1993. Northeastern bulrush (*Scirpus ancistrochaetus*) recovery plan. Hadley, Massachusetts.
- ZAWADZKAS, P.P. and W.G. ABRAHAMSON. 2003. Composition and tree-size distributions of the Snyder-Middlewarth old-growth forest, Snyder County, Pennsylvania. *Castanea* 68:31–42.

Received June 23, 2003; Accepted October 3, 2003.