CASTANEA 68(1): 31–42. MARCH 2003

Composition and Tree-Size Distributions of the Snyder-Middleswarth Old-Growth Forest, Snyder County, Pennsylvania

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ABSTRACT

We investigated the composition and spatial distribution of tree species and their environmental and edaphic correlates within the Snyder-Middleswarth Natural Area old-growth forest located in the narrow and steep ravine of Swift Run in central Pennsylvania. Eighty nested quadrats sampled along 5 topographic transects (16 quadrats each) encountered eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), black birch (*Betula lenta*), chestnut oak (*Quercus montana*), red maple (*Acer rubrum*), striped maple (*A. pensylvanicum*), and eastern white pine (*Pinus strobus*). The occurrences of these species differed by topography. Increasing soil phosphorus and potassium, and elevation correlated significantly with shift from hemlock and yellow birch-dominated bottomlands to ridge tops dominated by chestnut oak and red maple. Increasing soil acidity was significantly correlated with the shift from yellow birch-dominated quadrats to those primarily occupied by hemlock. Size distributions suggest that hemlock and yellow birch populations are stable, while those of black birch indicate episodic recruitment that may follow tree falls and other perturbations. Size distributions for chestnut oak imply impacts from white-tail deer browsing.

INTRODUCTION

Old-growth forests have become increasingly rare in North America since the time of European colonization and today represent a tiny fraction of the total forested area of the eastern United States (Nowacki and Abrams 1994, Rooney 1995, Orwig and Abrams 1999). Old-growth forest is particularly rare in central Pennsylvania because of intensive logging for timber and charcoal production during the past 150 years (Nowacki and Abrams 1992, Abrams and Orwig 1996). As a consequence, eastern old-growth forest, and Pennsylvania old-growth forest in particular, exist in small stands that are isolated from other old-growth forests by an intervening matrix of successional forests (Smith 1989, Farr and Tyndall 1992, Tyrrell and Crow 1994).

The Snyder-Middleswarth Natural Area within the Bald Eagle State Forest is one of the few stands of old-growth forest remaining in Pennsylvania and is among the largest such stands existing within Pennsylvania state forests [Pennsylvania Bureau of Forestry (no date)]. Although several other Pennsylvania old-growth forests have been examined (e.g., Whitney 1984, Rooney 1995, Rooney and Dress 1997, Orwig and Abrams 1999), we are unaware of any formal vegetation studies at the Snyder-Middleswarth Natural Area.

Five tree species dominate the Snyder-Middleswarth landscape including eastern hemlock [*Tsuga canadensis* (L.) Carriere], yellow birch (*Betula alleghaniensis* Britton), black birch (*Betula lenta* L.), red maple (*Acer rubrum* L.) and chestnut oak [*Quercus montana* Willd.—here we follow the recommendations of J. W. Hardin (1979) and use the name *Q. montana* because of the confusion surrounding the application of the name *Q. prinus* L.]. Two additional tree species, eastern white pine (*Pinus strobus* L.) and striped maple (*Acer pensylvanicum* L.),

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are present but are far less common. The dominant tree species are visibly segregated within this forest perhaps owing to the environmental and edaphic variation ranging from the Swift Run bottomlands to the slopes and ridge tops, the adaptations of species to subsets of environmental and edaphic conditions, differential exposure to wind and storm events, and the years of competitive interactions among species. The Snyder-Middleswarth Natural Area has been described as "...an exceptional block of completely uncut virgin forest occupying the steep valley of Swift Run. The bottoms and north [-facing] slope are hemlock-white pine, the south [-facing] slope is mixed oak..." (Erdman and Wiegman 1974). While this statement over-emphasizes the occurrence of white pine, it does convey the marked variation in forest-canopy dominance. The bottomlands are dominated by hemlock and yellow birch and with increases in elevation up each ridge from Swift Run, the composition and abundances change and black birch, red maple, and chestnut oak occur in great numbers.

With a limited number of old-growth forests available, learning about the composition and structure of landscapes such as the Snyder-Middleswarth Natural Area serves to increase our understanding of vegetation dynamics while providing valuable information about the specific traits of the site and species examined. The striking gradient of vegetation that occurs within the Snyder-Middleswarth old-growth forest provides an opportunity to study what edaphic and topographic gradients correlate with the distributions of species.

We examined the tree species composition and size distributions of the Snyder-Middleswarth old-growth forest and correlated the vegetation pattern with a number of environmental, edaphic, and topographic parameters. Our goals were (1) to describe the vegetative pattern, (2) to discover what environmental, edaphic, and topographic factors correlate with this vegetative pattern, and (3) to examine the size distributions of the predominant species.

METHODS

Study Site

Our study was conducted within the Snyder-Middleswarth Natural Area, part of the Bald Eagle State Forest, 8 km northwest of Troxelville, Pennsylvania (40°48′N, 77°17′W). The site has a temperate climate with warm, humid summers and only moderately cold, humid winters. The region's highest average monthly temperature of 23°C occurs in July and the lowest of −3°C occurs in January. Mean annual precipitation for the region is 103 cm and is evenly distributed throughout the year (30-yr means, NOAA data for Williamsport, Pennsylvania).

The old-growth forest is located in a narrow and steep ravine between two ridges that run east to west; Buck Mountain lies to the north and Thick Mountain to the south. The ravine, created by Swift Run, has well-developed north-facing and south-facing slopes as well as a bottomland. Elevations in the sampled area ranged from 451 m to 548 m, with slopes varying in steepness from 1–68%. The predominant soils are extremely stony and sandy well-drained loams that have weathered from sandstone and shale and have low to moderate available water capacity (Eckenrode 1985). The soils of the bottomland, slopes, and Buck Mountain ridge top are mapped as Hazelton (mesic Typic Dystrochrept) or Clymer (mesic Typic Hapuldult) soils while the Thick Mountain ridge top is covered by Ungers (mesic Typic Hapludult) soils.

Thanks originally to the inaccessibility of this ravine and in 1965 to its preservation as a National Natural Landmark, the approximately 135-ha portion of this forest included in our study has never been logged. The extent of direct human impact to the area is a footpath that runs along the northern bank of Swift Run and loops back along the north-facing slope. Hunting of deer and other game is allowed in the adjoining state forestlands.

There have been many natural disturbances within this old-growth forest during the past three decades (Abrahamson, pers. obs.). Windstorms, especially those associated with snow or ice events, have toppled a number of the larger hemlock and yellow birch throughout the stand. Furthermore, the crowns of slope and ridge top trees frequently show evidence of wind and/or ice damage. Gypsy moth outbreaks have occurred periodically within central Pennsylvania since the mid-1970s and likely have markedly impacted the oak canopies within the study area during one or two growing seasons.

Sampling

Five independent topographic transects of 16 nested quadrats each were used to sample within the old-growth forest. Each transect of quadrats ran parallel to Swift Run, in order to follow the elevation contour. One transect was located on the bottomland, one was located approximately halfway up each ridge, and one was located along the top of each ridge. Each nested 10 × 10 m quadrat was separated by 20 m from the adjacent quadrats within the same transect. A nested 5 × 5 m quadrat shared its northeast corner with that of the 10 × 10 m quadrat. There were 80 such nested quadrats sampled within the old-growth forest. All woody stems >6 cm diameter at breast height (dbh) were identified and measured in the 10 × 10 m quadrats; all woody stems <6 cm dbh were identified and counted in the 5 × 5 m quadrat. Sampling occurred between May and October 2000.

Tree ages were not determined as no coring was performed; coring studies were beyond the scope of this initial study of this old-growth forest. We recognize the limitations of using size distributions when inferring past disturbances (Lorimer 1985), however, we feel that in the absence of tree-age data, size-distribution data provide at least some insight into the successional status of species.

All non-vegetation measurements were taken from the northeast corner of each nested quadrat. Quadrat coordinates were recorded using a Magellan® GPS 4000 XL and quadrat elevation was determined from a digital topographic map (DeLorme 1999) by inserting the GPS coordinates for each quadrat. Forest overstory density (i.e., canopy cover) was quantified with a Robert E. Lemmon spherical densiometer model-C. We measured canopy cover in each of the four cardinal directions and averaged these values to produce a single canopy-cover measure for each quadrat. Aspect, which was determined by compass, and slope, which was measured with a Suunto® clinometer, were also recorded for each quadrat. A soil sample was taken with a soil auger at the northeast corner of each nested quadrat to a depth of 10 cm. Forty-three of the 80 nested quadrats were covered by rocky "talus" where only organic soil materials could be sampled. Consequently, we lack particle-size data for these nested quadrats.

The Pennsylvania State University Agricultural Analytical Services Laboratory analyzed the 80 soil samples for soil pH, acidity (meq/100 g), cation exchange capacity (meq/100 g), as well as concentrations of phosphorus (ppm), potassium (ppm), nitrogen (ppm), magnesium (ppm), and calcium (ppm). In addition, particle-size analyses were performed on the 37 mineral-soil samples. Using these data (i.e., sand, silt, and clay content), we estimated potential wilting point (cm^3 H_2O/cm^3 soil), field capacity (cm^3 H_2O/cm^3 soil), bulk density (g/cm^3), saturation (cm^3 H_2O/cm^3 soil), hydraulic conductivity (cm/hr), and available water (cm^3 H_2O/cm^3 soil) (Saxton et al. 1986).

Data Analysis

Density (number of individuals per ha), dominance (basal area per ha), and frequency (proportion of quadrats occupied), as well as the relative values for each of these measures, were calculated for each species. The relative importance of each species was calculated as the average of these relative values. Small stems (<6 cm dbh) were not included in these calculations because small stem data were simple counts. However, all stems regardless of size were included in size-class distributions.

The means and standard errors of each environmental and edaphic variable (e.g., canopy cover, slope, soil pH, nitrogen, % sand) were calculated by topographic transect to enable comparisons among transects. All variables were first tested for equality of variance with a Levene's test of equality of error variances. Of those variables that did not pass Levene's test, several could be transformed so that they did so. Phosphorus, potassium, and magnesium concentrations had normal variances after a square-root transformation while the percentage of clay, wilting point, and field capacity data were normalized with a $\log_{10}$ transformation. All variables were then tested for among transects differences using an analysis of variance (ANOVA). SPSS® Version 10 statistical software was used for all analyses (SPSS Inc., Chicago, Illinois).

Table 1. Density, frequency, dominance and relative density, frequency, dominance, and relative importance for woody stems (>6 cm dbh) based on all 5 transects sampled within the old-growth Snyder-Middleswarth Natural Area

Species	Density (stems/ha)	Frequency (% quads)	Dominance (m^2/ha)	Relative Density	Relative Frequency	Relative Dominance	Relative Importance
Eastern Hemlock	470.0	79	30.6	50.3	33.9	58.7	47.6
Black Birch	117.5	48	4.8	12.6	20.4	9.2	14.1
Yellow Birch	108.8	35	6.4	11.7	15.1	12.3	13.0
Chestnut Oak	87.5	29	6.4	9.4	12.4	12.3	11.3
Red Maple	118.8	35	2.8	12.7	15.1	5.4	11.1
Striped Maple	20.0	5	0.2	2.1	2.2	0.4	1.6
White Pine	11.3	3	0.9	1.2	1.1	1.7	1.3
Totals	933.8	233	52.1	100.0	100.0	100.0	100.0

In order to examine the distributions of quadrats and species as well as to assess any correlation of environmental and edaphic parameters with the vegetation ordination, we used Detrended Correspondence Analysis (DCA), from PC-ORD Version 4 (McCune and Mefford 1999). DCA allows the use of two matrices, a primary matrix that in our study contained the dominance values for each species within each quadrat, and a secondary matrix that contained the environmental and edaphic data for each quadrat. Prior to analysis, the primary matrix was "standardized by the norm" (Greig-Smith 1983) to improve normality. We used DCA rather than another multivariate approach such as canonical correspondence analysis because DCA's ordination is created solely from the vegetation data. Environmental and edaphic variables are secondarily related to the vegetation ordination. Thus, DCA does not presume that all critical environmental and edaphic variables related to the observed species distributions have been measured. DCA reports correlations as both parametric r-values and non-parametric tau values. The non-parametric tau values proved useful as the measurements for slope, elevation, calcium, nitrogen, acidity, CEC could not be normalized by transformation.

RESULTS

Species Distributions

Our sampling encountered only 7 tree species with eastern hemlock having the highest relative importance (47.6), followed by black birch (14.1), yellow birch (13.0), chestnut oak (11.3), and red maple (11.1). Striped maple (1.6) and eastern white pine (1.3) had much lower importance values and together had a relative importance of <3 (Table 1).

These overall values, however, do not adequately represent the variations in the distributions of species observed in the bottomland, on the slopes, or ridge tops. For example, the southern Thick Mountain ridge top was dominated by hemlock and black birch while the bottomland was composed of hemlock and yellow birch and the northern Buck Mountain ridge top was principally chestnut oak and red maple (Table 2). Hemlock dominated in all topographic transects except the northern ridge top where it was not sampled and black birch occurred everywhere except in the bottomland. Black birch had substantial abundance on the Thick Mountain ridge top and north-facing slope but was considerably less abundant on the Buck Mountain south-facing slope and ridge top. Yellow birch, like hemlock, occurred everywhere except the northern ridge top, however, their abundance patterns differed. Chestnut oak was limited to Buck Mountain, occurring on its south-facing slope and ridge top. Particularly striking was the uniqueness of the species compositions of the bottomland versus the northern ridge top. Hemlock and yellow birch almost equally dominated the bottomland to the exclusion of other tree species whereas on the northern ridge top, chestnut oak, red maple, and black birch dominate but neither hemlock nor yellow birch was sampled.

Table 2. Density, frequency, dominance and relative density, frequency, dominance and importance for woody stems (>6 cm dbh) from each of the 5 topographic transects sampled within the Snyder-Middleswarth Natural Area

Species	Density (stems/ha)	Frequency (% quads)	Dominance (m^2/ha)	Relative Density	Relative Frequency	Relative Dominance	Relative Importance
Southern Ridge Top (Transect 3)							
Eastern Hemlock	1,075.0	100	49.5	77.8	48.5	77.8	68.0
Black Birch	268.8	75	11.2	19.5	36.4	17.6	24.5
Red Maple	25.0	19	2.5	1.8	9.1	4.0	5.0
Yellow Birch	12.5	13	0.4	0.9	6.1	0.6	2.5
Totals	1,381.3	206	63.6	100.0	100.0	100.0	100.0
North-facing Slope (Transect 4)							
Eastern Hemlock	618.8	100	51.3	66.9	44.4	78.8	63.4
Black Birch	168.8	63	6.8	18.2	27.8	10.5	18.8
Yellow Birch	125.0	50	5.0	13.5	22.2	7.7	14.5
Red Maple	12.5	13	2.0	1.4	5.6	3.0	3.3
Totals	925.0	225	65.1	100.0	100.0	100.0	100.0
Bottomland (Transect 1)							
Eastern Hemlock	381.3	100	28.3	52.6	51.6	53.3	52.5
Yellow Birch	343.8	94	24.8	47.4	48.4	46.7	47.5
Totals	725.0	194	53.1	100.0	100.0	100.0	100.0
South-facing Slope (Transect 5)							
Eastern Hemlock	275.0	94	26.0	51.2	39.5	65.9	52.2
Chestnut Oak	87.5	44	4.2	16.3	18.4	10.6	15.1
Red Maple	62.5	44	3.5	11.6	18.4	8.9	13.0
Black Birch	50.0	38	3.5	9.3	15.8	8.8	11.3
Yellow Birch	62.5	19	2.3	11.6	7.9	5.9	8.4
Totals	537.5	238	39.5	100.0	100.0	100.0	100.0
Northern Ridge Top (Transect 2)							
Chestnut Oak	350.0	100	28.0	37.1	39.0	75.8	50.6
Red Maple	493.8	100	6.3	52.3	39.0	17.1	36.1
Black Birch	100.0	56	2.6	10.6	22.0	7.1	13.3
Totals	943.8	256	36.9	135.7	100.0	100.0	100.0

Size Distributions

A histogram of the diameters for all hemlocks sampled as well as histograms of hemlock sizes on each topographic transect suggest stable distributions and indicate that hemlock is replacing itself within the community (Figure 1). The size-class histogram for all sampled yellow birch illustrates the distributions that we observed at each transect where yellow birch occurred. This histogram implies that substantial losses are occurring from the smallest to the second smallest size class nevertheless the distribution was indicative of a population that is replacing itself. Similarly, the combined histogram for chestnut oak represented the histograms for individual topographic transect size-class distributions. These histograms suggest that either the establishment of chestnut oak or its recruitment to larger size classes has been hindered in recent decades. Although numerous individuals were sampled in the smallest size class, few individuals were sampled in the subsequent size class. The combined as well as the individual transect size-class histograms for black birch suggest episodic recruitment, implying that natural disturbance such as wind storms may affect its recruitment. No stems of black birch <6 cm dbh were sampled and only a limited number of small size-class stems were recorded. In addition, there were very few large individuals of black birch likely because of its short longevity compared to hemlock and yellow birch.

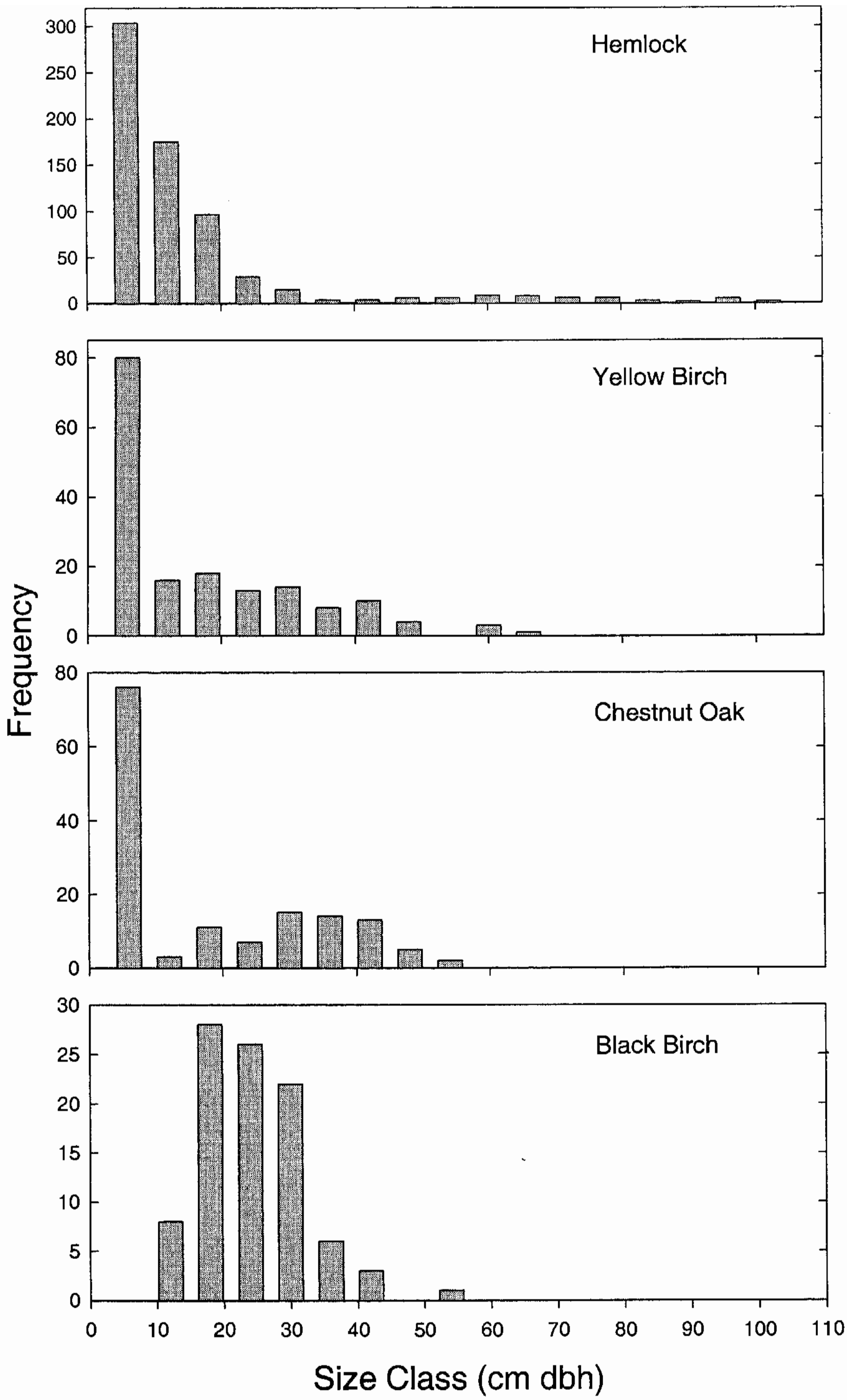

Figure 1. Size-class distribution for all eastern hemlock (top), yellow birch (second from top), chestnut oak (second from bottom), and black birch (bottom) stems sampled at the Snyder-Middleswarth Natural Area.

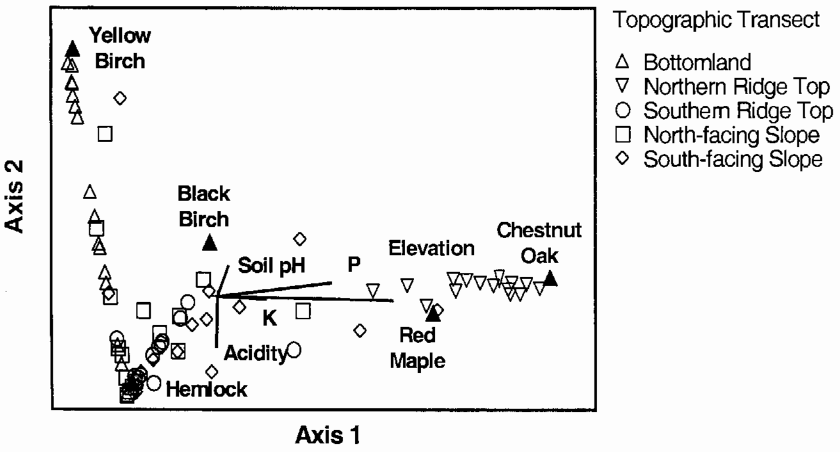

Figure 2. Detrended Correspondence Analysis plot based on woody stems >6 cm dbh sampled at the Snyder-Middleswarth Natural Area excluding eastern white pine and striped maple. The plot illustrates the distributions of the 80 quadrats and five tree species on axes 1 and 2 with an overlay of vectors for significant correlates with the first two axes. The vector direction indicates the path of the gradient.

Vegetative Patterns

Because of their minor combined relative importance (2.9), white pine and striped maple were excluded from the DCA ordination (Figure 2). DCA confirmed the expectation that each species occupied its own niche as indicated by their unique positions along the first three axes. The first axis accounted for 58% of the variation in the vegetation matrix, the second axis for 17%, and the third axis for 3%. Overall, the DCA ordination model explained 78% of the variation in the occurrences of species.

Axis 1 was correlated with the vegetation gradient from the chestnut oak and red maple transect on the northern ridge top to the hemlock/yellow birch bottomland transect. Chestnut oak and red maple correlated positively with axis 1 ($r = 0.91, 0.51$, respectively) while hemlock and yellow birch correlated negatively ($r = -0.66$ and -0.49, respectively). Axis 2 was correlated with the separation of the two birch species from hemlock. Yellow birch correlated positively ($r = 0.73$) while black birch had a weak, but still significant correlation ($r = 0.23$). Hemlock, on the other hand, correlated negatively ($r = -0.67$). Axis 3 was associated with the separation of chestnut oak and red maple as chestnut oak occurrence correlated negatively with axis 3 but red maple correlated positively ($r = -0.38$ and 0.82, respectively).

Variation in Environmental/Edaphic Measures

There was significant variation within the 29 environmental and edaphic measurements across transects with the exceptions of soil nitrogen concentration, clay content, estimated wilting point, and estimated hydraulic conductivity (Table 3). For example, the northern ridge-top soils were relatively high in phosphorus and potassium compared to the other sampled transects. Moreover, the slopes of both Thick and Buck Mountains had lower pH soils and higher potassium and magnesium concentrations than the bottomland soils. However, it is important to recognize that even these northern ridge-top soils are low in nutrients and are highly acidic compared to the agricultural-quality soils found in the nearby valleys. Consequently, any reference to high or low nutrient content is in terms relative to the conditions found within the sampled area.

Correlation of Vegetative and Environmental/Edaphic Measures

Several of the environmental and edaphic variables correlated with the axes of the DCA vegetation ordination (Figure 2). For example, the transformations of phosphorus and

Table 3. Means and standard errors for canopy cover, slope, elevation, soil-nutrient parameters, soil-particle size, and calculated values (based on particle-size proportions) for wilting point, field capacity, bulk density, saturation, hydraulic conductivity, and available water. Topographic transect means for a given variable followed by the same superscript are not statistically significant according to Student-Newman-Keuls post-hoc tests

	Bottomland	Northern Ridge Top	Southern Ridge Top	North-facing Slope	South-facing Slope	ANOVA
Total Canopy (%)	93 ± 4^{a}	92 ± 4^{a}	96 ± 1^{b}	$95 \pm 3^{a,b}$	92 ± 6^{a}	$F_{4,75} = 5.00, p = 0.001$
Greatest Slope (%)	2 ± 3^{b}	20 ± 4^{b}	21 ± 42^{b}	36 ± 33^{c}	52 ± 29^{a}	$F_{4,75} = 21.68, p < 0.001$
Elevation (m)	463 ± 7^{a}	544 ± 2^{d}	488 ± 13^{c}	478 ± 7^{b}	485 ± 11^{c}	$F_{4,75} = 194.46, p < 0.001$
Soil pH	3.8 ± 0.2^{b}	3.7 ± 0.3^{b}	3.4 ± 0.3^{a}	3.3 ± 0.1^{a}	3.3 ± 0.2^{a}	$F_{4,75} = 17.95, p < 0.001$
Acidity (meq/100g)	16.2 ± 6.8^{a}	22.7 ± 6.8^{b}	30.0 ± 4.2^{c}	28.9 ± 4.0^{c}	22.9 ± 8.4^{b}	$F_{4,75} = 12.69, p < 0.001$
CEC (meq/100g)	13.8 ± 3.6^{a}	18.2 ± 2.6^{b}	17.4 ± 0.8^{b}	17.3 ± 0.8^{b}	15.9 ± 3.6^{b}	$F_{4,75} = 7.30, p < 0.001$
P[1] (ppm)	8 ± 4^{a}	24 ± 10^{b}	8 ± 4^{a}	6 ± 2^{a}	8 ± 3^{a}	$F_{4,75} = 32.62, p < 0.001$
K[1] (ppm)	38 ± 14^{a}	116 ± 50^{c}	64 ± 24^{b}	66 ± 22^{b}	81 ± 28^{b}	$F_{4,75} = 15.91, p < 0.001$
Mg[1] (ppm)	34 ± 6^{a}	52 ± 50^{b}	45 ± 11^{b}	46 ± 11^{b}	43 ± 11^{b}	$F_{4,75} = 6.57, p < 0.001$
Ca (ppm)	140 ± 45^{a}	494 ± 494^{b}	$364 \pm 135^{a,b}$	$343 \pm 144^{a,b}$	$299 \pm 236^{a,b}$	$F_{4,75} = 3.82, p = 0.007$
N (ppm)	18.98 ± 19.70	11.09 ± 22.82	5.54 ± 1.54	16.44 ± 22.88	9.53 ± 6.96	NS
Sand (%)	$74.9 \pm 9.6^{b,c}$	$70.1 \pm 10.7^{a,b,c}$	$58.1 \pm 11.0^{a,b}$	54.6 ± 27.6^{b}	81.7 ± 10.7^{c}	$F_{4,32} = 4.82, p = 0.004$
Silt (%)	$16.9 \pm 6.5^{a,b}$	$21.4 \pm 8.0^{a,b}$	31.9 ± 10.6^{b}	28.1 ± 12.2^{b}	13.0 ± 11.3^{a}	$F_{4,32} = 4.70, p = 0.004$
Clay[1] (%)	8.2 ± 5.2	8.5 ± 3.6	10.7 ± 3.5	17.3 ± 15.6	5.3 ± 2.6	NS
Wilting Point[1,2] (cm^3 H_2O/cm^3 soil)	0.08 ± 0.02	0.08 ± 0.02	0.09 ± 0.01	0.12 ± 0.06	0.06 ± 0.02	NS
Field Capacity[1,2] (cm^3 H_2O/cm^3 soil)	$0.17 \pm 0.03^{a,b}$	$0.18 \pm 0.03^{a,b,c}$	$0.21 \pm 0.02^{b,c}$	0.23 ± 0.09^{c}	0.14 ± 0.04^{a}	$F_{4,32} = 4.33, p = 0.007$
Bulk Density[2] (gm/cm^3)	$1.62 \pm 0.08^{a,b}$	$1.60 \pm 0.08^{a,b}$	1.54 ± 0.05^{a}	1.49 ± 0.21^{a}	1.78 ± 0.22^{b}	$F_{4,32} = 4.12, p = 0.008$
Saturation[2] (cm^3 H_2O/cm^3 soil)	$0.39 \pm 0.03^{a,b}$	$0.40 \pm 0.03^{a,b}$	0.42 ± 0.02^{b}	0.43 ± 0.08^{b}	0.33 ± 0.08^{a}	$F_{4,32} = 4.12, p = 0.008$
Hydraulic Conductivity[2] (cm/hr)	4.66 ± 1.88	4.07 ± 1.93	2.65 ± 1.06	2.67 ± 3.17	8.41 ± 5.95	NS
Available H_2O^2 (cm^3 H_2O/cm^3 soil)	$0.09 \pm 0.01^{a,b}$	$0.10 \pm 0.01^{a,b}$	0.12 ± 0.02^{b}	0.12 ± 0.03^{b}	0.09 ± 0.02^{a}	$F_{4,32} = 4.67, p = 0.004$

[1] Variables that were transformed as described in the methods section prior to statistical or ordination analyses in order to meet normality assumptions.
[2] Calculated values based on particle-size analysis.

potassium concentrations correlated with axis 1 (r = 0.70 and 0.46, respectively), the axis related to the shift from quadrats dominated by hemlock and yellow birch to those that were predominantly chestnut oak and red maple. Elevation was another correlate of axis 1 (tau = 0.54). Thus, chestnut oak and red maple had greater dominance in quadrats located on soils with higher concentrations of phosphorous and potassium and at higher elevations than did hemlock or yellow birch.

Soil pH and acidity correlated (r = 0.34 and −0.44, respectively) with axis 2, the axis related to the separation hemlock from both birch species. Thus, yellow and black birch were more dominant within quadrats on soils with higher pH and hence, lower acidity than those where hemlock was predominant. None of the environmental or edaphic factors measured correlated with the third axis, which was related to the separation of chestnut oak and red maple. Regardless, the variation explained (3%) by axis 3 represents a minor fraction of the total variation explained by the ordination model. It is possible that some unmeasured variable, including disturbance history, may have influenced the vegetation patterns observed and would correlate with one or more of the three axes if historical data were available for these quadrats.

DISCUSSION

Species Distributions

Each of the five common tree species sampled in the Snyder-Middleswarth old-growth forest had distinct spatial patterns. For example, eastern hemlock and yellow birch completely dominated the Swift Run bottomland. However, hemlock was associated with more acidic soils as has been found elsewhere (Woods 2000b) and yellow birch was more common on less acidic soil (Erdmann 1990). In spite of its absence from the Buck Mountain ridge top, hemlock was the predominant species across the natural area. Its basal area constituted more than half of the basal area of all other species combined and its density was greater than that of all other species combined. Of the species sampled, hemlock is the most shade tolerant (Whitney 1990) and its dense canopy can have inhibitory effects on the regeneration of other species including yellow birch (Woods 2000b). Its ability to regenerate under low resource conditions (e.g., low light and low soil pH) sets up a positive feedback that can favor hemlock over other species (Catovsky and Bazzaz 2000). The current stem-size distributions suggest that hemlock will continue to dominate the Snyder-Middleswarth landscape into the foreseeable future. However, disturbances including catastrophic blow downs, fire, and herbivory by exotic pests such as the hemlock wooly adelgid, *Adelges tsugae* Annand, could reduce its future dominance enabling birch species, red maple, and even white pine to gain importance.

The ability of yellow birch to persist in hemlock-northern hardwood forests is dependent on episodic canopy disruption as yellow birch declines under a disturbance regime that creates only small gaps (Woods 2000a, b). Because of its relative shade intolerance, yellow birch has limited regeneration beneath dense hemlock canopies and hence, its regeneration occurs primarily in canopy gaps associated with nurse trees (Woods 1984, Runkle 1985, Catovsky and Bazzaz 2000). The persistence of yellow birch in the Snyder-Middleswarth forest may be due to the considerable canopy disturbance owing to frequent blow downs. Tip-up mounds and decaying down trees are common throughout the forest. Disturbance caused by high flows in Swift Run following large precipitation events may also contribute to the regeneration of yellow birch in the bottomland as large hemlock have occasionally been undercut by the erosive action of Swift Run.

Red maple and chestnut oak dominance increased with elevation on the south-facing slope and both species reached substantial density and dominance on the northern ridge top. Red maple exhibits characteristics of both early and late successional trees in that it can persist in late-successional forests but it can increase markedly following a wide range of disturbances (Lorimer et al. 1994, Abrams 1998, Orwig and Abrams 1999) including wind throws which are the primary source of canopy gaps in the Snyder-Middleswarth forest (Abrahamson, pers. obs.). Furthermore, the steepness (mean = 52%) of the south-facing slope and its southern exposure may generate sufficient disturbance (e.g., down-slope rock and/or soil movement, periodic xeric conditions limiting juvenile survival) to encourage opportunists like red maple and chestnut oak. Chestnut oak is typically associated with dry, well-drained, and often low-nutrient soils (Elias 1980, Greller 1988) and it responds favorably to disturbance (Nowacki and Abrams 1994). However, the stem-size distributions of chestnut oak suggest that it has not consistently recruited new individuals into its population. The shortage of smaller-sized individuals could be a consequence of episodic recruitment, periodic bouts of high mortality due to drought or other catastrophic events, or juvenile mortality due to deer browsing or insect herbivory including that of gypsy moths.

Black birch was the second most frequent species and it was particularly abundant on the north-facing slope and the southern ridge top and absent only in the bottomland. Perhaps because of this wide and abundant distribution, black birch occurrence had only a weak correlation with axis 2, the axis correlated with soil acidity. Alternatively, this general lack of correlation may be a consequence of black birch being dependent on episodic recruitment as an opportunistic invader of gaps. Within the Snyder-Middleswarth forest, relatively frequent blow downs cause marked local increases in light and possibly other resources. Black birch is strongly responsive to increased light whereas the dominant hemlock exhibits small changes in juvenile survival and growth under elevated light conditions (Catovsky and Bazzaz 2000).

The infrequent occurrence of white pine at the Snyder-Middleswarth Natural Area contradicts references to this forest as a hemlock-white pine forest [Erdman and Wiegman 1974, Pennsylvania Bureau of Forestry (no date)]. It is possible that white pine was once more abundant given that it is an early to mid-successional species that only recruits into old-growth forests following major disturbances (Abrams and Orwig 1996, Orwig and Abrams 1999). Medium to large-sized canopy gaps are required for its recruitment and some (Foster 1988, Rooney 1995) have suggested that a combination of wind throws and fire may be necessary for successful establishment. Thus, white pine can exist as a gap-phase species (Abrams et al. 1995) but substantial recruitment is dependent on larger-scale disturbances (Abrams and Orwig 1996, Abrams et al. 2000).

Even though elevation was a principal correlate of the vegetation gradient from the bottomland to the northern ridge-top community, it is unlikely that an absolute elevation difference of <100 m, in and of itself, is the cause of this acute change in species dominance. Rather, the elevation gradient is likely a reflection of the interactions of other gradients including the phosphorus and potassium concentration gradient that our analysis found and other unmeasured gradient such as soil moisture, water drainage, or occurrence of wind throws.

The increase of phosphorus and potassium from the bottomlands to ridge tops recorded in our study is the reverse of the more usual pattern of having richer colluvial aprons in the valleys within the Pennsylvania Ridge and Valley Province (Eckenrode 1985). We can hypothesize that the pattern we recorded is a consequence of Swift Run's bottomlands being scoured back to bedrock by late Pleistocene erosion while the ridge crests were less disturbed and hence remained richer (D. Marsh, pers. comm.). Detailed assessments of the valley's soils have yet to be performed.

The Snyder-Middleswarth Natural Area exhibits the expected characteristics of a well-developed old-growth forest, e.g., tree ages exceeding 300 yr (ages determined from fallen log sections), low tree densities distributed among all size classes, trees with diameters >70 cm, and volumes of dead wood (Spies and Franklin 1988, Tyrrell and Crow 1994). Consequently, we would expect that the observed distributions of species reflect both the distributions of key environmental and edaphic influences as well as historic and current disturbance events. Furthermore, we might posit that competition among tree species would amplify the correlation of species occurrences with environmental and edaphic factors because competitive interactions should act to reduce the number of individuals persisting on microsites to which they are poorly adapted.

Threats to the Snyder-Middleswarth Natural Area

White-tail deer browsing is currently among the most important agents of forest disturbance in the eastern United States. In Pennsylvania overbrowsing dates to the 1930s and its impacts are evident even in old-growth areas such as the hemlock-white pine-northern hardwoods at Heart's Content (Whitney 1984, Rooney and Dress 1997). Such browsing can shift the balance of canopy species because of differential recruitment by less-preferred and often light-requiring species such as red maple, black birch, and yellow birch (Whitney 1984, 1990; Rooney 1995; Abrams et al. 2000, 2001). There is evidence of deer use (droppings) and browse within the Snyder-Middleswarth old-growth forest. The gap in the smaller size classes of chestnut oak may be a consequence of juvenile mortality due to deer browsing. However, we did not see the same gap in smaller size classes with hemlock, a species that can be used as winter browse by deer in areas with high deer densities (Anderson and Loucks 1979). On the other hand, small hemlock stems only a few cm in diameter can be more than a century old (M.D. Abrams pers. comm.). Consequently, even though small individuals of hemlock are present, it is possible that there has been limited hemlock recruitment for several decades.

The continued domination of the Snyder-Middleswarth old-growth forest by hemlock could also be appreciably impacted by an outbreak of the hemlock woolly adelgid. This exotic herbivore was first reported in southeastern Pennsylvania in the late 1960s (McClure 1987) and it is present in central Pennsylvania (Abrahamson, pers. obs.). Should appreciable hemlock mortality occur, black birch would likely gain considerable importance (Orwig et al. 1998). Other herbivores including the elongate hemlock scale, spruce spider mite, hemlock rust mite, and cryptomeria scale could also threaten hemlock survival at the Snyder-Middleswarth Natural Area.

ACKNOWLEDGMENTS

We thank Jonathan Paliotta, Amy Whipple, Duane Griffin, Marc Abrams, Ben Marsh, Irene Kralick, and Norm Conrad for field assistance, technical support, or helpful advice. Permission to study this site was granted by the Pennsylvania Department of Conservation and Natural Resources, Bureau of Forestry. The Katherine Mabis McKenna Foundation and David Burpee Endowment of Bucknell University provided financial support. This study represents a portion of a senior thesis submitted for the B.S. degree in Environmental Studies at Bucknell University by P.P.Z.

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Received December 18, 2001; Accepted July 17, 2002.