RESEARCH ARTICLE

Successional Dynamics and Restoration Implications of a Montane Coniferous Forest in the Central Appalachians, USA

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ABSTRACT: Central Appalachian montane red spruce (*Picea rubens* Sarg.) communities have been greatly reduced in extent and functional quality over the past century. This community decline has put several plant and animal species, such as the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus* Shaw), at risk from habitat loss, and has resulted in the elimination of these forests as a commercially important type. Where feasible, red spruce restoration efforts may help mitigate these regional trends and provide valuable lessons for community restoration efforts elsewhere. In a pilot study designed to better understand second-growth spruce structure, we inventoried trees and downed coarse woody debris in an isolated montane red spruce forest in West Virginia, USA. We quantified stand characteristics and compared them to structural characteristics of old-growth forest communities of similar composition. At this relict forest, stand initiation occurred in the early 1920s following a period of watershed-wide timber harvesting. Live tree basal area ≥ 10 cm dbh (44.5 m^2 ha^{-1}), snag density ≥ 10 cm dbh (256 ha^{-1}), and total fallen log volume (86.2 m^3 ha^{-1}) were similar to old-growth attributes. However, snag basal area ≥ 10 cm dbh (4.6 m^2 ha^{-1}), height of dominant and co-dominant red spruce (24.7 m), and maximum red spruce dbh (48.0 cm) were significantly less than would be expected in old-growth forests of similar composition. Red spruce comprised > 40% of dominant crown class trees and often was a main canopy emergent. However, eastern hemlock (*Tsuga canadensis* [L.] Carr.) had the highest relative importance value (51.7%), with red spruce (18.0%) and red maple (*Acer rubrum* L.) (16.7%) representing lesser fractions. Stocking at 147% of threshold full stocking was correlated with slow growth rates for red spruce and eastern hemlock. Growth and yield simulations indicated current conditions would support a thinning in smaller size classes that could accelerate individual tree growth rates and decrease time required to attain additional old-growth structural characteristics.

Dinámica Sucecional y Implicancias de la Renovación de un Bosque Montano de Coníferas en los Apalaches Centrales, USA.

RESUMEN: Las comunidades montanas de *Picea rubens* Sarg en los Apalaches Centrales han sido altamente reducidas en extensión y en calidad durante el último siglo. Esta disminución de la comunidad ha puesto a muchas especies de plantas y animales, tales como la Ardilla voladora del Norte de Virginia (*Glaucomys sabrinus fuscus* Shaw), en riesgo de pérdida de hábitat, y ha resultado en la pérdida de la importancia comercial de este bosque. Donde es posible, los esfuerzos de renovación de *P. rubens* pueden ayudar a paliar esas tendencias regionales y proveer lecciones valiosas para los esfuerzos de renovación en otros lugares. En un estudio piloto, desarrollado para mejorar el entendimiento del crecimiento secundario de *P. rubens*, inventariamos los árboles y los bastos troncos en descomposición en un bosque aislado de *P. rubens* en Virginia del Oeste, USA. Cuantificamos las características de los árboles y las comparamos con las características de comunidades de bosques maduros de composición similar. En este relicto de bosque, los árboles más viejos son de la década del 20, posteriores a un período de extracción madedera. El área basal de los árboles vivos ≥ 10 cm dap (44.5 m^2 ha^{-1}), la densidad de nudos ≥ 10 cm dap (256 ha^{-1}), y el volumen total de madera caída (86.2 m^3 ha^{-1}) fueron similares a los atributos de un bosque maduro. No obstante, el área basal de los árboles con nudo ≥ 10 cm dap (4.6 m^2 ha^{-1}), la altura de *P. rubens* dominantes y co-dominantes (24.7 m) y el dap máximo de la especie (48.0 cm) fueron significativamente menores que lo que se hubiese esperado de un bosque maduro de composición similar. *P. rubens* comprende >40 % de las copas dominantes y a menudo fue el emergente más importante. No obstante *Tsuga canadiensis* [L.] Carr. tuvo el valor de importancia relativa más alto (51.7%), con *P. rubens* (18.0%) y *Acer rubrum* L. (16.7%) representando los menores porcentajes. El stock al 147% del umbral de stock lleno fue correlacionado con las lentas tasas de crecimiento de *P. rubens* y *Tsuga canadiensis* [L.] Carr. Simulaciones de crecimiento y producción indicaron que bajo las condiciones actuales se soportaría una extracción en las clases pequeñas que podría acelerar la tasa de crecimiento individual de los árboles y disminuir el tiempo requerido para lograr las otras características estructurales de bosque maduro.

Index terms: central Appalachians, eastern hemlock, forest structure, old-growth forest, red spruce

INTRODUCTION

Central and southern Appalachian montane coniferous forest communities of red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* [L.] Carr.), Fraser fir (*Abies fraseri* [Pursh] Poir.), and balsam fir (*A. balsamea* [L.] Mill.) and combinations thereof are considered among the most threatened forested ecosystems in the United States (Noss et al. 1995, Christensen et al. 1996). Most central

Appalachian red spruce forests in the Allegheny Mountains subsection of Virginia and West Virginia have never returned to pre-exploitation conditions following the railroad logging era and subsequent widespread fires from 1880 to 1930 (Pielke 1981, Stephenson and Clovis 1983, White and Cogbill 1992). Following exploitive logging practices, livestock producers in West Virginia often repeatedly burned cut-over forest to create high-elevation summer range (Stephenson 1993). Repeated fires degraded soil conditions by consuming the ecologically critical humus layer characteristic of montane and boreal conifer ecosystems (Brooks 1908, Clarkson 1964). Degraded red spruce forests often were converted to low-quality northern hardwood forests or shrub-dominated glades (Brooks 1911, Stephenson 1993). In West Virginia, red spruce-dominated montane forests have declined from > 200,000 ha at the time of the Civil War to 20,000 ha today (Stephenson and Clovis 1983, Stephenson 1993).

Currently, red spruce forest recovery in the central and southern Appalachians is being hindered by a variety of biotic and abiotic factors. These include atmospheric acidic deposition, hemlock adelgid (*Adelges tsugae* Annand) and balsam woolly adelgid (*Adelges piceae* Ratzeburg) infestations, excessive white-tailed deer (*Odocoileus virginianus* Zimmerman) herbivory, surface mining, and recreational/second-home development (Friedland et al. 1984, Schroeder 1988, McLaughlin et al. 1990, Battles et al. 1992, Micheal 1992, Mohnen 1992, White and Cogbill 1992, McDonald 1993, Hollingsworth and Hain 1994, Fredrickson 1998, Jenkins et al. 1999, Parker et al. 1999, Odom et al. 2001). Nonetheless, after approximately 100 years of postfire ecosystem processes, there are indications that partial restoration in central Appalachian red spruce forests is occurring and could be accelerated by active management. Red spruce can successfully compete with associated hardwoods in central Appalachian ecotones below elevations believed optimal for red spruce (Cogbill and White 1991). Moreover, the elevation of this ecotone may be decreasing (Adams et al. 1999). Red spruce also may be stabilizing in some locations in the southern Appalachians (Busing et al. 1988). Experimental thinning of dense second-growth red spruce stands reversed decades-long declines in individual tree vigor (Hornbeck and Kochenderfer 1998). In West Virginia, the presence of extensive areas with low-quality northern hardwood overstories and red spruce and eastern hemlock understories, suggests that management efforts such as overstory thinning to release the conifer-dominated understory could be used to accelerate montane red spruce forest recovery.

Accelerating red spruce forest recovery in the central Appalachians potentially could lead to enhanced or increased habitat for two federally listed species—Cheat Mountain salamander (*Plethodon nettingi* Green) and Virginia northern flying squirrel (Odom et al. 2001). Several species of concern such as the saw-whet owl (*Aegolius acadicus* Gmelin), northern goshawk (*Accipter gentiles* L.), snowshoe hare (*Lepus americanus* Erxleben), and fisher (*Martes pennanti* Erxleben) also would benefit from red spruce forest recovery (Hall 1983, Smith 1993). Despite being poorly surveyed by invertebrate ecologists, regional red spruce forests harbor several relict and endemic insect and spider species, and are believed to host species that are not yet described (Acciavatti et al. 1993).

Second-growth patches of red spruce or mixed red spruce–eastern hemlock 0.1 ha to > 1000 ha in size are present in the Allegheny Mountains in West Virginia and Virginia above approximately 900–1000 m (Bailey and Ware 1990, Cogbill and White 1991, Stephenson 1993, Hornbeck and Kochenderfer 1998). In West Virginia, these small stands may represent viable foci at which to begin restoration efforts aimed at improving habitat quality for special concern species and increasing the extent of montane red spruce communities on the 700,000 ha of land above 900 m (DiGiovanni 1990). The existence of these stands raises two questions. First, can second-growth red spruce stands be "restored" using active management to provide a better habitat for problematic or imperiled flora and fauna? Second, can small, isolated patches of red spruce actually provide functionally usable high-elevation montane habitat?

Before restoration plans can proceed, however, a better understanding of the structural and functional characteristics of extant montane red spruce forests is needed. Accordingly, we evaluated characteristics of an isolated second-growth red spruce–eastern hemlock stand on the Mead-Westvaco Ecosystem Research Forest (MWERF). As a logical first step toward restoration, we felt it was important to document structural characteristics of second-growth spruce forests, which constitute most of the existing spruce forest in the region. Previous work has focused on the few remaining old-growth remnants (Adams and Stephenson 1989), but second-growth red spruce provides the opportunity for improving montane habitat at wider landscape and regional scales. We also modeled future stand development to examine how management decisions are likely to affect desired future structural and functional characteristics such as red spruce size and relative abundance, amounts of downed coarse woody debris (CWD), and overstory canopy structure.

METHODS

Site Description

The 3360-ha MWERF is located in the Unglaciated Allegheny Mountain and Plateau physiographic province of West Virginia (Fenneman 1938) on the Rich Mountain Massif in southwestern Randolph County (N 38° 42', W 80° 3'). Established by Westvaco Corporation in 1994, the area is reserved for the study of forest management in central Appalachian ecosystems. Oldest forests on the MWERF are second-growth stands that were established by natural regeneration following widespread railroad logging that occurred in this portion of West Virginia in the 1900s–1920s (Clarkson 1993). Elevations range from 740 to 1200 m. Topography consists of steep side slopes with broad, plateau-like ridgetops and narrow valleys with small, high-gradient streams. The climate is cool and moist, with average annual precipitation exceeding 155 cm (Strausbaugh and Core 1978). Area soils are acidic, welldrained Inceptisols that are considered frigid above 1000 m, particularly in sheltered positions. Most forest cover on the MWERF is primarily a northern hardwood type dominated by American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), red maple (*A. rubrum* L.), black cherry (*Prunus serotina* Ehrh.), Fraser magnolia (*Magnolia fraseri* Walt.), and red spruce. Higher elevations (> 1000 m) and riparian areas are characterized by increased dominance of red spruce and eastern hemlock. Throughout, rosebay rhododendron (*Rhododendron maximum* L.) and striped maple (*A. pensylvanicum* L.) form dense understory thickets. An artifact of recent forest harvesting and excessive white-tailed deer herbivory, dense cover of hay-scented fern (*Dennstaedtia punctilobula* [Michx.] Moore) occurs where the shrub layer is absent and the overstory canopy is not continuous (Ford and Rodrigue 2001). Although the bulk of montane red spruce in the Allegheny Mountains occurs eastward on the Cheat, Backbone, Allegheny, and Back Allegheny Mountain ranges, several small patches (0.5–5 ha) of red spruce and eastern hemlock, and a disjunct, small population of the Virginia northern flying squirrel, occur on Rich Mountain at the MWERF and neighboring Kumbrabow State Forest.

Data Collection

In September 1999, we located eight fixed-area circular plots (0.04 ha) along transects at 25-m intervals to sample vegetation and coarse woody debris (CWD) in the "Spruce Rocks" area of the MWERF. Plots were 25 m or more from the adjacent northern hardwood forest. We recorded tree species, diameter at breast height (dbh; 1.3 m for trees ≥ 10 cm), and crown class. Our classification of individual tree crowns consisted of dominant, co-dominant, intermediate, overtopped, or standing dead according to commonly used criteria (Smith et al. 1997). Downed CWD sampling (> 2.54 cm in diameter) included piece length and endpoint and midpoint diameters (Maser et al. 1979, Barker 1997). An estimate of downed CWD decay was recorded but is not reported here because CWD exhibited minimal variability (most downed wood exhibited little decomposition). Within each main plot quadrant, we randomly selected one red spruce and one eastern hemlock for coring (consequently all crown classes were sampled) and subsequent radial growth analysis ($n = 71$). We cored as close to ground level as practical to better determine individual stem establishment dates. Cores generally were removed from trees perpendicular to surrounding terrain slope to avoid sample compression.

Data Analysis

We prepared tree cores for ring-width measurements by sanding core surfaces with sandpaper to enhance ring visibility under magnification. We measured ring widths using a Velmex measuring stage calibrated to 0.01 mm in conjunction with MeasureJ2X software (North Sandwich, N.H.) to record tree-ring measurement files. Following tree-ring measurement cross-dating using marker years based on consistently narrow years (e.g., 1988), we used COFECHA to statistically validate the cross-dating of ring-measurement series for individual species (Grissino-Mayer et al. 1997).

Stem wood radial growth patterns and stem establishment dates were used to assess past stand dynamics (Lorimer and Frelich 1989). We distinguished past stand disturbances from climatic effects based on release periods. Drought effects in eastern mesic forests have been shown to last only for several years (McIntyre and Schnur 1936, Cook and Jacoby 1977). Release events signifying major canopy disturbances persist longer and often are measured as percent growth changes (%GC). We used established methodology to calculate annual %GC by comparing preceding to superseding 10-year radial means (McCarthy and Bailey 1996, Nowacki and Abrams 1997, Schuler and Fajvan 1999).

We summarized plot vegetation data and initial percent stocking using FlexFIBER software (Thomas Brann, University of Maine, Orono, pers. com.). Relative importance value was calculated for each species as the mean of relative density (stems), relative dominance (basal area), and relative frequency (Cottam and Curtis 1956). We used the Forest Vegetation Simulator (FVS) (Teck et al. 1996) with the NE-TWIGS variant (Teck 1990) to project stand growth and yield characteristics for the next 50 years using different management scenarios. We graphically depicted individual tree and stand structure characteristics using the Stand Visual System (SVS) (McGaughey 2001).

We compared stand structure characteristics from Spruce Rocks to old-growth forest attributes as compiled by Tyrrell et al. (1998). Inventory characteristics at Spruce Rocks were compared to live tree basal area ($n = 25$), snag density ($n = 13$), dead tree basal area ($n = 11$), and maximum red spruce dbh ($n = 66$) for montane and allied spruce-fir old-growth study sites (Tyrrell et al. 1998). Due to insufficient CWD data associated with this forest type ($n = 3$), Spruce Rocks CWD was compared to CWD data from old-growth study sites classified as conifer-northern hardwood forests ($n = 26$) (Tyrrell et al. 1998). Normal probability plots were generated for all variables to check for outlying observations and the assumption of normal distribution before proceeding with hypothesis testing. Mid-range smoothers were used to assess how closely plotted points followed a line connecting the first and third quartiles. One snag density observation from Reiners and Lang (1979), which used a smaller minimum dbh, appeared to be an extreme value and was omitted from further analysis. We used two-sample t-tests not dependent on equal variances for hypothesis testing (Montgomery 1991).

We evaluated different thinning strategies to understand effects on future stand structure changes relative to no management. Our simulated management scenarios for the next 50 years represent a range of management options and include two thinning scenarios: a low-thinning regime and a crown-thinning regime. We also projected an uncut reference stand for the same period. Both thinning scenarios reduced tree numbers to the fewest that still could utilize all of the growing space, otherwise known as the "B-line stocking level" (Gingrich 1967). Thinnings were simulated to occur immediately and then again after 30 years. Thinnings from below were limited to trees > 12 cm dbh to incorporate commercial feasibility. Crown thinning re-

Table 1. Inventory characteristics of a mixed red spruce and eastern hemlock forest at the Mead-Westvaco Ecosystem Research Forest, Randolph County, West Virginia, 1999.

Species	Density (stems ha^{-1})	Relative Density (%)	Dominance (m^2 ha^{-1})	Relative Dominance (%)	Frequency (# plots)	Relative Frequency (%)	Relative Importance (%)
Tsuga canadensis	931	71.2	26.4	58.4	8	24.2	51.3
Picea rubens	159	12.2	8.6	18.9	8	24.2	18.4
Acer rubrum	138	10.6	8.5	18.7	7	21.2	16.8
Betula alleghaniensis	62	4.7	1.3	3.0	6	18.2	8.6
Amelanchier arborea	9	0.7	0.2	0.3	2	6.1	2.4
Ilex sp.	6	0.5	0.0	0.0	1	3.0	1.2
Prunus serotina	3	0.2	0.3	0.7	1	3.0	1.2
TOTALS	1,308		45.2		33		

moved the largest diameter trees in the stand until stocking level criteria were achieved. Species removal preferences were red maple, eastern hemlock, and red spruce, respectively, when trees of the same dbh were incurred by the simulator's thinning algorithm. The thinning from below was designed to increase growth rates of the stand's larger trees. The thinning from above was designed to simulate removal of the most valuable timber and fiber products. Applicable simulators such as FIBER and NE-TWIGS have been calibrated for northeastern conifers and are based on data from New England (Schuler et al. 1993). We are not aware of empirical simulators specifically calibrated for central Appalachian high-elevation coniferous forests. Furthermore, we do not suggest our growth and yield simulations determine optimality for stand structure characteristics. We compared widely different thinning strategies to illustrate the importance of today's management decisions on future conditions. We recognize that other silviculture strategies might do more to improve forest structure relative to the needs of species such as the Virginia northern flying squirrel.

RESULTS AND DISCUSSION

Current Conditions

In terms of relative importance, the Spruce Rocks area is dominated by eastern hemlock, with red spruce and red maple representing about equal lesser fractions (Table 1). The large importance value of eastern hemlock was due to both high relative density (stems) and high relative dominance (basal area). Eastern hemlock was present in most diameter classes and had a mean dbh of 17.3 cm (SE = 0.4, n = 300) (Figure 1). Red spruce also was present throughout most diameter classes but trended larger (mean dbh = 24.3 cm, SE = 1.4, n = 51). Red maple, unlike associated conifers, was not present in diameter classes below 11 cm and had a mean dbh of 26.6 cm (SE = 1.3, n = 44). Overall diameter distribution of sampled trees formed a unimodal size-class distribution typical of single-cohort stands undergoing stem exclusion.

Red spruce was often emergent above the stand's upper continuous canopy. Red spruce comprised 40% of dominant crown class trees (Figure 2) and was consistently the tallest dominant and codominant species (mean height = 24.7 m, SE = 0.9, n = 8; eastern hemlock: mean height =

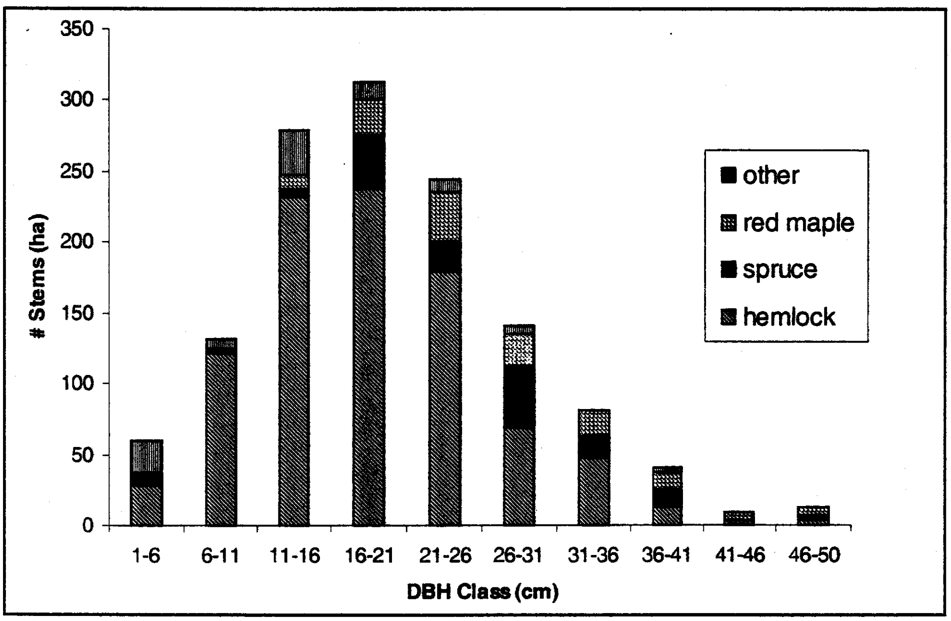

Figure 1. Inventoried diameter class distribution for tree species at Spruce Rocks, Randolph County, West Virginia.

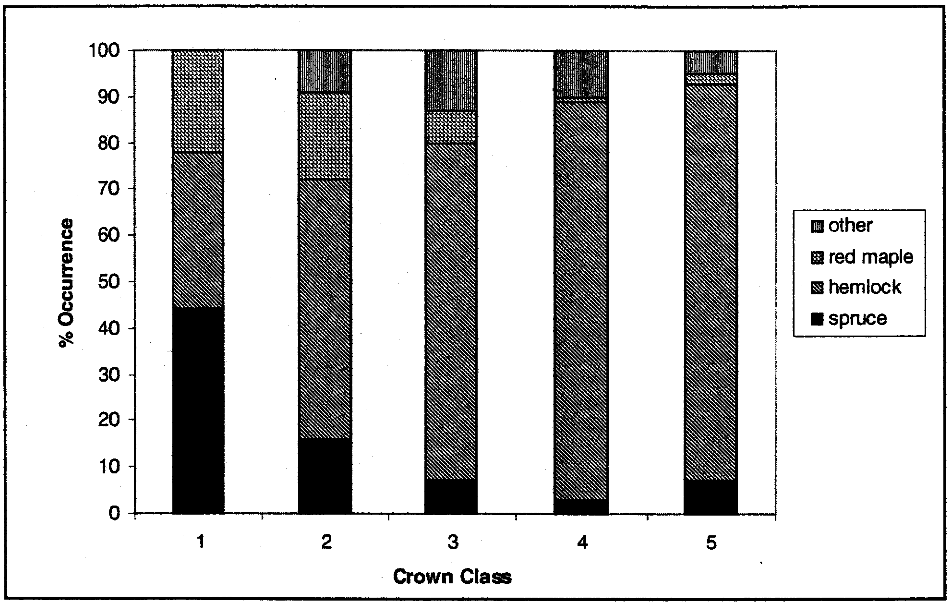

Figure 2. Relative distributions of tree species within five crown classes (1 = dominant, 2 = codominant, 3 = intermediate, 4 = overtopped, 5 = dead) at Spruce Rocks, Randolph Country, West Virginia.

20.8 m, SE = 0.5, n = 4; red maple: mean height = 22.4 m, SE = 0.2, n = 3). From our size sampling alone, it was unclear whether this structural characteristic was attributable to growth or age-related differences among tree species present.

Structural characteristics for the Spruce Rocks stand reflected both old-growth and second-growth attributes, as compared to published data from similar forest types. Stand basal area of live stems greater than 10 cm dbh did not differ significantly from that of montane and allied spruce-fir old-growth forests in the eastern United States (Table 2). This stand exceeded full stocking (147% of the B-line stocking) and accordingly would be expected to exhibit slow individual tree growth with high density-dependent mortality of overtopped and intermediate crown class individuals. Indeed, total standing snag density was high and did not differ from old-growth forests of similar composition (Table 2). Most standing dead stems were eastern hemlock (86%), with red spruce (8%), yellow birch (3%), and red maple (3%) at lesser fractions. Downed CWD was prominent throughout and did not differ in mean total volume from old-growth structural attributes (Table 2). Downed CWD mean diameter at the largest end was 9.4 cm (SE = 0.60 n = 8); largest downed CWD diameter at log's end and maximum downed CWD length across all plots and all pieces was 28.0 cm and 13.0 m, respectively. These piece sizes are indications that fallen log volume was a result of tree mortality in smaller size classes.

Not all structural characteristics of the stand were indicative of old-growth conditions. In addition to overall live tree size class distribution (Figure 1), maximum red spruce dbh, and dead tree basal area were indicative of second-growth time frames for stand development (Table 2). In addition, mean height of dominant and codominant red spruce was not indicative of old-growth sites in the central Appalachians, where red spruce can exceed 31 m in total height (Adams and Stephenson 1989). Dead tree basal area indicated that mortality was limited mostly to smaller trees.

Although stand structure exhibited both old-growth and second-growth attributes, it was clear from ages of cored trees that Spruce Rocks was a second-growth stand as suspected (Figure 3a). Most trees originated or were released after 1920, which coincides with original watershed-wide timber harvesting (ca. 1921) by the Moore-Kleppel Company (Roger Sherman, Mead-Westvaco, Rupert, W.Va., pers. com.). Cohort recruitment during the stand-initiation stage continued for approximately 30 years, from 1920 to about 1950. No new signif-

Table 2. Comparison of tructural characteristics of Spruce Rocks red spruce–eastern hemlock forest at the Mead-Westvaco Ecosystem Research Forest, Randolph County, West Virginia, and regional old-growth attributes of similar forest type.

Attribute	Spruce Rocks	Old-Growth	Method	t	df	P
Live tree basal area (m^2 ha^{-1})	44.5	39.3[a]	Two-sample, separate variance	-1.767	24.1	0.090
Snag density (stems ha^{-1})	256.0	211.0[a]	Two-sample, separate variance	-0.774	17.2	0.449
Downed CWD (m^3 ha^{-1})	86.2	121.4[b]	Two-sample, separate variance	1.972	12	0.072
Dead tree basal area (m^2 ha^{-1})	4.6	10.7[a]	Two-sample, separate variance	3.119	14.4	0.007
Maximum red spruce dbh (cm)	48.0[c]	62.9[a]	One-sample	8.432	65	0.000

[a] Attribute from montane and allied spruce-fir old-growth forests (Tyrrell et al. 1998).

[b] Attribute from conifer–northern hardwood old-growth forests (Tyrrell et al. 1998).

[c] Observed maximum at Spruce Rocks study site, Randolph County, West Virginia.

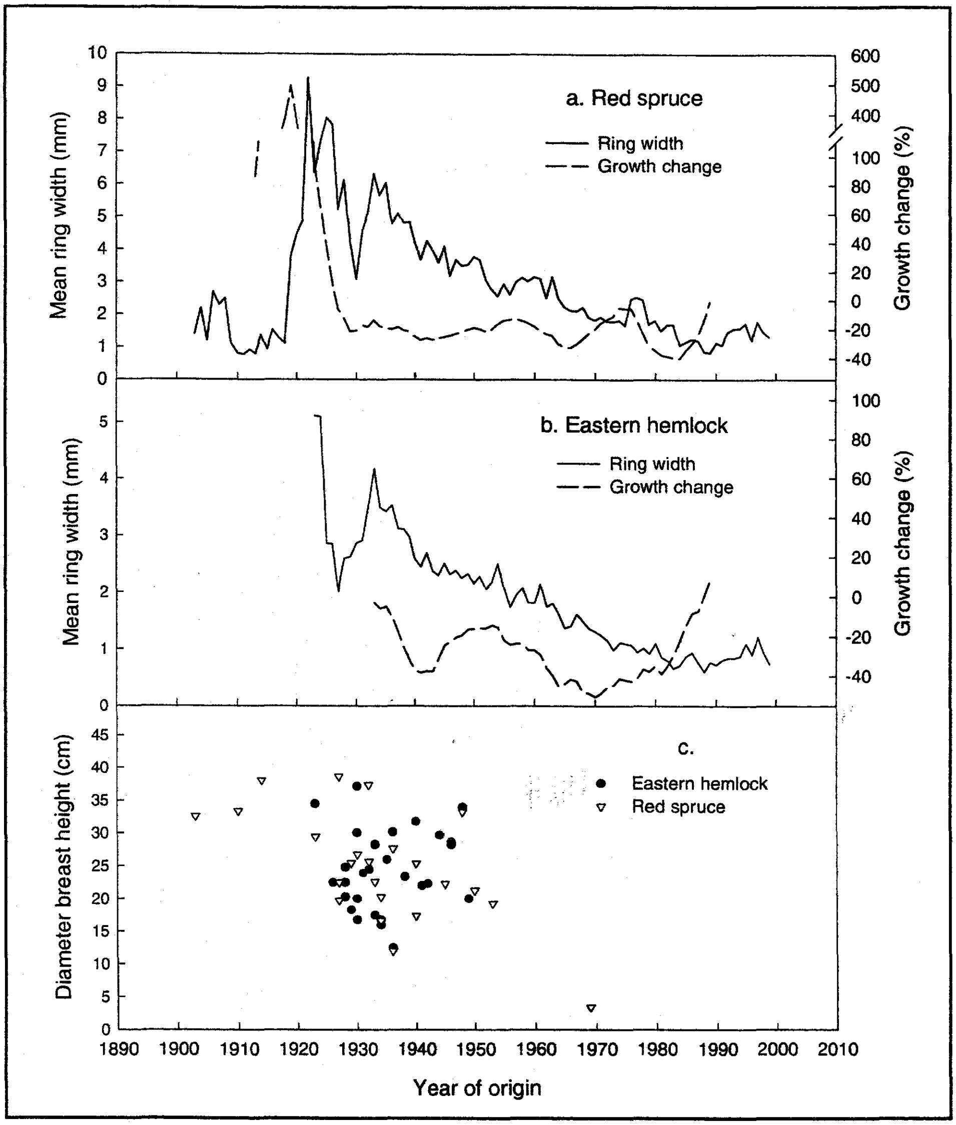

Figure 3. Age, mean ring width, and percent growth change relationships for all cored (a) red spruce and (b) eastern hemlock; age and diameter relationship for (c) all cored trees at Spruce Rocks, Randolph County, West Virginia.

icant recruitment has occurred since. Red spruce mean annual radial growth rates peaked in 1922 and %growth change (%GC) exceeded 100% from 1914 to 1922 (Figure 3b). Overall, red spruce radial growth declined from about 1930 to 1990, a decline which is typical of single-cohort stands during the stem-exclusion stage. Eastern hemlock growth rates were similar to those of red spruce and displayed the same negative exponential trend (Figure 3c). For the past decade, eastern hemlock and red spruce growth rates have stabilized, as indicated by recent trends in %GC (Figure 3b and 3c).

Future Conditions

Simulated management scenario comparisons illustrate the importance of current management decisions on future stand structural characteristics (Table 3). Coarse woody debris, quadratic mean stand diameter (QMD), frequency of living and dead trees $\geq$ 50.8 cm dbh, percent red spruce, and standing volume varied substantially among the three management scenarios we evaluated. Coarse woody debris contributions to the stand over the next 50 years are greatest when no commercial thinning or harvesting operations are performed. This is because thinnings were designed to reduce stocking levels so that expected tree mortality over the simulation period would be greatly reduced. However, CWD could be increased by thinnings if selected trees were cut or deadened by artificial means such as girdling or herbicides but not removed from the stand, as is done during precommercial operations. If such an approach were used, then crown thinning would maximize total volume of CWD contributions during the next 50 years (Table 3). Perhaps the most striking difference in the future conditions that we observed in our simulations was the relative frequency of larger trees (e.g., dbh > 50 cm) (Table 3). When we inventoried, we did not find any trees with a dbh as large as 50 cm; yet expected stand development over the next five decades would result in about 37 trees ha^{-1} that exceed this size. Furthermore, the low thinning doubles larger tree density relative to the unmanaged reference stand. As predicted by FVS and NE-TWIGS, size class distribution of trees in the year 2049 (as measured by QMD) achieved by low thinning would take an additional 50 years (2099) to attain without active management. Of course, the crown-thinning scenario prevents larger trees from occupying the stand during the simulation period.

The predicted structural differences in the year 2049 among the three considered options are apparent when they are graphically depicted (Figure 4). Inventory conditions in 1999 reflect structural characteristics of a single-cohort stand with mixed species in the stem-exclusion stage (Figure 4a). Vertical stratification within and among species is not yet well developed, although dominant, codominant, intermediate, and suppressed crown classes are present. By 2049, without external influences such as thinning or a pest outbreak (e.g., hemlock wooly adelgid), stand development will remain in the stem-exclusion stage, and species composition will remain relatively constant (Figure 4b, Table 3). Crown thinning effectively retards stand development, and future conditions approximate current conditions (Figure 4c). However, the low-thinning regime is expected to cause substantial change in structural characteristics (Figure 4d). As simulated, the second low thinning in 2029 to

Table 3. Current and alternative future conditions of Spruce Rocks red spruce–eastern hemlock forest at the Mead-Westvaco Ecosystem Research Forest, Randolph County, West Virginia.

Year	Downed CWD[a] (m^3 ha^{-1})	QMD[b] (cm)	Live Trees ≥ 50.8 cm ha^{-1}	Dead trees ≥ 50.8 cm ha^{-1}	% RS[c] (IV)	Standing Volume[d] (m^3ha^{-1})	Harvested Volume (m^3ha^{-1})	Gross Volume[e] (m^3ha^{-1})
1999	86	19.6	0	0	18.4	265.5		265.6
2049 with								
no management	180	32.0	37.3	3.5	14.0	565.5		565.5
2 thinnings (below)	97	42.9	70.6	3.5	30.8	321.2	195.8	517.2
2 thinnings (above)	40	28.4	0	0	16.4	365.8	372.3	738.2

[a] CWD (coarse woody debris) in 2049 includes standing mortality projected from 2000 to 2049, excludes 1999 CWD, and does not account for decomposition during the projection period.

[b] Quadratic mean stand diameter.

[c] Percent red spruce.

[d] Cubic volume includes all trees 12.7 cm dbh and larger.

[e] Gross volume is the sum of standing volume and harvested volume.

about 30 m^2 ha^{-1} of residual basal area creates canopy gaps that persist for at least 20 years (Figure 4d). Of course, actual stand structure would depend on residual tree spatial arrangement. Gaps could be favored by removing trees in clumps rather than evenly spacing residual trees. Such gaps may lead to understory re-initiation (caveat: understory re-initiation cannot be empirically predicted by NE-TWIGS and is not depicted in Figure 4). Oliver and Larson (1996) refer to the understory re-initiation stage as "transition old-growth" and strongly suggest that many functional "old-growth" forests fit this category. Structural attributes of such late-successional stands, such as large CWD, large cavity trees, and canopy heterogeneity, would benefit the Virginia northern flying squirrel (Urban 1988, Weigl et al. 1999). Moreover, because age limits of red spruce and eastern hemlock are approximately 400 and 1000 years, respectively (Burns and Honkala 1990), the transition old-growth stage represents the most plausible desired future condition.

CONCLUSIONS

Old-growth red spruce forests were once widespread throughout the central Appalachians. Currently, red spruce forests that display old-growth characteristics represent less than 1% of the remaining type and are extremely isolated. Existing second-growth red spruce forests may provide some characteristics of old-growth structure and function, as suggested by the regional persistence of rare, threatened, or endangered species thought to prefer old-growth structure. Our study at Spruce Rocks, West Virginia, found that some elements of old-growth forest structure, and possibly habitat, are present but that others, such as larger living and dead trees, are lacking. Larger trees provide larger snags and longer lasting cavity trees for saw-whet owls (DeGraff and Yamasaki 2001), better drey nest sites for Virginia northern flying squirrel (Jennifer Menzel, West Virginia University, Morgantown, pers. com.), larger canopy gaps following windthrow and new recruitment in them, greater variability of vertical structure from recruitment in gaps, and larger CWD.

Forest stands free of human disturbance are rare, and some levels of human disturbance are compatible with old-growth conservation values (Hunter and White 1997). The harvest of forest products and management for endangered species generally are regarded as mutually exclusive resource objectives. However, rare species habitat protection and active stand management are often without conflict when appropriate mitigations are used (Kittredge 1996, Schnepf et al. 1998, Stanturf et al. 1998). Game management has long been a component of silvicultural practice (Smith et al. 1997), but management for nongame species also is increasingly incorporated (e.g., DeGraff and Shigo 1985, Kittredge 1996, Rudolph and Conner 1996, Schnepf et al. 1998). Active management can benefit both game and nongame species (Bender et al. 1997, Healy 1997). Moreover, the practice of improving forest health through appropriate silviculture is gaining acceptance (Oliver et al. 1994, Kaufmann and Regan 1995, Stone et al. 1999).

We propose that some stand manipulations can be used to hasten the onset of later successional red spruce forest attributes that are poorly represented in the central Appalachians. This strategy can be incorporated into large-scale forest restoration activities, which would include forest structure enhancement that leads to better representation of rare conditions (Keddy and Drummond 1996). Consistent with our recommendations, thinning has been used successfully in secondary red spruce forests as long as no more than one-fourth to one-half of the basal area is

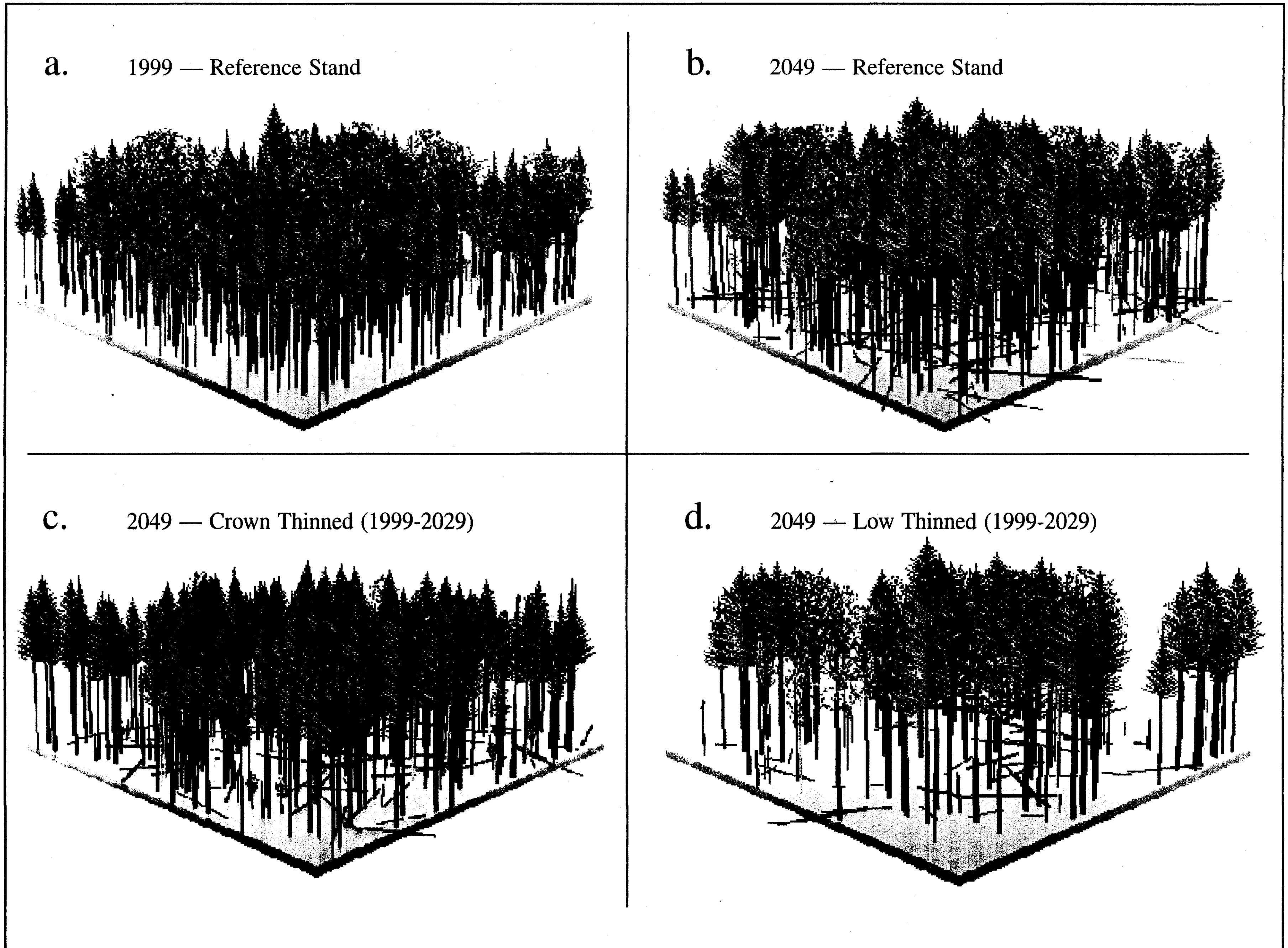

Figure 4. Stand structural characteristics at Spruce Rocks, Randolph County, West Virginia (a) in 1999, (b) as predicted in 2049 without major external disturbances, (c) as predicted in 2049 assuming a crown-thinning regime, and (d) as predicted in 2049 assuming a low-thinning regime.

removed, thereby avoiding problems of excessive windthrow (Frank and Bjorkbom 1973, Frank and Blum 1978). Although the precision of our simulations should be viewed cautiously, predicted patterns reflect robust forest successional patterns. We further recommend adaptive management procedures to test and refine silvicultural treatments aimed at developing forest structure that more accurately reflects old-growth conditions. Future research efforts related to restoring montane coniferous forests in the central Appalachians should incorporate the spatial context of second-growth stands so that efforts can be prioritized based on potential use by species that are dependent on later successional stages.

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LITERATURE CITED

Acciavatti, R.E., T.J. Allen, A.R. Miller, L.L. Pechuman, B.C. Kondratieff, R.F. Kirchner, A.G. Wheeler, S.M. Clark, E. van der Berghe, and W.J. Arnold. 1993. Insects and spiders of the upland forest. Pp. 143-178 *in* S.L. Stephenson, ed., Upland Forests of West Virginia. McClain Printing, Parsons, W.Va.

Adams, H.S. and S.L. Stephenson. 1989. Old-growth red spruce communities in the mid-Appalachians. Vegetatio 85:45-56.

Adams, H.S., S.L. Stephenson, M.B. Adams, and D.M. Lawrence. 1999. Ecological status of Mid-Appalachian red spruce communities. Pp. 235 *in* R.P. Eckerlin, ed., Proceedings of the Appalachian Biogeography Symposium, Special Publication Number 7, Virginia Museum of Natural History, Martinsville.

Bailey, C.M. and S. Ware. 1990. Red spruce forests of Highland County, Virginia: biogeographical considerations. Castanea 55:245-258.

Barker, K.G. 1997. Relationships between salamander communities and cove hardwood stand age in the southern Appalachians. M.S. thesis, University of Georgia, Athens. 69 pp.

Battles, J.J., A.H. Johnson, T.G. Siccama, A.J. Friedland, and E.K. Miller. 1992. Red spruce death: effects on forest composition and structure on Whiteface Mountain, New York. Bulletin of the Torrey Botanical Club 119:418-430.

Bender, L.C., D.L. Minnis, and J.B. Haufler. 1997. Wildlife responses to thinning red pine. Northern Journal of Applied Forestry 14:141-146.

Brooks, A.B. 1911. West Virginia Geological Survey, Vol. 5: Forestry and Wood Industries. Acme Publishing, Morgantown, W.Va. 481 pp.

Brooks, F.E. 1908. The top of West Virginia. The Illustrated Monthly West Virginian 2:11-18.

Burns, R.M. and B.H. Honkala (tech coords.). 1990. Silvics of North America, 1: Conifers. Agriculture Handbook 654, U.S. Department of Agriculture, Forest Service, Washington, D.C. 675 pp.

Busing, R.T., E.E.C. Clebsch, C.C. Eager, and E.F. Pauley. 1988. Two decades of change in a Great Smoky Mountains spruce-fir forest. Bulletin of the Torrey Botanical Club 115: 25-31.

Christensen, N.L., A.M. Bartuska, J.H. Brown, S. Carpenter, C.D. D'Antonio, R. Francis, J.F. Franklin, J.A. MacMahon, R.F. Noss, D.J. Parsons, C.H. Peterson, M.G. Turner, and R.G. Woodmansee. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. Ecological Applications 6:665-691.

Clarkson, R.B. 1964. Tumult on the Mountains. McClain Printing, Parsons, W.Va. 410 pp.

Clarkson, R.B. 1993. Destruction of the upland forests by lumbering and fire. Pp. 35-46 *in* S.L. Stephenson, ed., Upland Forests of West Virginia. McClain Printing, Parsons, W.Va.

Cogbill, C.V. and P.S. White. 1991. The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian Mountain chain. Vegetatio 94:153-175.

Cook, E.R. and G.C. Jacoby. 1977. Tree ring-drought relationships in the Hudson Valley, New York. Science 198:399-401.

Cottam, G. and J.T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

DeGraff, R.M. and A.L. Shigo. 1985. Managing cavity trees for wildlife in the Northeast. General Technical Report NE-101, U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Broomall, Penn. 21 pp.

DeGraff, R.M. and M. Yamasaki. 2001. New England Wildlife Habitat, Natural History, and Distribution. University Press of New England, Hanover, Conn. 981 pp.

DiGiovanni, D.M. 1990. Forest statistics for West Virginia—1975 and 1989. Resource Bulletin NE-114, U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, Penn. 172 pp.

Fenneman, N.M. 1938. Physiography of the Eastern United States. McGraw-Hill, New York. 714 pp.

Ford, W.M. and J.L. Rodrigue. 2001. Soricid abundance in partial overstory removal harvests and riparian areas in an industrial forest landscape of the central Appalachians. Forest Ecology and Management 152:159-168.

Frank, R.M. and J.S. Bjorkbom. 1973. A silvicultural guide for spruce-fir in the Northeast. General Technical Report NE-6, U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Broomall, Penn. 29 pp.

Frank, R.M. and B.M. Blum. 1978. The selection system of silviculture in spruce-fir stands: procedures, early results, and comparisons with unmanaged stands. Research Paper NE-425, U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Broomall, Penn. 15 pp.

Fredrickson, T.S. 1998. Impacts of logging and development on central Appalachian forests. Natural Areas Journal 18:175-178.

Friedland, A.J., R.A. Gregory, L. Karenlampi, and A.H. Johnson. 1984. Winter damage to foliage as a factor in red spruce decline. Canadian Journal of Forest Research 14:963-965.

Gingrich, S.F. 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the Central States. Forest Science 13:38-53.

Grissino-Mayer, H.D., R.L. Holmes, and H.C. Fritts. 1997. The international tree-ring data bank program library version 2.1 user's manual. University of Arizona, Laboratory of Tree-Ring Research, Tucson. 106 pp.

Hall, G.A. 1983. West Virginia Birds. Special Publication no. 7, Carnegie Museum of Natural History, Pittsburgh, Pa. 180 pp.

Healy, W.M. 1997. Thinning enhances New England oak stands to enhance acorn production. Northern Journal of Applied Forestry 14:152-156.

Hollingsworth, R.G. and E.P. Hain. 1994. Balsam wooly adelgid: effects of growth and abnormal wood production in Fraser fir seedlings as influenced by seedling genetics, insect source, and soil source. Canadian Journal of Forest Research 24:2284-2294.

Hornbeck, J.W. and J.N. Kochenderfer. 1998. Growth trends and management implications for West Virginia's red spruce forests. Northern Journal of Applied Forestry 15:197-202.

Hunter, M.L. and A.S. White. 1997. Ecological thresholds and the definition of old-growth forest stands. Natural Areas Journal 17:292-296.

Jenkins, J.C., J.D. Aber, and C.D. Canham. 1999. Hemlock wooly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Canadian Journal of Forest Research 29:630-645.

Kaufmann, M.R. and C.M. Regan. 1995. Ecosystem management, forest health, and silviculture. Pp. 46-52 *in* L.G. Eskew, ed., Forest Health through Silviculture. General Technical Report RM-267, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Keddy, P.A. and C.G. Drummond. 1996. Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. Ecological Applications 6:748-762.

Kittredge, D.B. 1996. Protection of habitat for rare wetland fauna during timber harvesting in Massachusetts. Natural Areas Journal 16:310-317.

Lorimer, C.G. and L.E. Frelich. 1989. A method for estimating canopy disturbance frequency and intensity in dense temperate forests. Canadian Journal of Forest Research 19:651-663.

Maser, C., R.G. Anderson, K. Cromack, J.T. Williams, and R.E. Martin. 1979. Dead and down woody material. Pp. 78-95 *in* J.W. Thomas, ed., Wildlife Habitats in Managed Forests of the Blue Mountains of Oregon and Washington. General Technical Report RM-166, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

McCarthy, B.C. and D.R. Bailey. 1996. Composition, structure, and disturbance history of Crabtree Woods: an old-growth forest of western Maryland. Bulletin of the Torrey Botanical Club 123:350-365.

McDonald, B.R. 1993. Rare plants of the upland forest. Pp. 67-86 *in* S.L. Stephenson, ed., Upland Forests of West Virginia. McClain Printing, Parsons, W.Va.

McGaughey, R.J. 2001. Stand visualization system. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Ore. [Available at *www.fs.fed.us/pnw/svs/*]

McIntyre, A.C. and G.L. Schnur. 1936. Effects of drought on oak forests. Bulletin Number 325, Pennsylvania Agriculture Experiment Station, State College. 7 pp.

McLaughlin, S., C.J. Anderson, N.T. Edwards, W.K. Roy, and P.A. Layton. 1990. Seasonal patterns of photosynthesis and respiration of red spruce saplings from two elevations in declining southern Appalachian stands. Canadian Journal of Forest Research 20:485-495.

Micheal, E.D. 1992. Impact of deer browsing on regeneration of balsam fir in Canaan Valley, West Virginia. Northern Journal of Applied Forestry 9:89-90.

Mohnen, V.A. 1992. Atmospheric deposition and pollutant exposure of eastern U.S. forests. Pp. 64-124 *in* C. Eagar and M.B. Adams, eds., Ecology and Decline of Red Spruce in the Eastern United States. Springer-Verlag, New York.

Montgomery, D.C. 1991. Design and Analysis of Experiments. John Wiley and Sons, New York. 649 pp.

Noss, R.F., E.T. LaRoe, and J.M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Biological Report 28, National Biological Service, Washington, D.C.

Nowacki, G.J. and M.D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecological Monographs 67:225-249.

Odom, R.H., W.M. Ford, J.W. Edwards, C.W. Stihler, and J.M. Menzel. 2001. Developing a habitat model for the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in the Allegheny Mountains of West Virginia. Biological Conservation 99:245-252.

Oliver, C.D., A.E. Harvey, H.S. Malany, J.M. Mandzak, and R.W. Mutch. 1994. Managing ecosystems for health: an approach and the effects on uses and values. Journal of Sustainable Forestry 2:113-133.

Oliver, C.D. and B.C. Larson. 1996. Forest Stand Dynamics. John Wiley and Sons, New York. 520 pp.

Parker, B.L., M. Skinner, S. Gouli, T. Ashikaga, and H.B. Teillon. 1999. Low lethal temperature for hemlock wooly adelgid. Environmental Entomology 28:1085-1091.

Pielke, R.A. 1981. The distribution of spruce in west-central Virginia before lumbering. Castanea 46:201-216.

Reiners, W.R. and G.E. Lang. 1979. Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. Ecology 60:403-417.

Rudolph, D.C. and R.N. Conner. 1996. Red-cockaded woodpeckers and silvicultural practice: is uneven-aged silviculture preferable to even-aged? Wildlife Society Bulletin 24:330-333.

Schnepf, K.A., J.A. Heselmeyer, and D.O. Ribble. 1998. Effects of cutting Ashe juniper woodlands on small mammal populations in the Texas Hill Country. Natural Areas Journal 18:333-337.

Schroeder, F.G. 1988. Southern Appalachians. Pp. 106-107 *in* B. Krahl-Urban, H.E. Papke, K. Peters, and C. Schimansky, eds., Forest Decline. U.S. Environmenal Protection Agency, Corvallis, Ore.

Schuler, T.M. and M.A. Fajvan. 1999. Understory tree characteristics and disturbance history of a central Appalachian forest prior to old-growth harvesting. Research Paper NE-710, U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Radnor, Penn. 12 pp.

Schuler, T.M., D.A. Marquis, R.L. Ernst, and B.T. Simpson. 1993. Test of four stand growth simulators for the northeastern United States. Research Paper NE-676, U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, Penn. 14 pp.

Smith, R.L. 1993. Wildlife of the upland forests. Pp. 211-230 *in* S.L. Stephenson, ed., Upland Forests of West Virginia. McClain Printing, Parsons, W.Va.

Smith, D.M., B.C. Larson, M.J. Kelty, and P.M.S. Ashton. 1997. The Practice of Silviculture: Applied Forest Ecology. 9th Ed. John Wiley and Sons, New York. 537 pp.

Stanturf, J.A., C.J. Schweitzer, S.H. Schoenholtz, J.P. Barnett, C.K. McMahon, and D.J. Tomczak. 1998. Ecosystem restoration: fact or fancy? Pp. 376-383 *in* Transcripts of the 63rd North American Wildlife and Natural Resources Conference, Orlando, Fla. Wildlife Management Institute, Washington., D.C.

Stephenson, S.L. 1993. An introduction to the upland forest region. Pp. 1-9 *in* S.L. Stephenson, ed., Upland Forests of West Virginia. McClain Printing, Parsons, W.Va.

Stephenson, S.L. and J.F. Clovis. 1983. Spruce forests of the Allegheny Mountains in central West Virginia. Castanea 48:1-12.

Stone, J.E., T.E. Kolb, and W.W. Covington. 1999. Effects of restoration thinning on presettlement *Pinus ponderosa* in northern Arizona. Restoration Ecology 7:172-182.

Strausbaugh, P.D. and E.L. Core. 1978. Flora of West Virginia. 2nd Ed. Seneca Books, Morgantown, W.Va.

Teck, R.M. 1990. NE TWIGS 3.0: An individual-tree growth and yield projection system for the northeastern United States. Compiler 8:25-27.

Teck, R., M. Moeur, and B. Eav. 1996. Forecasting ecosystems with the Forest Vegetation Simulator. Journal of Forestry 94:7-10.

Tyrrell, L.E., G.J. Nowacki, T.R. Crow, D.S. Buckley, E.A. Nauertz, J.N. Niese, J.L. Rollinger, and J.C. Zasada. 1998. Information about old growth for selected forest type groups in the eastern United States. General Technical Report NC-197, U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minn. 507 pp.

Urban, V. 1988. Home range, habitat utilization and activity of the endangered northern flying squirrel. M.S. thesis, West Virginia University, Morgantown. 59 pp.

Weigl, P.D., T.W. Knowles, and A.C. Boyton. 1999. The distribution and ecology of the northern flying squirrel, *Glaucomys sabrinus* fuscus in the southern Appalachians. North Carolina Wildlife Resources Commission, Raleigh. 93 pp.

White, P.S. and C.V. Cogbill. 1992. Spruce-fir forests of eastern North America. Pp. 1-39 *in* C. Eagar and M.B. Adams, eds., Ecology and Decline of Red Spruce in the Eastern United States. Springer-Verlag, New York.