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Proceedings from the Conference on the Ecology and Management of High-Elevation Forests in the Central and Southern Appalachian Mountains

Abstract

Proceedings of the Conference on the Ecology and Management of High-Elevation Forests in the Central and Southern Appalachian Mountains held May 14-15, 2009, at Snowshoe Mountain Resort, near Slatyfork, WV. The proceedings includes 18 peer-reviewed papers and 40 abstracts pertaining to acid deposition and nutrient cycling, ecological classification, forest dynamics, avifauna, wildlife and fisheries, forests pests, climate change, old-growth forest structure, and regeneration, and restoration.

Cover photo: An old-growth red spruce-northern hardwood forest as seen from Gaudineer Scenic Area on the Monongahela National Forest. Photo used with permission by David Ede, U.S. Forest Service, Monongahela National Forest.

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Conference on the Ecology and Management of High-Elevation Forests in the Central and Southern Appalachian Mountains

Proceedings of a Conference held at Snowshoe Mountain Resort, Slatyfork, WV, May 14-15, 2009

Edited by:

James S. Rentch, West Virginia University
Thomas M. Schuler, U.S. Forest Service

Sponsored by:

The Nature Conservancy
U.S. Forest Service, Northern Research Station and the Monongahela National Forest
West Virginia University, Division of Forestry and Natural Resources
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Foreword

The Conference on the Ecology and Management of High Elevation Forests in the Central and Southern Appalachians was conceived to bring together managers, practitioners, and researchers working to better understand the unique issues relevant to high-elevation forests in the central and southern Appalachians. We invited Charles Cogbill (Harvard Forest) to summarize the biogeography of high-elevations forests in the central and southern Appalachians, Carolyn Copenheaver (Virginia Tech) to provide insight into the historical conditions of high-elevation forests in the region, Greg Nowacki (U.S. Forest Service) to summarize the current state of the forest, and Mark Anderson (The Nature Conservancy) to address how climate change may influence these forests in the future. The conference also consisted of 42 offered oral presentations and 14 posters. Concurrent sessions were organized to cover topics relevant to acid deposition and nutrient cycling, ecological classification and forest dynamics, avifauna, wildlife and fisheries, forests pests and climate change, and regeneration and restoration. A plenary session was also devoted to a panel discussion to highlight the efforts of the informally chartered High Elevation Conservation Working Group and to invite new cooperators to this multi-partner initiative. The conference concluded with a field trip to Snowshoe Mountain Resort sites that exemplified conservation issues relevant to high-elevation wetlands, the recently delisted West Virginia northern flying squirrel, the threatened Cheat Mountain salamander, silvicultural options for active restoration of high-elevation forests, and soil characteristics unique to high-elevation spruce forests not impacted by high-intensity wildfires. Interest in continuing this conference on a reoccurring basis was expressed by many in attendance.

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Review Procedures

Manuscripts for oral presentations were assigned to one of the editors and peer-reviewed by at least two reviewers assigned by the editors. Reviews were returned to editors, summarized, and sent to the authors with recommendations. Authors revised their manuscripts and returned them to the editors. Revised manuscripts were then reviewed again by the editors and once finalized, were submitted to the Northern Research Station, U.S. Forest Service for final editing and publishing.

The Steering Committee wishes to thank the following people for reviewing manuscripts within these proceedings:

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ABSTRACTS OF POSTER PRESENTATIONS

THE ISOLATED RED SPRUCE COMMUNITIES OF VIRGINIA AND WEST VIRGINIA

Harold S. Adams, Steven L. Stephenson, Adam W. Rollins, and Mary Beth Adams[1]

Abstract.—Quantitative data on the composition and structure of coniferous forests containing red spruce in the mountains of central and southwestern Virginia and eastern central West Virginia, based on sampling carried out in 67 stands during the 1982 to 1984 field seasons, are provided. The average importance value ([relative basal area + relative density/2]) of red spruce was 46.8, and no other tree species occurred in all 67 stands. Yellow birch, eastern hemlock, Fraser fir, and balsam fir were the only other tree species with an average importance value >5, but the two species of fir were restricted to just a few stands. The general study area encompasses three different physiographic provinces (Appalachian Plateau, Ridge and Valley, and Blue Ridge), and compositional differences were apparent when the groups of stands sampled in the three provinces were compared. For example, fewer tree species (16) were recorded in the tree stratum in the Blue Ridge than in either the Ridge and Valley (21) or the Appalachian Plateau (22). Because the data presented herein were collected more than 25 years ago, they represent a baseline for future studies of montane coniferous forests in the Central Appalachians.

INTRODUCTION

Red spruce (*Picea rubens* Sarg.) is the most characteristic species of the montane coniferous forests that occupy higher peaks and ridges of the Central and Southern Appalachians from Virginia and West Virginia to Tennessee and North Carolina (Oosting and Billings 1951, Whittaker 1956). In many instances, these forests form a distinct dark "cap" on the high-elevation peaks and ridges where they occur. Red spruce has a restricted distribution in the mountains of central and southwestern Virginia and eastern central West Virginia. Presumably, distribution is limited because few areas in this region of the Appalachians reach the elevations necessary to provide the cool, moist conditions that this species requires to grow and reproduce. Paleobotanical studies have indicated that coniferous forests containing red spruce occurred throughout much of Virginia and West Virginia during the height of Wisconsin Glaciation and were still present at relatively low elevations (<500 m) in the southern portion of the Shenandoah Valley in Virginia as recently as 9,500 yrs BP (Harrison et al. 1965, Craig 1969, Whitehead 1972). With climatic warming, however, these coniferous forests were replaced by deciduous forests at all but the highest elevations (Watts 1979). At present, the approximate lower limit for red spruce in central and southwestern Virginia is 975 m, although well developed spruce communities generally do not occur at elevations below 1,200 m. In West Virginia, red spruce generally occurs in areas above 915 m but in a few places can be found at elevations below 800 m. However, forests where the species is dominant are found only at the very highest elevations (>1,200 m). Because the period from 8,000 to 4,000 yrs BP is believed to have been warmer and drier than at present (Delcourt and Delcourt 1984), it seems plausible that red spruce was restricted to even higher elevations during this earlier period.

Today, stands of red spruce are extant at fewer than 20 sites in central and southwestern Virginia (Hoffman 1950, Mazzeo 1966, Adams and Stephenson 1984), and at only two of these (Mount Rogers and Whitetop Mountain in

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extreme southwestern Virginia) is the species relatively abundant. Pielke (1981) suggested that red spruce formerly was much more widely distributed in the higher elevations of Virginia than is currently the case, but little evidence supports such a hypothesis. However, red spruce is known to have once been more abundant at some localities but was reduced in extent as a result of logging and (often) subsequent fire (Korstian 1937, Shields 1962).

In contrast, red spruce occurred over large areas (estimated at >200,000 ha) in the late 19th century in the mountains of eastern central West Virginia (Millspaugh 1891). However, logging between 1880 and 1920 (Clarkson 1964) almost completely eliminated these original forests. The red spruce forests that exist today are much more limited in extent (probably no more than about 24,000 ha) and commonly contain admixtures of various northern hardwoods, including yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and red maple (*Acer rubrum*) (Stephenson and Clovis 1983).

Balsam fir (*Abies balsamea*), often a co-dominant species with red spruce in the Northern Appalachians, reaches its southernmost limit in the Blue Ridge Mountains of northern Virginia (Adams and Stephenson 1985). There it occurs as a minor understory component in a few stands dominated by red oak (*Quercus rubra*) (Stephenson and Adams 1989). In West Virginia, the species is known from just four localities (Stephenson and Adams 1986). Fraser fir (*A. fraseri*), commonly a co-dominant species with red spruce at higher elevations in the Southern Appalachians, reaches its northernmost limit on Mount Rogers in southwestern Virginia, where it occurs as a dominant component of the tree stratum at the highest elevations (Stephenson and Adams 1984).

Interestingly, old-growth stands of red spruce that were never subjected to logging still exist at a limited number of localities in southwestern Virginia and eastern central West Virginia (Adams and Stephenson 1989). The best known of these are the War Spur stand in the Mountain Lake Wilderness Area in Giles County, VA, and the Gaudineer Scenic Area on Shavers Mountain in Randolph County, WV. The latter, which is actually a mixed red spruce/northern hardwood forest, is the most extensive old-growth example of this forest type in the Central Appalachians.

White and Eager (1984) reviewed the extensive body of literature on the status of Southern Appalachian red spruce (including spruce-fir) communities. However, relatively little has been published on the red spruce communities of the Central Appalachians (Stephenson and Clovis 1983). Pauley (1988) described the composition and structure of a second-growth red spruce forest in Pocahontas County, WV, whereas Adams and Stephenson (1989) examined old-growth red spruce communities at three localities in Pocahontas, Tucker, and Randolph Counties. The isolated red spruce communities in central and southwestern Virginia have never been studied intensively, and published reports are limited to those of Shields (1962), Stephenson and Adams (1984), and Rheinhardt (1984), all of which focused on the spruce-fir communities of Mount Rogers and adjacent areas. Other studies include those of Bailey and Ware (1990), who studied the red spruce forests of Highland County, and Adams and Stephenson (1991), who provided a general description of the red spruce forest type in Virginia. For the most part, published information on red spruce communities is found in brief notes (e.g., Chappell 1972).

A general pattern of growth-trend decline that began during the 1960s and early 1970s was documented for red spruce throughout eastern North America, including Virginia and West Virginia, in the latter part of the last century (Adams et al. 1985, McLaughlin et al. 1987, Stephenson 1987, Stephenson and Adams 1993, Hornbeck and Kochenderfer 1998). The exact cause of the observed decline is still not known, but both natural stand dynamics (e.g., competition among individual trees in an over-stocked stand) and various anthropogenic factors (e.g., acid deposition) have been suggested (e.g., Eagar and Adams 1992). Whatever the cause, any significant degradation of red spruce forests probably will have profound consequences for endemic wildlife and local biodiversity. For example, the red spruce forest type is the habitat for several sensitive and endangered species, among them the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*), restricted to high-elevation forests of the Central Appalachians across Virginia and West

Virginia (Ford et al. 2004, Menzel et al. 2006). Moreover, all known populations of the Cheat Mountain salamander (*Plethodon nettingi*) occur above 900 m in the mountains of four counties in West Virginia and are closely associated with this forest type (Pauley 1993, Dillard et al. 2008).

The overall objective of the studies we report herein was to obtain quantitative data on composition and structure of all strata of vegetation at the Virginia and West Virginia localities where the red spruce forest type occurs. However, the data presented herein are limited largely to the tree stratum.

THE GENERAL STUDY AREA

Forest communities with red spruce in Virginia and West Virginia occur within three general physiographic provinces from east to west: Blue Ridge, Ridge and Valley, and Appalachian Plateau. The high-elevation areas in the mountains of central and southwestern Virginia where red spruce occurs include portions of both the Blue Ridge and Ridge and Valley physiographic provinces of the Southern Appalachian Mountains (Fenneman 1938), whereas in eastern central West Virginia red spruce is limited to some of the higher areas of the Appalachian Plateau. However, the Appalachian Plateau occupies a considerably greater area than either the Blue Ridge or Ridge and Valley physiographic provinces. As such, the Appalachian Plateau has a larger variety of habitats where red spruce is found. These range from bogs and valleys to side slopes and ridgetops. Ridge and Valley localities are generally restricted to high-elevation ridges and upper slopes, are typically limited in extent (usually only a few hectares), and are isolated from one another. There are only a few localities (mostly high-elevation ridges but with red spruce also extending to upper side slopes and drainages) where red spruce is found in the Blue Ridge as well, although these localities support the largest and most extensive stands in Virginia.

Blue Ridge

The mountains of the Blue Ridge are located to the east of the Ridge and Valley province and consist of two rather distinct sections separated by the Roanoke River, the southernmost stream cutting through this ridge system. The northern section, separated from the ridges of the Ridge and Valley by the broad, flat Shenandoah Valley, is an irregular range of relatively rugged, broad-topped mountains that only occasionally exceed 1,200 m. The southern section consists of an elevated plateau deeply cut by stream valleys. The highest mountains in Virginia occur in this section of the Blue Ridge; two peaks (Mount Rogers and Whitetop) exceed 1,680 m. The Blue Ridge is composed primarily of metamorphosed igneous rocks.

Ridge and Valley

The mountain ridges of the Ridge and Valley province generally run in a southwest-northeast direction and form a relatively narrow belt along the western boundary of Virginia. These ridges are rather level-crested, often with steep slopes, and are usually capped with Clinch (Tuscarora) sandstone of Silurian age. The less resistant (mostly Ordovician) shales and limestones have eroded away, producing the intervening valleys. Elevations in the region generally range from 300 to 1,050 m, but many ridgetops exceed 1,200 m and a few reach heights in excess of 1,375 m.

Appalachian Plateau

In West Virginia, red spruce forests are found within the Allegheny Mountain Section of the Appalachian Plateau (Fenneman 1938). The mountains of this region tend to have broad, flat summits underlain by resistant sandstones and conglomerates, with shales and limestones exposed on side slopes (Core 1966). Much of this part of West Virginia is above 915 m in elevation, with the highest point (Spruce Knob in Pendleton County) reaching 1,480 m above sea level.

Climate

Climatological data for high-elevation areas in the mountains of central and southwestern Virginia and eastern central West Virginia are limited, but data from a U.S. Weather Bureau station established in November 1971 at the University of Virginia Mountain Lake Biological Station (elevation 1,168 m) in Giles County, give some indication of the climate of the general study area during the approximately 10 years immediately prior to the time that our sampling was carried out. The average annual precipitation, based on the period of 1972-1983, is 136.3 cm. The average monthly precipitation ranges from a low of 8.9 cm in August to a high of 14.8 cm in June. The mean annual temperature is 8.1 °C. Average monthly temperatures range from a low of -3.7 °C in January to a high of 18.5 °C in July. The lowest temperature of record is -31.7 °C, and the record maximum temperature is 31.1 °C. The average frost-free season is about 142 days (U.S. Department of Commerce 1972-1984). Data from the Cranberry Glades region (elevation 1,030 m) of Pocahontas County, WV, indicate similar climatic conditions, with a mean annual precipitation of approximately 130 cm, a mean annual temperature of 5.6 °C, and an average frost-free season of about 140 days (Darlington 1943). Canaan Valley (elevation 975 m) in Tucker County, WV, based on the information available for 1945-1964, is characterized by an average annual precipitation of 136 cm. Mean annual temperature is 8.1 °C and average monthly temperatures range from a low of -2.2 °C in January to a high of 18.4 °C in July. The frost-free period is relatively short, presumably because of cold-air drainage into the valley, and averages only about 92 days (Weedfall and Dickerson 1965).

MATERIALS AND METHODS

For most of the 67 stands considered herein, quantitative data on topographic variables and composition and structure of the tree stratum were obtained from sampling during the 1982 to 1984 field seasons. Some additional data were collected between 1992 and 2001. Thirty of the 67 stands are located in central and southwestern Virginia; 14 in the Blue Ridge physiographic province; and 16 in the Ridge and Valley or, in one instance, in a region of transition between the latter province and the Appalachian Plateau (Fig. 1). All 37 stands in West Virginia are located within the Allegheny Mountain Section of the Appalachian Plateau. Criteria for selection of the unit of vegetation (stand) actually sampled were that (1) vegetation be relatively homogeneous (with respect to floristics and plant structure) and at least 1 hectare in size; (2) topography of the area be uniform; (3) there be no obvious evidence that a major disturbance (e.g., logging, fire) had occurred during the lifetime of the trees sampled; and (4) red spruce be present in the tree stratum. We recorded slope inclination and aspect at several locations within each stand, and elevation was estimated using U.S. Geologic Survey 7.5-minute quadrangle maps, benchmarks, and obvious topographic features. In each stand, we recorded diameters at breast height (d.b.h., 1.37 m above ground level) of all live stems of trees (≥2.5 cm d.b.h.) in a single 20-m by 50-m (0.1 ha) quadrat. In two stands, both located on Spruce Knob of the Appalachian Plateau region, we used two 10-m by 10-m plots due to the high tree density and low biodiversity of the stands. We tallied stems of seedlings (individuals of tree species <1.0 m high) and shrubs (including vines) by species in either ten 1-m by 20-m, two 10-m by 10-m, or four 5-m by 5-m quadrats placed at regular intervals along a 50-m tape used to establish the center line of the larger quadrat. In most stands, we estimated percent cover of herbaceous plants, exposed rock, wood debris, and bryophytes from ten 1-m by 1-m quadrats spaced at 5-m intervals along the baseline tape. Cover values were determined with the use of a cover-class rating scale described by Daubenmire (1968). We also recorded any additional species not encountered within the quadrats but observed within the stand.

In most localities, we extracted cores at breast height from at least five representative larger red spruce trees to determine their approximate ages (*sensu* Adams et al. 1985). After cores were air dried, glued in grooved boards, and sanded, we counted growth rings using a binocular microscope.

We pooled quadrat data for each locality and calculated relative basal area and relative density values separately for size classes designated as trees (stems ≥10 cm d.b.h.) and small trees (stems <10 cm d.b.h. but ≥2.5 cm d.b.h.). For each locality, we calculated species importance value indices for trees and small trees as one-half the sum of relative basal area and relative density. Vascular plant nomenclature used herein follows Radford and others (1968), except that *Betula alleghaniensis* is used instead of *B. lutea*.

RESULTS AND DISCUSSION

Mean values for vegetation and site characteristics of red spruce stands sampled in each physiographic province are

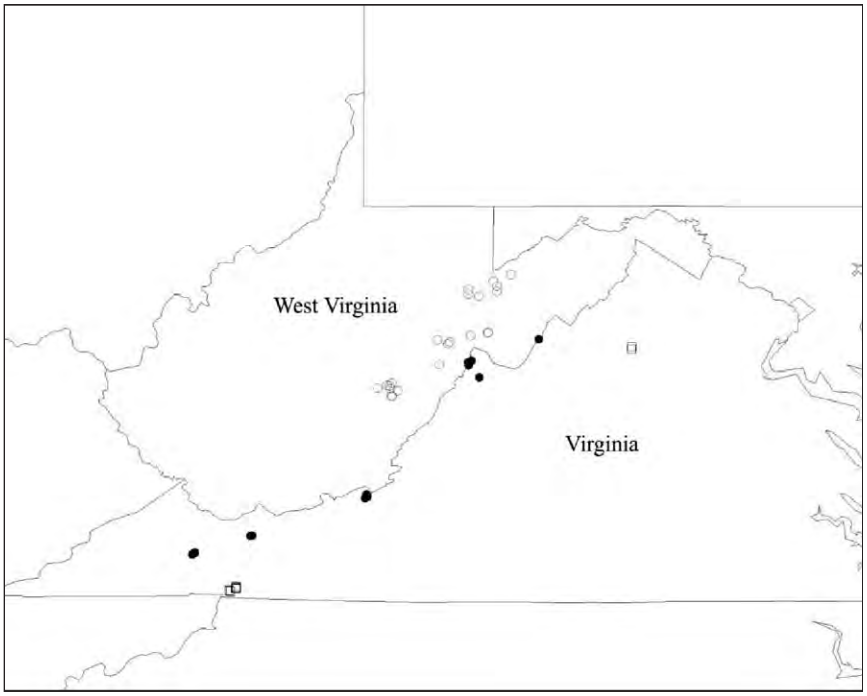

Figure 1.—General locations of stands sampled in southwestern Virginia and eastern central West Virginia. Note: squares = Blue Ridge, closed circles = Ridge and Valley, and open circles = Appalachian Plateau.

provided in Table 1. The highest average elevation (1,568 m) and slope inclination (20 percent) occurred in the Blue Ridge, whereas lowest values for these parameters (1,158 m and 11 percent, respectively) were recorded in the Appalachian Plateau. Based on values of aspect transformation, the Appalachian Plateau stands would seem to occur on drier (0.96) slope exposures on average than either the Blue Ridge (1.12) or Ridge and Valley (1.21), although values of other parameters measured or determined in each of the stands (e.g., bryophyte cover [41 percent]) suggest otherwise. Highest values for rock cover (22 percent), herbaceous cover (115 percent), tree density (899/ha), and small-tree density (842/ha) were recorded in the Blue Ridge Province. Conversely, richness of vascular plants (20 species) was lowest in this province. Lowest values for rock cover (2 percent), bryophyte cover (18 percent), small-tree basal area (1.19 m^2/ha), and sapling density (702/ha) were noted in the Ridge and Valley, although the highest value for tree basal area (44.7 m^2/ha) was calculated here. In fact, except for number of tree seedlings, the overall understory component in this province was less well developed than in the two other provinces. This result might suggest that stands in this province are, on average, more mature than those sampled in the Blue Ridge or Appalachian Plateau. The lowest values for basal area of trees and density of seedlings were recorded in Appalachian Plateau Province (35.2 m^2/ha and 32,698/ha, respectively). Generally speaking, values for tree density are comparable to those of hardwood stands we have sampled in the mid-Appalachian region, although basal areas are somewhat higher (Adams et al., personal observations; Rheinhardt and Ware 1984; Stephenson and Adams 1989). It is also interesting to note that the values recorded for small-tree density in all provinces were less than those recorded for trees, which is opposite the condition usually noted in mid-Appalachian hardwood forests (Adams et al., personal observation). It may be that the denser canopy coverage typical of red spruce stands hinders development of this stratum. Most certainly the dense cover suppresses red spruce saplings. The first two authors have determined age of small saplings (1 to 1.5 m tall) to be up to 75 years.

Thirty-two species of trees were tallied in the 67 stands sampled (Table 2). Red spruce, with an average importance value of 46.81, was dominant and the only species occurring in all stands. Its importance value ranged from 1.2 in a stand in the Fernow Experimental Forest to 100.0 in a second-growth stand on Cheat Mountain, both stands located in the Appalachian Plateau. Only four other species (yellow birch, eastern hemlock [*Tsuga canadensis*], Fraser fir, and balsam fir, in decreasing rank) had average importance values exceeding 5. Among species other than red spruce, yellow birch was the most consistently present species (occurring in 53 stands), red maple was present in 37 stands, hemlock was present in 32, and American beech and serviceberry (*Amelanchier arborea*) each occurred in 20 stands. Black birch (*Betula lenta*) and black cherry (*Prunus serotina*) were recorded in 19 and 17 stands, respectively. All other species (24) were present in ten or fewer stands; seven species were found as trees in only one stand each.

Of the 32 species recorded as trees, 10 occurred in all three regions, seven in two of the three, and 15 in only one region. Yellow birch was more consistently present in the Blue Ridge and Appalachian Plateau provinces, whereas red maple, eastern hemlock, and serviceberry were more consistently present in the Ridge and Valley and Appalachian Plateau provinces. The frequency of occurrence of American beech was proportionally comparable for all provinces, but that of black birch was greater in the Ridge and Valley and black cherry was more frequent in the Appalachian Plateau.

Eleven species were present in both the Blue Ridge and Ridge and Valley provinces. Of those, only white oak (*Q. alba*) did not also occur in the Appalachian Plateau. The Blue Ridge and Appalachian Plateau provinces had 12 species in common; of these, fire cherry (*Prunus pensylvanica*) and mountain ash (*Sorbus americana*) were not recorded in the Ridge and Valley province. Of the 14 species tallied in both the Ridge and Valley and Appalachian Plateau, four (sugar maple [*Acer saccharum*], cucumber magnolia [*Magnolia acuminata*], mountain holly [*Ilex ambigua*], and yellow-poplar [*Liriodendron tulipifera*]) were absent from the Blue Ridge province. The three species

Table 1.—Mean values for vegetation and site characteristics of red spruce stands sampled in the mid-Appalachians of Virginia and West Virginia. Note: n = 9-14 for the Blue Ridge, 14-16 for the Ridge and Valley, and 11-37 for the Appalachian Plateau. Species richness values are based on presence of all vascular plants recorded in plots.

Parameter	Blue Ridge Province	Ridge and Valley Province	Appalachian Plateau Province
Elevation (m)	1,568	1,244	1,158
Slope (%)	20	17	11
Aspect (°)	0-295	5-350	0-350
Transformed aspect[a]	1.12	1.21	0.96
Exposed rock (%)	22	2	6
Wood (%)	15	13	13
Stand age (yr)[b]	92	92	87
Tree basal area (m^2/ha)[c]	40.9	44.7	35.2
Tree density (N/ha)[c]	899	727	814
Small-tree BA (m^2/ha)[d]	1.77	1.19	1.76
Small-tree density (N/ha)[d]	842	443	588
Tree saplings (N/ha)[e]	3,131	702	1290
Tree seedlings (N/ha)[f]	138,300	158,990	32,698
Shrubs (N/ha)	7,261	4,368	6,741
Herb cover (%)	115	21	24
Bryophyte cover (%)	41	18	41
Species richness	20	25	25

[a] Beers and others (1966)

[b] Based on data at least 5 cored trees per stand where done, then averaged for all stands per province

[c] Stems ≥10 cm d.b.h.

[d] Stems 2.5-9.9 cm d.b.h.

[e] Stems <2.5 cm d.b.h. but ≥ 1 m tall

[f] Stems <1 m tall

Table 2.—Mean importance values for trees (stems ≥10 cm d.b.h.) within each of the three physiographic provinces and the overall mean importance value for all 67 stands.

Species	Blue Ridge Province (n = 14)	Ridge and Valley Province (n = 16)	Appalachian Plateau Province (n = 37)	All Stands (n = 67)
Picea rubens	42.5	63.4	41.3	46.8
Betula alleghaniensis	11.2	6.3	14.8	12.0
Tsuga canadensis	3.4	9.1	11.7	9.4
Abies fraseri	30.7	–	–	6.4
A. balsamea	–	–	10.1	5.6
Acer rubrum	0.1	5.3	6.5	4.9
Fagus grandifolia	1.0	2.4	5.0	3.5
Quercus rubra	6.3	4.3	<0.1	2.4
Prunus serotina	0.3	0.2	3.4	2.0
Betula lenta	0.3	3.0	2.0	1.9
Acer saccharum	–	<0.1	1.8	1.0
Amelanchier arborea	0.1	1.8	0.8	0.9
Sorbus americana	2.4	–	0.2	0.6
Acer pensylvanicum	0.4	0.6	0.4	0.5
Magnolia acuminata	–	0.5	0.6	0.5
Tilia heterophylla	–	–	0.7	0.4
Quercus alba	0.8	0.9	–	0.4
Ilex ambigua	–	0.7	<0.1	0.2
Prunus pensylvanica	0.1	–	0.2	0.1
Nyssa sylvatica	–	0.5	–	0.1
Magnolia fraseri	–	–	0.2	0.1
Sassafras albidum	–	0.3	–	<0.1
Acer spicatum	0.3	–	–	<0.1
Pinus strobus	–	0.2	–	<0.1
Hamamelis virginiana	–	0.2	–	<0.1
Alnus rugosa	–	–	0.1	<0.1
Crataegus sp.	–	–	<0.1	<0.1
Liriodendron tulipifera	–	<0.1	<0.1	<0.1
Fraxinus nigra	–	–	<0.1	<0.1
Carya tomentosa	–	0.1	–	<0.1
Castanea dentata	–	<0.1	–	<0.1
Fraxinus americana	<0.1	–	–	<0.1
Total Number of Species	16	21	22	32

(Fraser fir, mountain maple [*Acer spicatum*], and white ash [*Fraxinus americana*]) found only in the Blue Ridge tend to prefer more mesic conditions, whereas five of the six species (the exception being white pine [*Pinus strobus*]) found only in Ridge and Valley tend to favor less mesic situations. Of the six species of trees tallied only in the Appalachian Plateau, all but hawthorn (*Crataegus* spp.) typically have a preference for more mesic environments.

Overall, based on average importance values (IVs) for species represented in the tree stratum, the Blue Ridge and Ridge and Valley tree composition had a similarity value of 59.3 percent (based on 100 – [sum of differences in IV of all species]); the Ridge and Valley and Appalachian Plateau, 68.6 percent; and the Blue Ridge and Appalachian Plateau, 58.4 percent. The greater similarity of the Ridge and Valley and Appalachian Plateau provinces most likely can be attributed to their proximity to one another. It also is interesting to note that fewer species (16) were recorded in the tree stratum of the Blue Ridge than in either the Ridge and Valley (21) or Appalachian Plateau (22) provinces. In the Blue Ridge, only two species (red spruce and yellow birch) were tallied in 75 percent or more of all sampled stands, in the Ridge and Valley only one (red spruce) was this frequent, and in the Appalachian Plateau four species (red spruce, yellow birch, eastern hemlock, and American beech) were tallied in >75 percent of all stands. In every instance, the majority of species recorded were found in fewer than 25 percent of the number of sampled stands (12 in the Blue Ridge, 14 in the Ridge and Valley, and 10 in the Appalachian Plateau). Red spruce was the leading dominant in all three provinces. Fraser fir was the second-leading dominant in the Blue Ridge, owing to its abundance in six of seven stands on Mount Rogers. Yellow birch and hemlock shared roles as second- and third-leading dominants in the Ridge and Valley and Appalachian Plateau. Two other species (red maple and northern red oak) occupied important ecological positions in two provinces (the Blue Ridge and Ridge and Valley).

Eleven species shared the role of leading dominant in the 67 sampled stands, but only five species shared this role in the Blue Ridge, four in the Ridge and Valley, and nine in the Appalachian Plateau. Of the species tallied as leading dominants, only Fraser fir and northern red oak did not share that role in the Appalachian Plateau. Red spruce was the leading dominant in 32 stands, hemlock in nine, balsam fir in seven, Fraser fir in six, and yellow birch in five. Two species (northern red oak and black cherry) were the leading dominant in each of two stands, and four additional species were the leading dominant in one stand each.

Either yellow birch or red spruce was the second-leading dominant in just more than half of all stands studied. In addition, red maple occupied this position in the Ridge and Valley and Appalachian Plateau provinces, whereas American beech and eastern hemlock were also second-leading dominants in the Appalachian Plateau. One stand in the Appalachian Plateau had no second-leading dominant since all of the trees were red spruce. Although 12 species were recorded as second-leading dominants, only four of these were recorded in the Blue Ridge. The Ridge and Valley and Appalachian Plateau had nine and ten species, respectively. The leading dominants when yellow birch was the second-leading dominant were red spruce (five stands) and eastern hemlock (one stand) in the Blue Ridge; red spruce and eastern hemlock (one stand each) in the Ridge and Valley; and red spruce (six stands), eastern hemlock (two stands), and beech and sugar maple (one stand each) in the Appalachian Plateau. When red spruce was the second-leading dominant, leading dominants were Fraser fir (five stands) and yellow birch (one stand) in the Blue Ridge; hemlock (two stands) and yellow birch (one stand) in the Ridge and Valley; and balsam fir (five stands) and hemlock (two stands) in the Appalachian Plateau. These data suggest that it is not uncommon for a reciprocal relationship, with respect to leading dominant and second-leading dominant, to exist between red spruce and yellow birch and between red spruce and eastern hemlock.

The 67 stands sampled in the present study were similar in that all contained red spruce. As already noted, however, compositional differences were apparent when the groups of stands sampled in the three provinces were compared. Moreover, four basic subtypes of the red spruce forest type can be distinguished. These are (1) the red spruce-dominated (red spruce IV>60); (2) the bog type with two different expressions (eastern hemlock-dominated and balsam fir-dominated); (3) the Fraser fir type; and (4) the red spruce/hardwood admixture with two different expressions (northern hardwood and “oak”). The red spruce-dominated subtype occurs in all three physiographic provinces and typically is found on higher-elevation ridgetops and upper slopes. Red spruce had an average importance value of 85.6 in stands representing this subtype, although 16 other species were present at low importance values. The bog type red spruce community typically occurs at lower elevations in low-lying areas. The eastern hemlock-dominated bog type is found in all three provinces, although only one such stand was sampled in the Blue Ridge (Limberlost in the northern Blue Ridge in Shenandoah National Park). Eastern hemlock, red spruce, and yellow birch had a combined importance value of 88.0 in the eastern hemlock-dominated bog type. The balsam fir-dominated bog type, found only in the Appalachian Plateau province, is dominated by balsam fir, red spruce, eastern hemlock, and yellow birch (with a collective importance value of 89.5). Yellow birch is not as important as in the eastern hemlock bog type.

The Fraser fir/red spruce subtype is found only in the southern Blue Ridge province at Mount Rogers. The elevation of Mount Rogers exceeds that of any other mountain in Virginia and West Virginia. Mount Rogers is unique in that it is the only known location of naturally occurring Fraser fir outside of the Southern Appalachians of Tennessee and North Carolina. Fraser fir, red spruce, and yellow birch had a combined importance value of 94.2 in the Fraser fir/red spruce subtype, and only four other tree species were present. The northern hardwood/red spruce admixture subtype was not found in the Blue Ridge province and only one stand occurred in the Ridge and Valley province. Three species (yellow birch, American beech, and red spruce) had a combined importance value of 64.0 in this subtype. Collectively, five species (northern red oak, red maple, white oak, black birch, and red spruce) had an importance value of 85.3 in the “oak”/red spruce subtype community. These communities are not common and only one example of each was found in each of the three physiographic provinces.

In summary, montane coniferous forests containing red spruce are much less extensive today than they were in the late 19th century, and this forest type is now considered to be endangered (Noss et al. 1995). Management options are not as yet clearly defined but have been addressed in several recent studies (e.g., Hornbeck and Kochenderfer 1998, Schuler et al. 2002, Rentch et al. 2007). Subsequent research on natural stand dynamics in montane coniferous forests in the Central Appalachians could use the data presented herein as a baseline representing conditions more than 25 years ago.

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CHANGES IN CANOPY COVER ALTER SURFACE AIR AND FOREST FLOOR TEMPERATURE IN A HIGH-ELEVATION RED SPRUCE (*PICEA RUBENS* SARG.) FOREST

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Abstract.—The objective of this study is to describe winter and summer surface air and forest floor temperature patterns and diurnal fluctuations in high-elevation red spruce (*Picea rubens* Sarg.) forests with different levels of canopy cover. In 1988, a series of 10- x 10-meter plots (control, low nitrogen [N] addition, and high nitrogen addition) were established on Mount Ascutney, VT, to examine the influence of N fertilization on red spruce and balsam fir (*Abies balsamea* Mill.) forest N cycling, tree mortality, and forest growth. As a result of N addition to the plots, species mortality has occurred on the low N and high N plots with the control plots experiencing very little mortality. Consequently, the mortality experienced on the low N and high N plots reduced forest cover and created both patchy and open forest canopies. In 2002, we installed temperature probes on the existing high-elevation red spruce to begin describing surface air (2 cm above ground) and forest floor temperature (~ 2 cm below ground) patterns under different levels of canopy cover. In June 2006 we established four new 10- x 10-meter red spruce plots, girdling 50 percent of the trees in two plots and 100 percent in the other two plots to further test surface air and forest floor temperature ranges under an altered forest canopy. Summer diurnal fluctuations in surface air temperature were highest on the high N plots (9.5 °C to 12.8 °C) during all years except 2007, where the 100 percent girdled plots had the highest summer diurnal value, 19.7 °C. Winter diurnal fluctuations in surface air temperature were lowest on the high N plots for all years. Summer diurnal fluctuations in forest floor temperature were highest on the high N plots for all years, while the winter diurnal fluctuations in forest floor temperature showed little variability between plots. Summer mean maximum, mean minimum, and mean surface air and forest floor temperatures were higher on the high N and/or 100-percent girdled plots in any given year. Summer mean maximum air temperature was highly related to percent canopy cover ($r^2 = 0.94$, $p=0.006$). As a result of direct solar radiation and the hot air that reaches and heats the ground surface through gaps and open canopies, 1- or 2-year-old red spruce seedlings might be negatively affected.

INTRODUCTION

The degree to which seasonal surface air and forest floor temperature changes under different levels of canopy shading in red spruce (*Picea rubens* Sarg.) forests has not been described. In this study, the Mount Ascutney, VT, red spruce plots that were established in 1988 provide an opportunity to report seasonal surface air and forest floor temperature across plots with different levels of forest cover and forest floor characteristics (McNulty et al. 2005). Gap areas and forest canopy cover structure and composition influence how surface air and forest floor temperature means, maximums, minimums, and diurnal fluctuations are moderated (Balisky and Burton 1995). Duff thickness and soil moisture content have been shown to be secondary in controlling soil temperature. Percent canopy cover is the primary control on soil temperature in high-elevation Engelmann spruce (*Picea engelmannii Parry ex. Engelm.*)-subalpine fir forests (Balisky and Burton 1995). Forest canopy cover also controls forest floor litter accumulation and input that may in turn control red spruce regeneration

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and establishment by limiting the contact between seedling roots and available soil nutrients (Klein et al. 1991). Spruce is an important tree species for the wood products industry, especially in the Northeast, as well as an important habitat and food source for birds, porcupines, and other area wildlife (Hart 1959, McIntosh and Hurley 1964).

During the 1980s, high rates of spruce decline and mortality were observed across New England and the southern Appalachians (Bruck 1984, Nicholas et al. 1992, Aber et al. 1998), and over the past 20 years many papers have shown a direct link between experimentally applied nitrogen (N) and N saturation, and forest decline and mortality (Schaberg et al. 2002, Magill et al. 2004, McNulty et al. 2005). These forests have also shown a lack of red spruce seedling establishment after a disturbance, but there is evidence of increases in birch (*Betula* spp.) regeneration and density in red spruce forests that have significant gaps or open canopies (Perkins et al. 1988, Klein et al.1991). Other changes that can occur during and after forest mortality or disturbances include increases in sunlight at the forest floor due to a loss of canopy cover (Perkins et al. 1988), increases in the forest floor thickness (Klein et al. 1991), increases in nutrient loss through leaching and displacement (McNulty et al. 2005), and increases in soil temperature and decreases in soil moisture content (Balisky and Burton 1995). Nutrients are available for plant uptake only when there is enough moisture in the soil to bring them into solution, thus soil moisture is critically important in tree species regeneration, establishment, and growth.

Cloud immersion has been linked to maximizing photosynthetic carbon gains in spruce-fir forests (Reinhardt and Smith 2008), suggesting that changes in cloudy conditions due to loss of canopy cover and changes in climate may affect species productivity and sustainability over the long term. Increases in regional mean annual air temperature can also affect area red spruce forests by altering their species composition via upslope migration of lower elevation deciduous forests into higher-elevation conifer forests (Beckage et al. 2008). These increases in mean annual air temperature, coupled with canopy cover alterations or loss in forest canopy shading, may exacerbate or speed up the influence of surface air and forest floor temperature on soil moisture content and the rate at which deciduous and conifer species regenerate and establish in these forests. Temperature data in high-elevation red spruce forests that have experienced accelerated rates of mortality and decreased canopy shading are limited. Thus, the objective of this study is to report and describe changes in seasonal and yearly mean surface air and forest floor temperature in red spruce forests with varying degrees of canopy cover.

MATERIALS AND METHODS

In 1988, we established a series of 10- x 10-meter paired plots (two controls, low N addition, and high N addition) on Mount Ascutney to examine the influence of N inputs on red spruce and balsam fir (*Abies balsamea* Mill.) forest N cycling, tree mortality, and forest growth. (See McNulty and Aber 1993 for detailed methodology and site description.) The low N and high N plots have experienced tree species mortality while very little mortality has occurred on the control plots. Mortality on the low N and high N plots reduced forest cover, creating both patchy (60-percent cover) and open forest canopies (45-percent cover). Because of the variability in canopy cover, these plots provide a gradient of surface air, forest floor temperature characteristics, and light inputs. In 2002, we installed four temperature probes in a fan pattern on the existing high-elevation red spruce to begin describing surface air (2 cm above ground) and forest floor temperature (~ 2 cm below ground) patterns under different levels of canopy cover. In June 2006 we established and installed temperature sensors on four new 10- x 10-meter red spruce plots, girdling 50 percent (referred to as “girdled50”) of the trees in two paired plots and 100 percent (referred to as “girdled100”) in the other two paired plots to further test surface air and forest floor temperature ranges under an altered forest canopy. Canopy cover was estimated for each plot based on visual observations. Duff layers were estimated during sensor installation.

We used Hobo H8 outdoor 4-channel external temperature loggers (Onset Corporation, Bourne, MA) to measure surface air and forest floor temperature across the 10- x 10-meter plots. Temperature measurements were recorded continuously at 1-hour intervals and summarized as summer (defined as June, July, August) and winter (defined as December of the previous year, and January, February, March of the following year) mean maximums, mean minimums, means, and diurnal fluctuations on each plot. If temperature data values were missing due to battery or logger failure, we estimated the missing temperature values using a linear model that was developed between paired plots as long as the r^2 was at least 0.90 and $p < 0.001$. A model outside of these criteria was not used to estimate temperature data.

RESULTS

Estimates of canopy cover using visual observations varied across plots, ranging from 30 percent to 90 percent (Table 1). Estimates of the duff layers are based on field observations and are shown in Table 1.

Diurnal Fluctuation

Summer diurnal fluctuations in surface air temperature were highest on the high N plots (9.5 °C to 12.8 °C) during all years except 2007, where the 100-percent girdled plots had the highest summer diurnal value, 19.7 °C (Table 2). Winter diurnal fluctuations in surface air temperature were lowest on the high N and girdled plots, the plots with the lowest percent canopy cover. Summer diurnal fluctuations in forest floor temperature were highest on the high N plots for all years. Winter diurnal fluctuations in forest floor temperature showed little variability between plots (Table 2).

Mean Maximum Temperature

The pattern of summer mean maximum surface air temperature was similar to that for diurnal fluctuations, where the highest values occurred on the high N plots during all years except 2007; the 100-percent girdled plots had the highest mean maximum surface air temperature value, 32 °C (Fig. 1a). Winter mean maximum surface air temperature was lower on the low N plots during all years except 2003/04 (i.e., December 2003/January, February, March 2004) when compared to the other plots (Fig. 1b). Summer mean maximum forest floor temperature was always higher on the high N plots for all years (Fig. 1c). Winter mean maximum forest floor temperature was lower on the control plots than on the other plots (Fig. 1d).

Mean Minimum Temperature

Plots with the lowest summer mean minimum surface air temperature varied across years (Fig. 2a). Winter mean minimum surface air temperature was lowest on the low N plots during all years except 2003/04 when compared to the other plots (Fig. 2b). Summer mean minimum forest floor temperature was always lowest on the control plots, averaging 0.9 °C lower than the low N plots and 1.2 °C lower than the high N plots (Fig. 2c). Winter mean minimum forest floor temperature was always lower on the control plots than on the other plots (Fig. 2d).

Mean Temperature

Summer mean surface air temperature was highest on the high N plots during all years except 2007, where the 100-percent girdled plots had the highest mean surface air temperature value, 17.8 °C (fig. 3a). Winter mean surface air temperature was lowest on the low N plots during all years except 2003/04 when compared to the other plots (Fig. 3b). Summer mean forest floor temperature was always higher on the high N plots than on the other plots (Fig. 3c). Winter mean forest floor temperature was lower on control plots when compared to the other plots (Fig. 3d).

Table 1.—Characterization of canopy cover. Cover values are based on visual observations in a high-elevation red spruce forest, Mount Ascutney, VT. The 2007 data are also shown for the girdled plots because the treatment (girdled in 2006) did not take effect until 2007. Estimates of the duff layers are also shown.

		Estimated canopy cover[a] (%)	
Plots	Duff layer[b] (cm)	2006	2007
Control	10	75	na
LowN	5	60	na
HighN	5	45	na
Girdled50	10	90	65
Girdled100	10	80	30

[a] Canopy cover was estimated for each plot based on visual observations. All the trees that were girdled did not die, thus, there is some canopy cover on the girdled100 plots.

[b] Approximately 50% of HighN plot surface has exposed organic soil, patchy duff layer.

Table 2.—Summer and winter mean diurnal fluctuations in original control and N addition plots and new girdled plots in a high-elevation red spruce forest, Mount Ascutney, VT. Summer defined as June, July, and August and winter defined as December of previous year and January, February, and March of following year. na = not available.

		Surface air temperature (°C)					Forest floor temperature (°C)				
Season	[a]Year	Control	LowN	HighN	Girdled 50	Girdled 100	Control	LowN	HighN	Girdled 50	Girdled 100
Summer	2002	7.9	9.5	12.3	na	na	105	1.2	1.6	na	na
Summer	2003	7.7	9.6	9.9	na	na	1.2	1.3	1.6	na	na
Summer	2004	7.3	9.4	9.5	na	na	1.3	1.4	1.6	na	na
Summer	2005	7.3	10.4	11.9	na	na	1.3	1.6	1.8	na	na
Summer	2006	6.8	11.7	10.7	6.0	6.3	3.4	4.1	4.8	2.4	2.1
Summer	2007	7.7	12.8	12.8	9.4	19.7	4.2	4.6	5.9	3.3	4.7
Winter	2003/04	2.5	2.8	0.8	na	na	0.3	0.2	0.1	na	na
Winter	2004/05	1.8	1.2	0.2	na	na	0.5	0.1	0.1	na	na
Winter	2005/06	4.2	4.2	3.0	na	na	0.5	0.1	0.2	na	na
Winter	2006/07	3.6	2.9	2.1	3.2	1.8	1.1	0.4	0.6	0.5	0.5

[a] Data for 2002 is for August only.

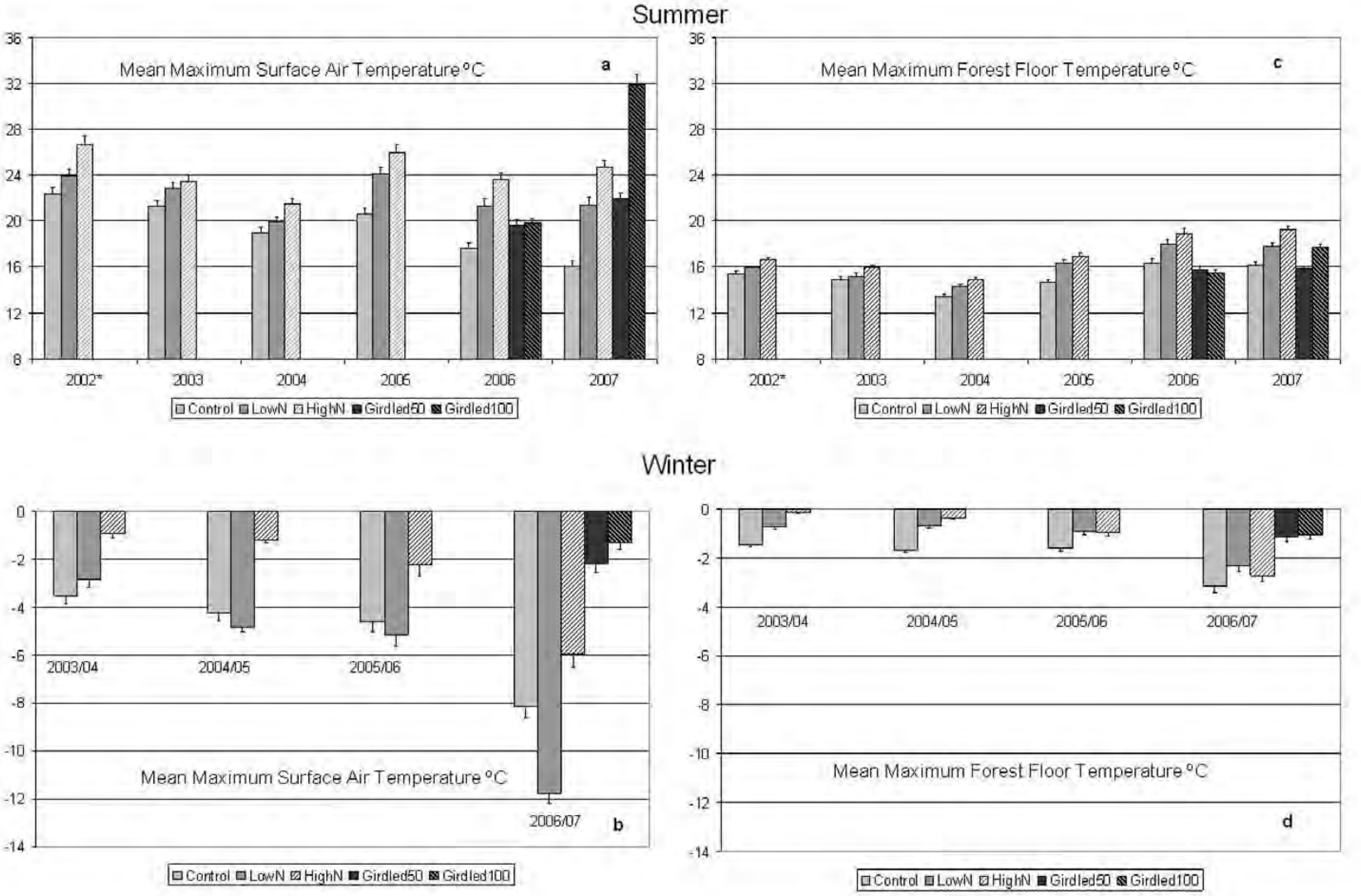

Figure 1.—Summer and winter mean **maximum** surface air and forest floor temperature in original control and N addition plots and new girdled plots in a high-elevation red spruce forest, Mount Ascutney, VT. Summer defined as June, July, and August and winter defined as December of previous year and January, February, and March of following year. *August 2002 only.

DISCUSSION

Summer and Winter Mean Maximum Temperature

We found the largest difference in summer mean maximum air temperature occurred in 2007 between the control and girdled100 plots, 15.8 °C. The largest difference in summer mean maximum forest floor temperature occurred in 2006 between the control and high N plots, 3 °C, suggesting that forest floor characteristics are moderating the effects of reduced canopy cover on summer mean maximum forest floor temperature by minimizing wide fluctuations. Research by Balisky and Burton (1995) found a 7- to 8- °C difference in daily mean maximum soil temperature when comparing the temperature in bare soil areas (no canopy cover) to areas covered with vegetation ranging from herbaceous to conifer trees 5 meters in height. Our summer mean maximum surface air and forest floor temperature patterns were fairly consistent across plots in that those with the lowest percent canopy cover (i.e., high N and girdled100) had the highest summer mean maximum surface air and forest floor temperatures during any year (Figs. 1a and 1c). The winter mean maximum surface air and forest floor temperatures were also consistent across plots, with the highest percent canopy cover generally having the lowest mean maximum surface air and forest floor temperatures in any given year (Figs. 1b and 1d).

Mean maximum temperatures are controlled by several factors including canopy cover, duff thickness, soil moisture, topographic shade, seasonal variations, air temperature, and other climatic and soil variables (Bonan 1991, Friedland et al. 2003, Rutherford et al. 2004). Solar radiation, air

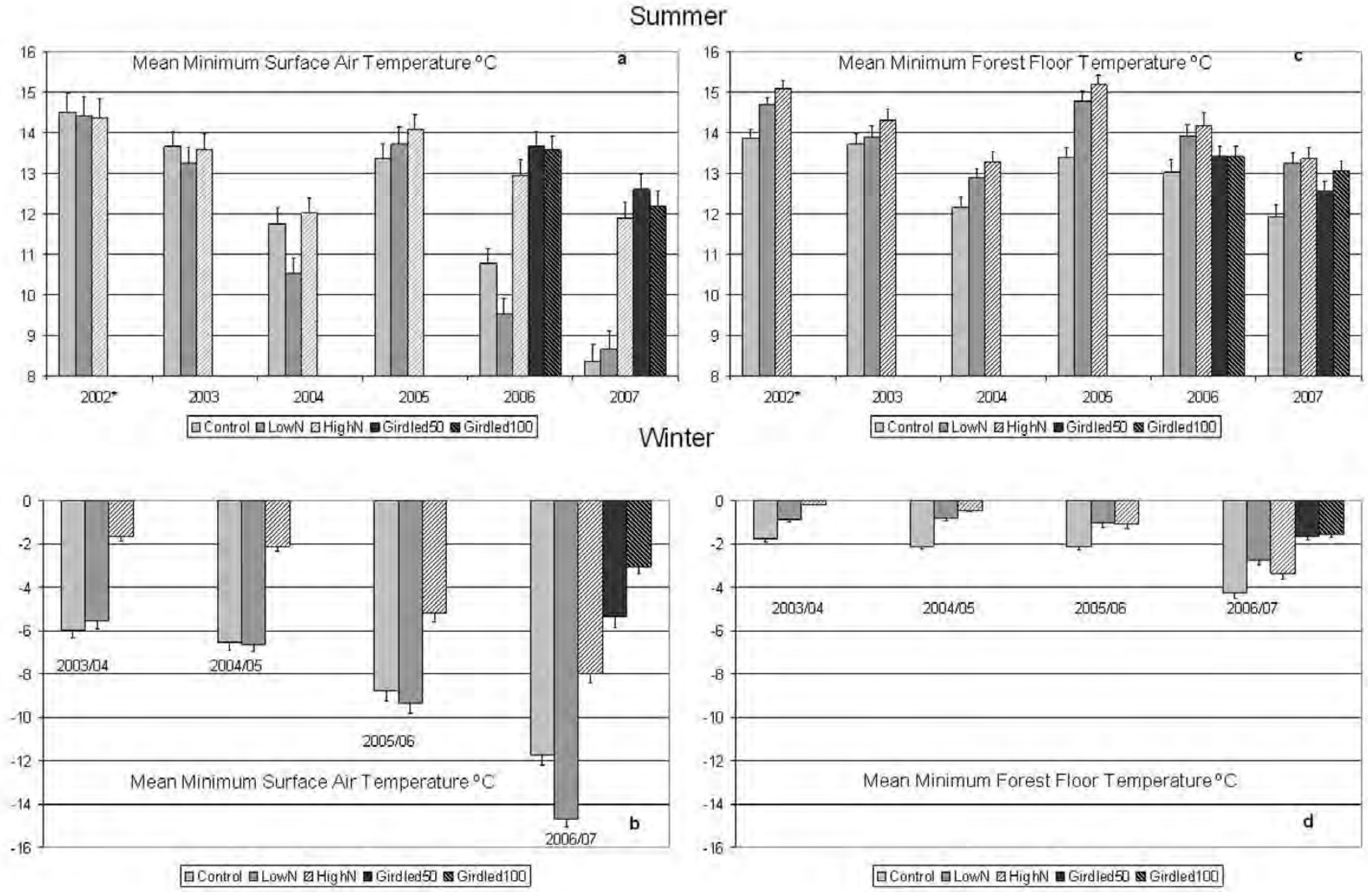

Figure 2.—Summer and winter mean **minimum** surface air and forest floor temperature in original control and N addition plots and new girdled plots in a high-elevation red spruce forest, Mount Ascutney, VT. Summer defined as June, July, and August and winter defined as December of previous year and January, February, and March of following year. *August 2002 only.

temperature, and topographic shape across the plots on Mount Ascutney were similar with some spatial microclimate and microsite differences (Geiger 1965). Our linear regression model suggests percent canopy cover is the principle control on summer mean maximum surface air temperature across all plots ($r^2 = 0.94$, $p = 0.006$); that is, components of the forest canopy structure are causing increases or decreases in summer mean maximum surface air temperature (Fig. 4a). In contrast, a mixture of canopy cover and non-canopy cover attributes (i.e., forest floor moisture and/or duff thickness) is probably controlling summer mean maximum forest floor temperature across plots as the relationship between percent canopy cover and summer mean maximum forest floor temperature ($r^2 = 0.33$, $p = 0.30$) is less connected than what was found between percent canopy cover and summer mean maximum surface air temperature (Figs. 4a and 4b).

Further evidence suggests that forest floor characteristics such as duff thickness and soil moisture are helping to moderate the effects of percent canopy cover on summer mean maximum forest floor temperature. For example, in 2007 the summer mean maximum surface air temperature was highest on the girdled100 plots, reaching 32 °C and accompanied by a summer mean maximum forest floor temperature of 18 °C (Figs. 1a and 1c). The high N plots had a summer mean maximum surface air temperature of only 25 °C and a summer mean maximum forest floor temperature of 19 °C (Figs. 1a and 1c). Although the girdled100 plots had a significantly higher summer mean maximum surface air temperature when compared to the high N plots, their summer mean maximum forest floor temperature was lower by 1 °C. The high N plots had a sparse intact duff layer and exposed organic soil, indicating the potential for high heat capacity and thermal conductivity.

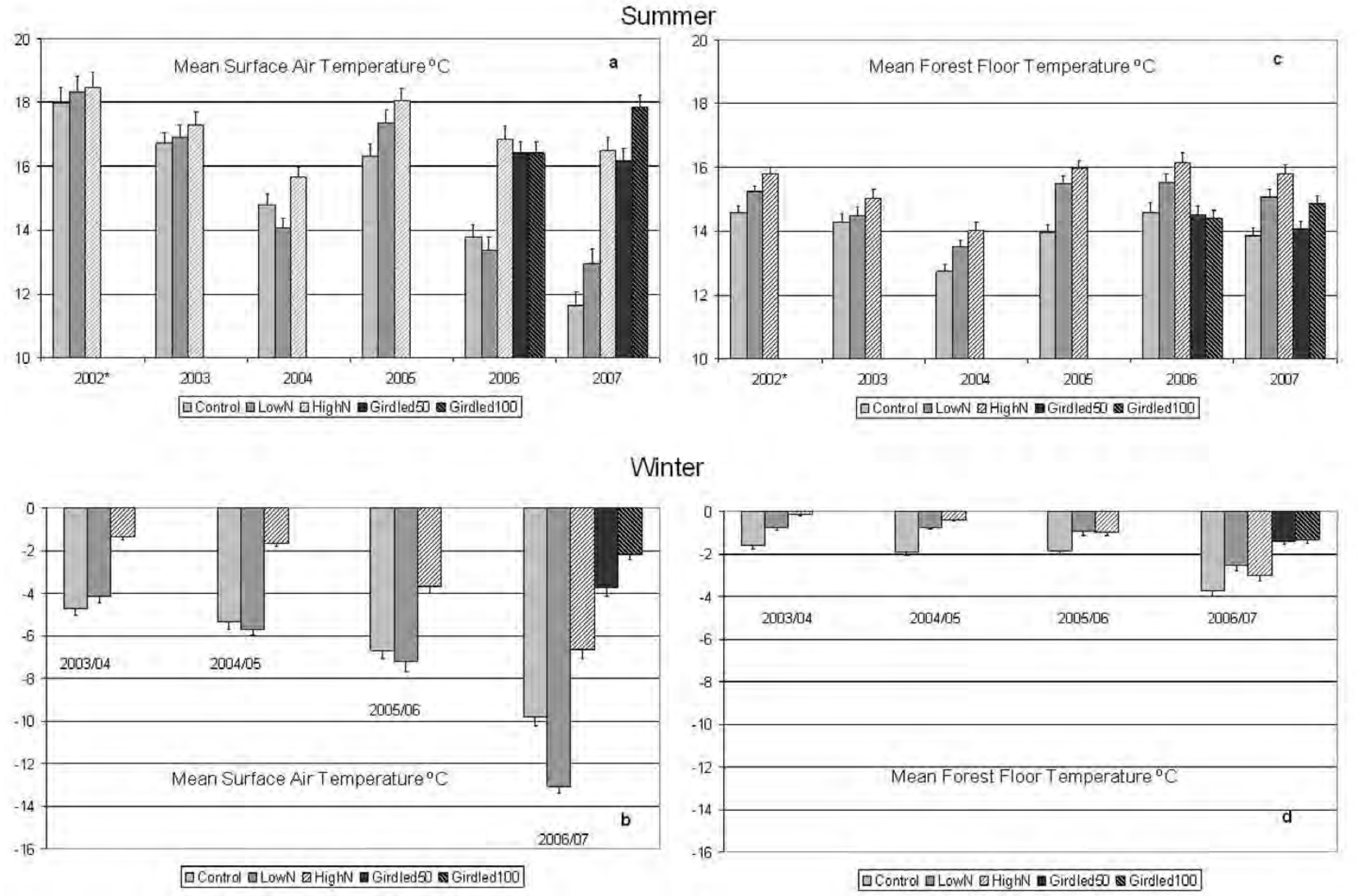

Figure 3.—Summer and winter mean surface air and forest floor temperature in original control and N addition plots and new girdled plots in a high-elevation red spruce forest, Mount Ascutney, VT. Summer defined as June, July, and August and winter defined as December of previous year and January, February, and March of following year. *August 2002 only.

Summer and Winter Mean Minimum Temperature

The summer mean minimum forest floor temperature in all years was higher than the summer mean minimum surface air temperature (Figs. 2a and 2c). This summer pattern in mean minimum temperatures was not surprising because the forest floor, having warmed up from the sun during the day, cools slower during the night than the surface air, resulting in slightly higher mean minimum temperatures.

Shading from the canopy cover had an effect on both winter surface air and forest floor temperature, with cooler temperatures occurring in the surface air (Fig. 2b) when compared to the forest floor (Fig. 2d). Forest floor temperature values were lower because components of the forest floor are buffering against the effects of extreme winter temperatures. Low soil temperature and winter temperature conditions have been studied to determine their relative role in species regeneration and establishment (Butt 1990, Friedland et al. 2003). Friedland and others (2003) and Vostral and others (2002) indicated that the lack of species establishment at higher elevations on Mount Ascutney is not due to winter temperature conditions but was maybe due to summer temperature controls. Summer soil temperatures ranging from 10 °C to 12 °C have been found to reduce conifer seedlings' growth potential (Vapaavuori et al. 1992). Our lowest summer mean minimum forest floor temperature occurred in 2007 on the control plots, 11.9 °C.

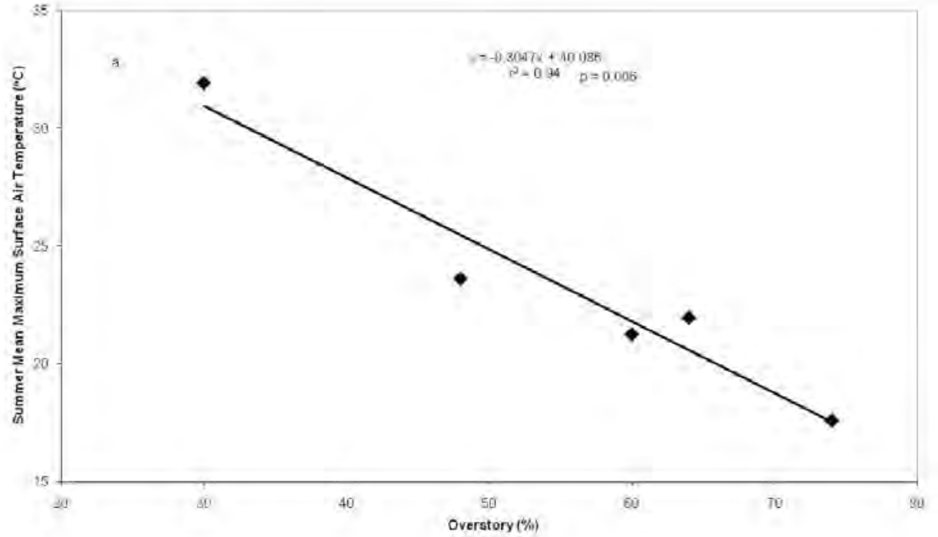

Figure 4a.—Regression analysis between estimated percent canopy cover and summer mean maximum surface air temperature across the original and girdled plots.

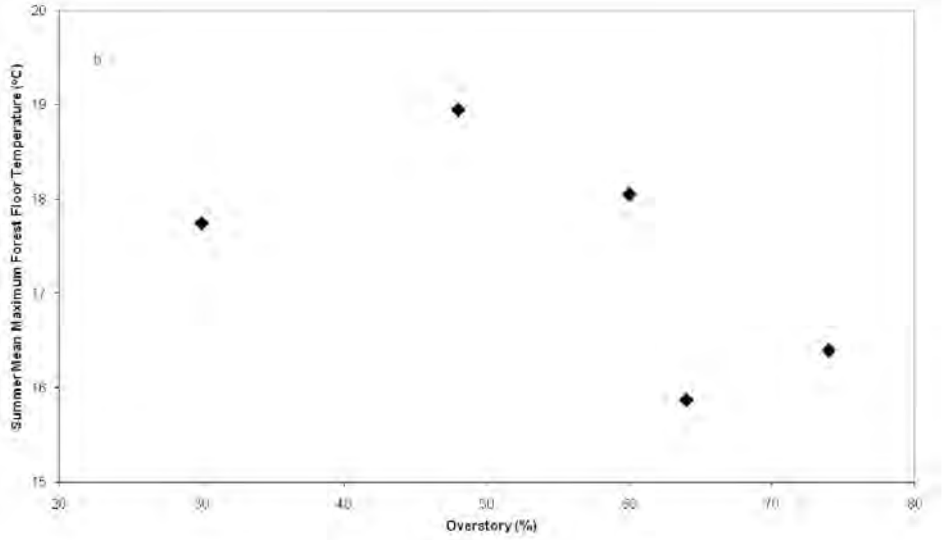

Figure 4b.—Relationship between estimated percent canopy cover and summer mean maximum forest floor temperature across the original and girdled plots.

Summer and Winter Mean Temperature

Our results showed that there were significant differences in summer mean surface air and forest floor temperature as a consequence of reduced levels of shade caused by species mortality on the original plots and tree canopy manipulation on the girdled plots (Figs. 3a and 3c). The most significant differences in the summer mean surface air temperature occurred between the control and girdled100 plots, with a difference of 5.5 °C in 2007. Summer mean forest floor temperature followed a similar pattern as the summer mean maximum forest floor temperature. The forest floor temperature on the high N plots was significantly higher than on the other plots. Plausible explanations for the summer mean air and forest floor temperature patterns are the same as outlined under the summer and winter mean maximum temperature section above.

CONCLUSIONS

Our results indicate that reductions in canopy cover in red spruce forests alter surface air and forest floor temperatures. However, surface air and forest floor temperatures respond differently to air temperature and radiation inputs. For example, our regression model showed that the relationship between percent canopy cover and summer mean maximum surface air temperature was more coupled than percent canopy cover and summer mean maximum forest floor temperature. This finding suggests that summer mean maximum forest floor temperatures were buffered by factors such as soil moisture content and duff thickness. In the long term, gaps in the forest canopy caused by species mortality may affect red spruce regeneration and establishment as seeds can be permanently damaged when exposed to temperatures higher than 33 °C (Hart 1965). A more detailed assessment of canopy cover using the fisheye method to estimate canopy openness may refine the relationship between canopy cover and temperature patterns. In addition, measurements of soil moisture regimes and microsite characteristics across our plots may help to explain how forest floor conditions are moderating canopy cover effects.

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STAND DYNAMICS OF RELICT RED SPRUCE IN THE ALARKA CREEK HEADWATERS, NORTH CAROLINA

Beverly Collins, Thomas M. Schuler, W. Mark Ford, and Danielle Hawkins[1]

Abstract.—Disjunct red spruce (*Picea rubens* Sarg.) forests in the southern Appalachians can serve as models for understanding past and future impacts of climate change and other perturbations for larger areas of high-elevation forests throughout the Appalachians. We conducted a vegetation and dendrochronological survey to determine the age, size class, and condition of extant red spruce and composition of co-occurring woody and herbaceous vegetation in the Alarka Creek headwaters basin on the Nantahala National Forest in Swain County, NC. Using 10-m-wide belt transects, we measured the diameter of overstory red spruce and nearby saplings and seedlings, cored them, and mapped their location. We also examined red spruce for evidence of insect infestation. We noted the presence of all other woody species and recorded the diameter of other overstory trees. At 20-m intervals, we cored an overstory tree (other than red spruce) and quantified the herbaceous vegetation using 5-m x 10-m plots. Large red spruce, which averaged 755 cm^2 in basal area per tree, made up 18 percent of canopy trees. Serviceberry and sweet birch dominated the remainder of the overstory at 36 percent and 18 percent, respectively. Overall tree density averaged 450 stems/ha with 242 cm^2 basal area per tree, or 10.89 m^2/ha basal area. Great rhododendron and mountain laurel dominated the shrub layer, with red maple and sweet birch seedlings present throughout. Red spruce has been continuously recruited for the past century and new seedlings are still being established. Dendrochronological analysis indicates growth decline in the 1930s, followed by persistent recovery to near expected levels until a decade ago. Recent growth declines coincided with a heavy regional outbreak of southern pine beetles (*Dendroctonus frontalis* Zimm.), which may or may not have caused the decline. Red spruce growth was insensitive to precipitation, but improved with warm fall (previous year October, current year September, October) temperatures. Our assessment indicates that the Alarka Creek headwaters harbor a second-growth red spruce component still capable of self-replacement and partially buffered by site characteristics from climatic perturbations despite its relatively low elevation and southern latitude.

INTRODUCTION

Disjunct forests at the southern range of red spruce (*Picea rubens* Sarg.) can help reveal impacts of climate change and other perturbations, thereby serving as models for understanding other red spruce forests throughout the Appalachians. One such relict forest occurs in the headwaters basin of Alarka Creek in Swain County, NC. Situated at roughly 1,220 m, this site is among the southernmost and lowest-elevation forests with red spruce in the southern Appalachians (White and Cogbill 1992). Canopy red spruce trees occur along the periphery and are scattered throughout the basin. The basin itself is a forested wetland with gullied topography created by a network of small streams.

Previous research (Webb et al. 1993) has shown that red spruce in small, disjunct bog populations in New Jersey were longer-lived and more productive than those in adjacent upland populations. Although tree ring chronologies showed growth declines beginning in about 1975, the bog populations showed no climate sensitivity. In contrast, two

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upland populations appeared sensitive to spring and summer drought, with better growth in years with a wet March, wet June, or warm January. The authors suggest bogs offer a refugium from drought in the central Appalachians. At the southern distribution of red spruce, low-elevation bogs and other wetlands also might provide protection from drought or cloud- and fog-borne pollution, but perhaps only in sites where cold air drainage alleviates potential warm temperature stress. Red spruce is adapted to cool, shaded conditions (e.g., Alexander et al. 1995, Dumais and Prevost 2007). For example, understory red spruce exhibited maximum net photosynthesis rates between 15 and 20 °C; higher temperatures reduced photosynthesis rates and increased respiration rates (Alexander et al. 1995). These responses could lead to reduced growth rates or production in southern, low-elevation sites.

We conducted a vegetation survey to examine the size class and condition of extant red spruce and composition of co-occurring woody and herbaceous vegetation in the Alarka Creek headwaters basin. In addition, we used dendrochronology methods to determine age and history of red spruce in the basin. We asked: Is there evidence of a recent (post-1960) spruce decline or sensitivity to annual variation in temperature and precipitation as shown in high-elevation and more northern populations (e.g., McLaughlin et al. 1987)?

METHODS

The Alarka Creek headwaters basin (35°19'58" N; 83°21'35" W; Fig. 1), in the Big Laurel area of the Nantahala National Forest in Swain Co., NC, was acquired as part of a larger tract (ca. 900 ha) by the U.S. Forest Service in the 1990s. Monthly mean temperatures range from 1.4 °C in January to 22.1 °C in July; annual precipitation is 123 cm (data for 1971-2000 Swain County from National Climate Data Center, Asheville, NC). Elevation in the area ranges from 1,097 to 1,340 m. The basin encloses braided small stream channels, which have formed a network of gullies. Canopy red spruce and hardwoods are scattered, forming an incomplete cover over a patchy shrub layer of laurel. The surrounding Big Laurel area was logged at least once, and parts may have been logged twice, during the 1900s (Mike Wilkins, U.S. Department of Agriculture, Forest Service, pers. comm.), but there are no known records for the basin.

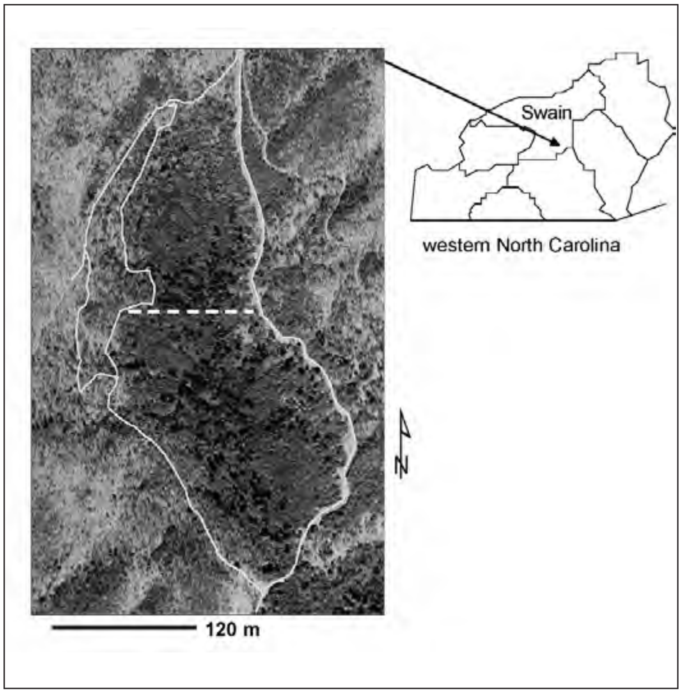

Figure 1.—Location and aerial photo of the Alarka Creek basin, showing trails (gray lines) and a representative sampling transect (dashed white line).

We surveyed the vegetation in the basin in summer 2007, using five 10-m-wide belt transects that were spaced 100 m apart along the long axis and extended across the short axis of the basin (Fig. 1). Transect lengths varied with width of the basin: T1 = 120 m, T2 = 100 m, T3 = 120 m, T4 = 80 m, and T5 = 85 m, for a total of 5,050 m^2, or 0.51 ha sampled. Within each transect, we measured tree diameter at breast height (d.b.h., 1.37 m above ground), cored, and mapped the location of overstory red spruce (>10 cm d.b.h.). Trees were cored at breast height with an increment borer; a single 0.52-mm core was removed from each tree. We also examined red spruce for evidence of insect infestation. We recorded height of spruce saplings and seedlings (<10 cm d.b.h.) and measured distance to the nearest overstory tree. We noted the presence of all other woody species and recorded the diameter of other overstory trees. At 20-m intervals along each transect, we cored an overstory tree (other than red spruce) at breast height and recorded presence of shrub and herbaceous species in a 5-m x 10-m plot for a total of 33 plots (or 1,650 m^2) sampled. We report shrub and herbaceous species occurrence as frequency or percent of the 33 plots.

Standard techniques of dendrochronology were used to process the tree cores (Fritts 1976). We used a Velmex tree-ring measuring system calibrated to 0.01 mm for the physical measurements. The samples were first validated by measuring each core twice and comparing the results graphically for measurement inconsistencies. We attempted to cross-date individual tree ring series using the same methodology. However, some apparent pattern inconsistencies could not be resolved as measurement errors or ring anomalies. We speculate that competitive interactions among individual trees may have weakened the response to climate. We caution the reader to recognize that our inability to positively resolve some annual dates may have degraded our ability to model the long-term growth and climate relationship. The series were analyzed using COFECHA to test the quality of the cross-dating (Holmes 1983). The computer program ARSTAN was used to develop a standardized chronology. ARSTAN uses time-series modeling to produce chronologies with reduced error variance by minimizing the age-trend and small-scale disturbance signals (Cook and Holmes 1986). We used negative exponential or straight line curve fits for most series to preserve the low-frequency variation, such as the potential climate signal and synchronous disturbance signals. We report both the raw and residual ARSTAN chronologies so that readers may better understand the nature of the chronology signal retained from the original unfiltered data. Because of the small sample size for earlier periods of the chronology, results should be interpreted with caution prior to about 1930.

Monthly mean surface air temperature and precipitation data for the western North Carolina region (Division 1) from 1894 through 2006 were obtained from the National Climate Data Center in Asheville, NC. We used Dendroclim2002 (Biondi and Waikul 2004) to examine the relationship between the residual red spruce chronology and climate over time. This program computes response functions, or coefficients of a multivariate Principal Components Analysis. We determined response functions using a forward 30-year "evolutionary window" beginning with the oldest samples and applying increments over time.

RESULTS

Red spruce was distributed over the range of sapling to canopy tree sizes, had greater representation than hardwoods in the larger (>45 cm d.b.h.) size classes, and was the largest (91 cm d.b.h.) tree in the sampled area (Fig. 2A). Red spruce trees averaged 31 cm d.b.h. (755 cm^2 per tree, 451 m^2/ha basal area) and composed 18 percent of canopy trees.

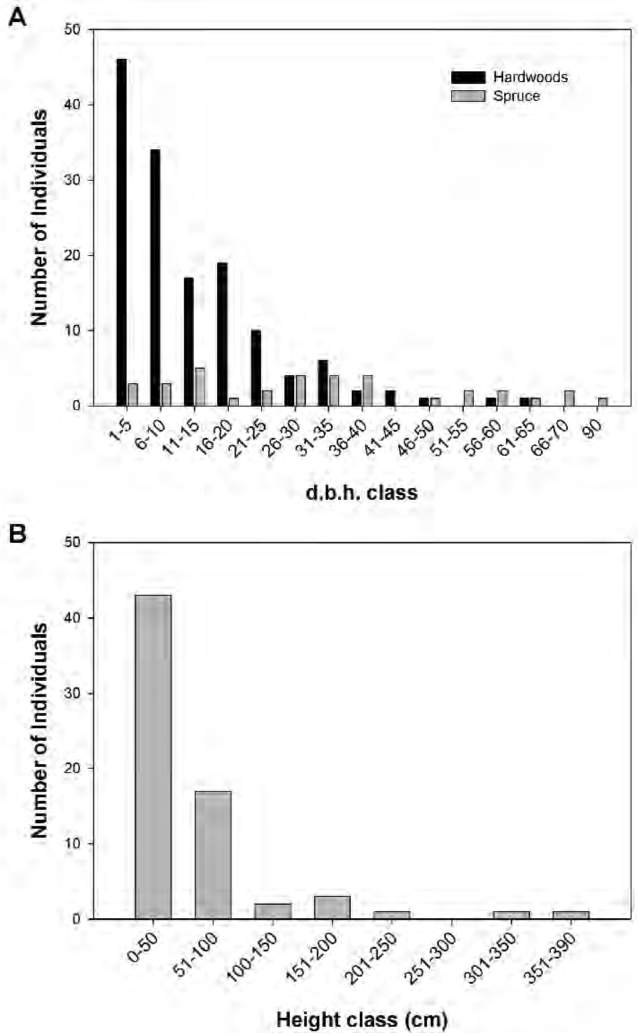

Figure 2.—A: Total number per 0.51 ha (summed over all transects) of hardwoods and red spruce in each of 14 size (d.b.h.) classes. B: Number of red spruce seedlings in each of eight height classes.

American serviceberry (*Amelanchier arborea* Michx.) (52 trees, 36 percent) and sweet birch (*Betula lenta* L.) (25 trees, 18 percent) made up more than 50 percent of the remaining trees in the sampled area; other species included red maple (*Acer rubrum* L.), common winterberry (*Ilex verticillata* [L.]) A. Gray), Fraser's magnolia (*Magnolia* fraser Walt.i) and white oak (*Quercus alba* L.). Many individuals of these species exhibited wetland or resprout growth form, with multiple-stemmed trunks. Overall tree density averaged 450 stems/ha with 242 cm^2 basal area per tree, or 10.89 m^2/ha basal area. Great rhododendron (*Rhododendron maximum* L.) (11 percent) and mountain laurel (*Kalmia latifolia* L.) (3 percent) made up the shrub layer, which was patchy and primarily on gully tops. The ground layer was a mixture of herbs, including *Trillium* species (primarily painted trillium [*T. undulatum* Willd.] and wake-robin [*T. erectum* L.] at 5 and 2 percent, respectively), *Sphagnum* moss (5 percent), wood fern (*Dryopteris marginalis* [L.] A. Gray) (3 percent), and tree seedlings of red maple and sweet birch at 7 and 3 percent, respectively. Red spruce seedlings and saplings (N = 68) in the sampled area averaged 64 cm in height, were distributed over height classes from less than 50 cm to almost 4 m (Fig. 2B), and, on average, were 6.4 m from a red spruce tree.

Tree ring analysis of 32 cores (mean age = 64 years) dated the oldest red spruce core to 1855. Linear population structure suggests nearly steady recruitment over the last 100 years (Fig. 3A). A significant (P = 0.001, r^2 = 0.41) linear relationship exists between tree age and d.b.h. (d.b.h. = 7.444 + 0.378 * age). Individuals present before 1995 likely were below the 10-cm d.b.h. threshold for coring and were included in the seedling survey. No relationship was found between tree age and distance from the edge of the basin (P = 0.92). There was, however, a weak positive (r^2 = 0.08; P = 0.07) relationship between d.b.h. and distance from the edge; the larger trees tended to be in the middle of the basin.

The raw tree chronology shows a sharp drop in growth in the 1930s (Fig. 3B); in the residual chronology, growth in each year between 1930 and 1933 was less than the year before. An apparent age-related decline in the raw chronology is not seen in the residual chronology for 1933 to 1993. Subsequently, an abrupt synchronous decline began in 1994, with recovery after 2003 evident in both the raw and ARSTAN residual chronologies (Fig. 3B). Ring widths showed no significant response to precipitation or the Palmer Drought Severity Index, but there was a significant positive response to previous year October, current year September, and current year October temperatures (Fig. 4).

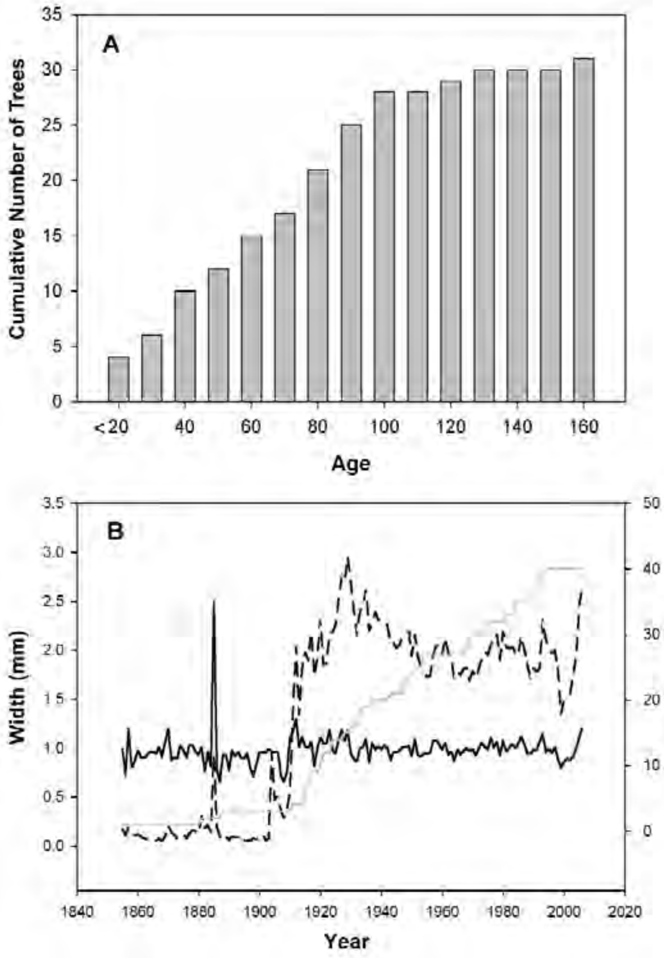

Figure 3.—A: Cumulative age distribution of red spruce cores. B: Raw (dashed line) and ARSTAN residual (solid black line) red spruce chronologies and sample number (solid gray line) over years.

DISCUSSION

Dendroecological studies of high-elevation red spruce in the Southern Appalachians show slower growth periods from 1850-1870 and after 1965, with above-average growth between 1900 and 1950 (Cook and Zedaker 1992). Tree ring chronology for red spruce in the Alarka basin indicates recruitment and growth beginning about 1915. Rather steady recruitment followed, suggesting the relatively low-elevation basin has offered protection from, or been resistant to, changes in atmospheric deposition and regional climate. However, an abrupt drop in red spruce growth in the 1930s correlates well with continental extreme drought conditions (Herweijer et al. 2007), although annual regional precipitation hovered around the average (114 cm) for most years between 1930 and 1940. We did not detect a post-1960 decline linked to climate. The second abrupt drop of spruce growth in the late 1990s coincides with a heavy regional outbreak of southern pine beetles (*Dendroctonus frontalis* Zimm). We cannot be certain whether the beetles were the causative agent, but southern pine beetles have been reported as a "serious pest" of spruce (Murphy 1917), were responsible for widespread destruction of spruce in West Virginia (Murphy 1917), and killed spruce trees in western North Carolina (McNulty 2009). Red spruce growth in the Alarka basin recovered rapidly, and damage possibly due to pine beetles was noted on only 20 percent (7 of 35 trees) during the vegetation sampling in 2007.

In high-elevation forests of the Northeast, above-average temperatures from 1925 (prior November, current July temperatures) or 1945 (prior August, December temperatures) through 1960 appear beneficial to red spruce growth (Cook and Zedaker 1992). In the Alarka basin, warm previous- and current-year fall (October) temperatures appear beneficial to growth, but red spruce growth was insensitive to monthly precipitation.These results suggest the basin provides protection from summer temperature stress and drought, whereas warm fall temperatures prolong the growing season.

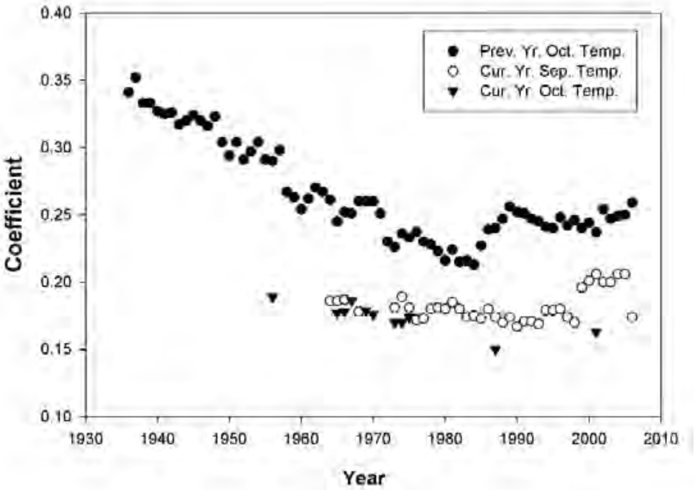

Figure 4.—Significant response values (coefficients) for average monthly temperature effects on residual chronology.

Although red spruce makes up less than 20 percent of the trees, they constitute most of the largest trees in the Alarka basin. Red spruce and hardwoods, including American serviceberry and sweet birch, are scattered throughout the basin, amidst a shrub-layer canopy of great rhododendron and mountain laurel. The presence of red spruce seedlings and saplings distributed over height classes from less than 50 cm to almost 4 m suggests that red spruce is still capable of self-replacement in the basin. In addition, positive growth response to warm September and October temperatures and recovery from the possible pine beetle outbreak indicate that larger, canopy red spruce trees generally have remained robust. The concave basin clearly provides cold air drainage, i.e., a favorable microclimate with protection from summer temperature and drought stress (Murphy 1917).

Persistence of red spruce through past climate fluctuations at the relatively low-elevation Alarka basin suggests higher-elevation populations, especially those in more sheltered landforms, may persist under future climate regimes in the southern and central Appalachians. Our results demonstrate, however, that exogenous disturbances such as insect outbreaks can rapidly alter long-term growth patterns and could lead to community replacement even though conditions are otherwise favorable for growth. Continued monitoring of vulnerable communities, such as the Alarka Creek red spruce community, is a crucial step for developing climate change strategies and deciding when and where to implement them. With continued monitoring, land-use practices that maintain favorable environmental conditions, and avoidance of stochastic stand-altering disturbances such as wind or ice storms, Alarka and similar scattered concave basins should continue to harbor low-elevation red spruce populations in the Southern Appalachians in the near term.

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HISTORICAL RECONSTRUCTIONS OF HIGH-ELEVATION SPRUCE FORESTS IN THE APPALACHIAN MOUNTAINS

Carolyn A. Copenheaver[1]

Abstract.—The objective of this study was to determine whether the historical distribution of a small, high-elevation red spruce stand could be reconstructed based upon historical records. The study site was Giles County, VA, where a small stand of red spruce exists today, indicating that it has been in this location for as long as the written record exists for this region. Working through three approaches, I attempted to locate this stand within public land survey records and their associated witness trees, historical photographs, and government documents. Each dataset originates from a different time period: the survey records from the early 1800s, the photographs from the late 1800s, and the government documents from the early 1900s. The witness-tree record from the land surveys contained no evidence that red spruce was present in Giles County. In the historical photographs, only three photographs out of 237 showed red spruce, and in the government documents there was no evidence of red spruce. These results indicate that in historical reconstructions of vegetation, it is highly likely that small populations will be missed. These reconstructions should be viewed as generalized representations of the forest communities of the past rather than thorough reconstructions.

INTRODUCTION

Historical reconstructions of vegetation allow land-use historians to set current vegetation conditions within a context of past vegetation, allow ecologists to witness the successional changes on the landscape, and provide land managers with a better understanding of the cause-and-effect of human activities on vegetation dynamics (Russell 1997). Reconstructing vegetation typically provides the most accurate representation of past vegetation when multiple data sources are combined. However, most reconstructions tend to focus on large, landscape-level trends with an accurate reconstruction at the stand level or examination of rare species. Therefore the objective of this project was to take a known entity and see whether it was identifiable in the historical record. Specifically, I worked with a small red spruce stand on the top of Salt Pond Mountain in Giles County, VA, and attempted to find references to it in the witness trees recorded in the public land surveys collected in the early 1800s, historical photographs taken in the late 1800s, and government documents describing the forest conditions in Giles County from the early 1900s. Results from this project will have important implications for management and conservation of high-elevation spruce-fir communities in the Appalachian Mountains (Foster et al. 1996).

STUDY AREA

Giles County is located in southwestern Virginia along the West Virginia border. The county was established as a political entity in 1806 and much of the early settlement was centered around agriculture. Almost 100 years later, natural resource extraction followed once the railroads entered the region. The major resources exported from Giles County were timber and limestone because the area lacked the coal resources common to other regions in the southern Appalachian Mountains (Copenheaver et al. 2007). The highest mountain in the county is Salt Pond Mountain, home to a small population of red spruce (*Picea rubens* Sarg.).

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METHODS

Three hundred fifty-four deed descriptions were transcribed from publicly available deed books located at the Giles County Courthouse in Pearisburg, VA. These deeds dated back to 1806-1830 and all deeds included metes-and-bounds descriptions of the parcel(s) of property exchanged. From these descriptions, witness trees (trees that "witness" the property corner) were tallied to identify species composition in Giles County from this early settlement period. Particular emphasis was placed on collecting deeds from the Mountain Lake area to increase the likelihood of including red spruce in the witness tree sample. In addition, 237 historical photographs taken by J.C. Porter in the 1880s and archived in Virginia Tech's Special Collections were examined for the presence of red spruce. A magnifying lens was used to assist with the identification, and two researchers verified identification of the red spruce. Last, two historical government assessments of the forest resources of Giles County were examined for references to red spruce (Snidow and McComas 1927, Humbert 1929).

RESULTS

According to the witness trees recorded in the Giles County deed records, the dominant tree species found in the county in the early 1800s were: white oak (*Quercus alba* L.), northern red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.), hickory (*Carya* spp.), chestnut oak (*Quercus prinus* L.), yellow-poplar (*Liriodendron tulipifera* L.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and scarlet oak (*Quercus coccinea* Muenchh.). Less dominant, but still relatively common, tree species included: ash (*Fraxinus* spp.), basswood (*Tilia americana* L.), beech (*Fagus grandifolia* Ehrh.), birch (*Betula* spp.), blackgum (*Nyssa sylvatica* Marsh.), black walnut *(Juglans nigra* L.), buckeye (*Aesculus flava* Aiton), chestnut (*Castanea dentata* (Marsh.)Borkh.), cucumber (*Magnolia acuminata* (L.)L.), dogwood (*Cornus florida* L.), ironwood (*Carpinus caroliniana* Walter), black locust (*Robinia pseudoacacia* L.), pine (*Pinus* spp.), post oak (*Quercus stellata* Wangenh.), sassafras (*Sassafras albidum* (Nutt.)Nees.), serviceberry (*Amelanchier* spp.), sycamore (*Platanus occidentalis* L.), and white walnut (*Juglans cinerea* L.). "Spruce pine" was mentioned three times, but an examination of common names from this period demonstrates that this was likely a reference to Virginia pine (*Pinus virginiana* Mill.) and not red spruce.

Among the 237 historical photos, only three showed red spruce. Two of these photographs were identified as being along Kimberling Creek (far from the current population of red spruce) and one, on Salt Pond Mountain (near the current population of red spruce).

The Humbert (1929) document identified spruce as a component of the chestnut ridge type, but this forest type was also characterized as being on exposed ridges, drier soils, and burned-over sections. These latter characteristics do not match the known silvical characteristics of red spruce. The Snidow and McComas (1927) document was the source of the Giles County forest description included in the Humbert (1929) document. Snidow and McComas (1927) described the chestnut ridge type as having "scrub or spruce pine," rather than the "spruce" recorded in Humbert (1929). Therefore, Humbert's (1929) reference to spruce was a typographical error rather than a true inclusion of red spruce in that forest type.

DISCUSSION

The presence of a small population of red spruce on the top of Salt Pond Mountain was undetectable in both the witness-tree record and the government documents, but the historical photographs revealed red spruce in Giles County, VA. The absence of this species from some information sources implies that when attempting to reconstruct historical species distributions or forest types known to be rare, we must employ multiple historical documents because each historical source comes with its associated biases (Black and Abrams 2001). By combining different sources, we can offset the biases inherent in a given dataset.

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MAINTENANCE OF EASTERN HEMLOCK FORESTS: FACTORS ASSOCIATED WITH HEMLOCK VULNERABILITY TO HEMLOCK WOOLLY ADELGID

Mary Ann Fajvan and Petra Bohall Wood[1]

Abstract.—Eastern hemlock (*Tsuga canadensis* [L.]) is the most shade-tolerant and long-lived tree species in eastern North America. The hemlock woolly adelgid (*Adelges tsugae*) (HWA), is a nonnative invasive insect that feeds on eastern hemlock and Carolina hemlock (*Tsuga caroliniana* Engelm.). HWA currently is established in 17 eastern states and is causing tree decline and wide-ranging tree mortality. Our data from West Virginia and Pennsylvania suggest that hemlock crown vigor (a ranking of amount of live crown) relates to a predictable pattern of hemlock vulnerability at light and moderate levels of HWA infestation. We found that crown variables, such as live crown ratio and crown density and transparency, are accurate predictors of hemlock decline; more vigorous trees appear to be less vulnerable to HWA. Thus, silvicultural thinning treatments may be a means for reducing stand densities and increasing crown vigor in colder areas where climate may slow HWA spread.

INTRODUCTION

The hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) is native to Asia and to western North America, where it has rarely exhibited outbreak dynamics on western hemlock species. HWA was first observed in eastern Virginia in 1951, and has since rapidly expanded its range. It is now found in 17 eastern states from southern Maine to northern Georgia, coinciding with the range of eastern hemlock (*Tsuga canadensis* [L.] Carr.) (Souto et al. 1996), its primary host, and Carolina hemlock (*T. caroliniana* Engelm.). Variations in the rates and direction of expansion are primarily influenced by landscape features and climate. Unlike most insects, HWA feeds, grows, and reproduces during the winter. Hence, periods of low winter temperatures can cause high HWA mortality and hinder population establishment, growth (Parker et al. 1999, Shields and Cheah 2005), and spread rates (Evans and Gregoire 2007). Likewise, the cold temperatures in the high elevations along the Appalachian Mountain Range have helped slow the rate of spread and establishment. HWA appears to spread more slowly in areas with mean minimum temperatures of -15 °F (plant hardiness zone 5B). Regionally, HWA is spreading to new areas at a rate of 15.6 km/year south of Pennsylvania and 8.13 km/year (or less) in the northern portion of the hemlock's range (Evans and Gregoire 2007). Hemlock mortality associated with HWA establishment can range from almost none to nearly 100 percent (Orwig and Foster 1998, Bair 2002, Mayer et al. 2002). Mortality can occur quickly and uniformly throughout a stand or can occur slowly and in patches over more than a decade. Indirect ecosystem effects of HWA include changes in vegetation structure and composition, changes in wildlife communities, altered nutrient cycling rates, and changes in aquatic communities. Because widespread chemical control is economically unfeasible and biocontrols are still being tested, scientists and managers are investigating strategies to increase hemlock survival.

In the central and southern Appalachian Mountains, hemlock is most frequently found at elevations of 610 to 1,520 m, where it overlaps with red spruce starting at 1,370 m. Most commonly, hemlock is found on north- and east-facing slopes, and in moist coves and valleys. In the northeastern and northern portions of hemlock's range, it

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grows from sea level to about 730 m. On the Allegheny Plateau most of the hemlock grows between 300 and 910 m (Godman and Lancaster 1990). Because of hemlock's high tolerance to shade, it is typically found throughout all canopy layers and can continue to grow slowly for hundreds of years at high stand densities (Godman and Lancaster 1990). Hemlock's slow growth in these crowded conditions can provide a unique habitat for wildlife and aesthetic appeal to landowners.

Results from some studies in the northern portion of its range have suggested that hemlocks growing on sites with adequate and consistent moisture generally survive HWA infestation longer than trees growing on droughty sites and southern aspects, or waterlogged sites (Sivaramakrishnan and Berlyn 2000, Mayer et al. 2002, Orwig 2002, Pontius et al. 2004). However, other studies either failed to find a correlation with site factors (Orwig and Foster 1998, Eschtruth et al. 2006), or had high variability in their results (Royle and Lathrop 2000, Rentch et al. 2009).

Tree crown size and vigor appear to have the strongest relationship to hemlock vulnerability to HWA. Hemlocks in dominant and codominant overstory crown class positions appear to survive HWA longer than intermediate and overtopped crown class trees (Orwig and Foster 1998, Eschtruth et al. 2006) because in the early stages of infestation, intermediate crown class trees showed a higher likelihood of decline than overtopped trees (Rentch et al. 2009). A study conducted in HWA-infested stands located in Delaware Water Gap National Recreation Area, PA, predicted the odds of hemlock radial growth decline based on the relationship between crown condition and HWA infestation. Tree-ring chronologies from increment cores were used to develop a binomial decline index based on 3 consecutive years of below-average growth. Hemlock decline was modeled as a function of an extensive array of tree crown and site variables that were collected during the first 11 years of HWA infestation. Crown variables such as live crown ratio (LCR, ratio of live crown height to total height), crown density (an ocular estimate of the fullness of the crown, based on the amount of skylight blocked by leaves, branches, bole, and fruits), crown dieback (percent of branches with newly dead twigs in the live crown), and foliage transparency (relative amount of light that passes through the live crown) had the most explanatory power in the model, and were relatively accurate predictors of hemlock decline (Rentch et al. 2009). Consequently, silvicultural thinning treatments are being tested as a means for reducing stand densities and increasing crown vigor in colder areas where climate may slow HWA spread (Fajvan 2008).

The objective of this paper is to examine crown vigor data from HWA-infested stands in two different study areas and at different years post-infestation to determine whether patterns in tree decline are correlated with crown characteristics as predicted by the model developed by Rentch and others (2009). Stands located in West Virginia have been infested for only 4 years and HWA populations are still building. Stands in Pennsylvania have been infested for up to 16 years and are considered heavily infested. Some of these stands were sampled in 2003 to develop the aforementioned prediction model (Rentch et al. 2009). Additionally for the West Virginia data, we relate crown vigor data to songbird richness because changes in bird communities often reflect changes in stand structure. Finally, we discuss silvicultural objectives for improving the vigor of stands threatened by HWA.

METHODS

Study Area Descriptions and Sampling Methods

Delaware Water Gap National Recreation Area (DEWA) occupies approximately 27,800 ha along the Delaware River in northeastern Pennsylvania and northwestern New Jersey. Forest stands are primarily dominated by eastern deciduous species with pure hemlock stands occupying about 5 percent of the landscape (Eschtruth et al. 2006). In the mixed stands, hemlock can occupy 30-70 percent of the basal area (Mahan et al. 2004). HWA infestations were first detected in the park in 1989 (Evans 1995) and declines in hemlock health were evident in 1992. From 1993-1995 a system of 81 permanent plots was established in five hemlock stands where no HWA had been previously detected (Rentch et al.

2009). Each plot consisted of 10 permanently tagged hemlocks. A sub-sample of these trees was monitored annually and the following observations were recorded: LCR, crown density, crown dieback, and foliage transparency. All crown ratings were assessed to the nearest 5 percent compared to an ideal, healthy tree, consistent with Forest Health Monitoring Visual Crown Rating methodologies (Schomaker et al. 2007). All sample trees were assigned a vigor rating category (Table 1) at each measurement year. For this paper, we used data collected in 2007 and 2008.

On the New River Gorge National River (NERI) and Gauley River National Recreation Area (GARI) in southeastern West Virginia, a long-term hemlock ecosystem monitoring project was established in 1998 prior to HWA infestation (Wood et al. 2008). Study plots (n = 36) cover an extensive area spanning approximately 97 km from north to south and range in elevation from 427-853 m. Three moisture levels—hydric, mesic, and xeric—were each replicated 12 times. Each plot was 400 m^2 (0.04 ha) in size, with dimensions similar to other HWA stand-level monitoring studies (Mahan et al. 1998, Orwig and Foster 1998). Depending on site conditions, plots were placed either within a hemlock stand or within an isolated patch of hemlock trees and were square (20 m x 20 m) or rectangular (10 m x 40 m). On sites where hemlock was a co-dominant rather than a dominant tree species, plot-centers were deliberately placed where there was a visible amount of hemlock canopy cover. Centers and corners of each plot were permanently marked. We initiated baseline surveys of adelgid presence and hemlock tree vigor, live crown ratio, and diameter in fall/winter 1998 (Wood 1999a, 1999b). These data were collected each fall/winter (except during 1999 and 2005) to coincide with the November-April period in which the current season's HWA population typically exhibits woolly characteristics (Onken et al. 1994). Adelgid presence was determined by scanning the canopy of each hemlock tree with binoculars in search of the woolly form. HWA was first detected on eight plots in 2004. All hemlock trees ≥ 8 cm diameter at breast height (d.b.h.) that were rooted within or intersecting the outside perimeter of each 400 m^2 plot were tallied and d.b.h. was measured. Each tree was given a crown-vigor class rating, which was an index of the health of the live crown based on Onken and others (1994). The entire crown was inspected using binoculars and ranked as 1-5 (Table 1). Additionally, the live crown ratio was visually estimated as the percentage of the total tree height with live foliage.

Plots were placed at least 250 m apart when possible to accommodate avian surveys. Eight pairs of points were <250 m apart; none were <100 m apart. Generally, 250 m between point count stations is considered sufficient for independence between avian sampling stations (Ralph et al. 1993), although some studies have used distances of 100 m (Pendleton 1995). Avian point count surveys were completed each breeding season (late May-end June) from 1999-2008 using standard sampling protocols (Ralph et al. 1993).

Analysis

In the earlier study at DEWA, variables that provided the best fit in the logistic regression model developed for predicting the probability of hemlock decline were: LCR, crown density, d.b.h., foliar transparency and dieback, and plot-level percent HWA infestation (Rentch et al. 2009). We could not test the model directly with the new Pennsylvania (DEWA) and West Virginia (NERI, GARI) data because not all of these variables were measured. For the 2007-08 DEWA measurements (15+ years post-infestation), a value for HWA infestation was not available for those trees, but we did have data for crown density, dieback, transparency, and live crown ratio collected from 682 live trees. For 119 live hemlock trees on the eight West Virginia plots first infested in 2004, the only crown feature that could be compared with the model was LCR. We calculated mean LCR for each crown vigor class in 2004 (first year of infestation), 2006 (2 years post-infestation), and 2008 (4 years post-infestation). For both sites, the individual tree crown features were summarized for each vigor class assigned in the field and compared with the average crown features of trees that were used to develop the previous model (Rentch et al. 2009). Because trees that were categorized as being "in decline" were experiencing reduced diameter growth (Rentch et al. 2009), we plotted these same crown features relative to averages predicted by the model to estimate growth decline.

Table 1.—Definitions for crown vigor classes for each study area.

Pennsylvania		West Virginia	
Vigor class	Definition	Vigor class	Definition
Healthy	tree appears healthy with <10% branch or twig mortality or foliage discoloration	1	>95% healthy crown
Light decline	branch or twig mortality, or foliage discoloration on 10-25% of crown	2	>75-95% healthy crown
Moderate decline	branch or twig mortality or foliage discoloration on 26-50% of crown	3	>50-75% healthy crown
Severe decline	branch or twig mortality or foliage discoloration on more than 50% of crown	4	>25-50% healthy crown
Dead	no live foliage	5	>0-25% healthy crown

Additionally for all 36 West Virginia plots, we related mean LCR and mean crown vigor rank to songbird species richness with Pearson product-moment correlation. Richness was the number of different songbird species detected on each plot in each year. This analysis allowed us to evaluate whether a change in vegetation structure might affect songbird richness.

RESULTS AND DISCUSSION

Annual declines in tree vigor were evident during the first 4 years of infestation in West Virginia. The number of healthy trees decreased as trees categorized with lower crown vigor increased (Fig.1). Mean LCRs for hemlocks ranked as vigor 1 or 2 were higher than the mean of 55.6 percent predicted by the model (Fig. 2). Very few trees, however, were ranked as vigor 1 after the first measurement year (Fig. 1). Trees with crowns ranked 3 or 4 had live crown ratios similar to or less than 55.6 percent (Fig. 2).

At DEWA, healthier trees, those in the light decline category, had LCRs equal to or greater than the mean (Fig. 3), but the number of trees in the light decline category was only 26. The mean LCR for trees classified as in moderate decline (N = 591 trees) was similar to the model mean of 55.6 percent. Trees in severe decline (N = 65 trees) tended to have LCRs below the model mean (Fig. 3), indicating a possible correlation between crown vigor and vulnerability to HWA at this time. After 15 years of infestation at DEWA, no trees were classified as healthy in the data examined (Fig. 3).

Similar trends were found for model comparisons of mean crown density (model = 35.8 percent), dieback (model = 21.1 percent), and transparency (model = 33.8 percent) with DEWA hemlocks (Fig. 3). Trees in light decline had crown features similar to the model mean values, and trees in severe decline had lower vigor crowns than the model predictions. Regardless of time since infestation, crown features of hemlocks that were classified as being healthy, in light decline, or in severe decline are consistent with the model.

After 15-16 years of infestation, however, crown features varied more for DEWA trees classified as being in moderate decline. A more in-depth look indicated that 58 percent had crown density values that were lower than the model mean, and 42 percent had densities greater than the model mean. Dieback values followed a similar trend with 60 percent of the trees having more dieback than the model mean. Crown transparency measurements for trees classified as in moderate decline were the most consistent with the model. Most (88 percent) of the crown transparency values for those trees were greater than the model mean.

Based on the estimates for crown density and dieback, about 40 percent of the trees classified as moderate in the 2007-08 measurement may not yet be showing diameter growth

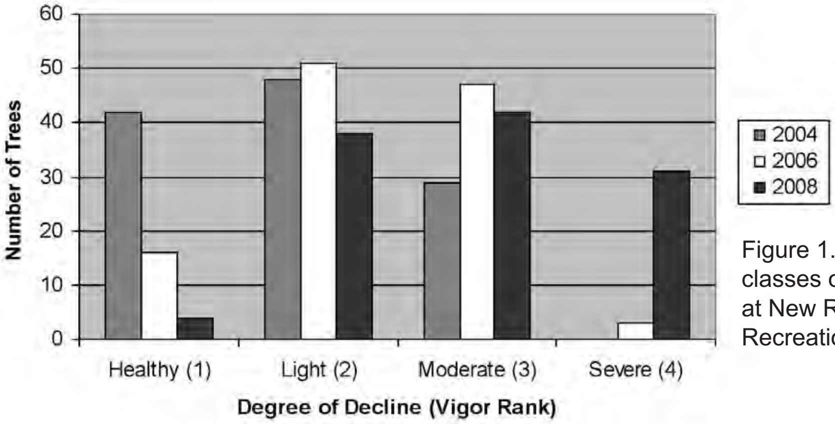

Figure 1.—Number of hemlock trees in four crown vigor classes on 8 plots infested by hemlock woolly adelgid in 2004 at New River Gorge National River and Gauley River National Recreation Area, WV.

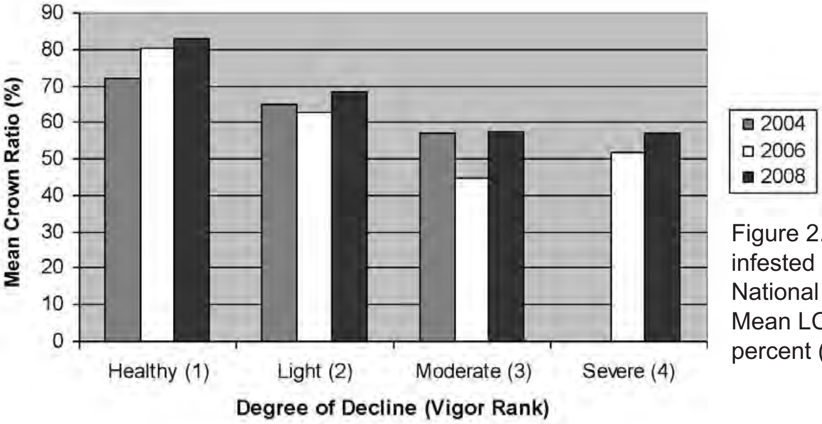

Figure 2.—Hemlock LCR in four crown vigor classes on 8 plots infested by hemlock woolly adelgid in 2004 at New River Gorge National River and Gauley River National Recreation Area, WV. Mean LCR predicted by the model for trees in decline was 55.6 percent (Rentch et al. 2009).

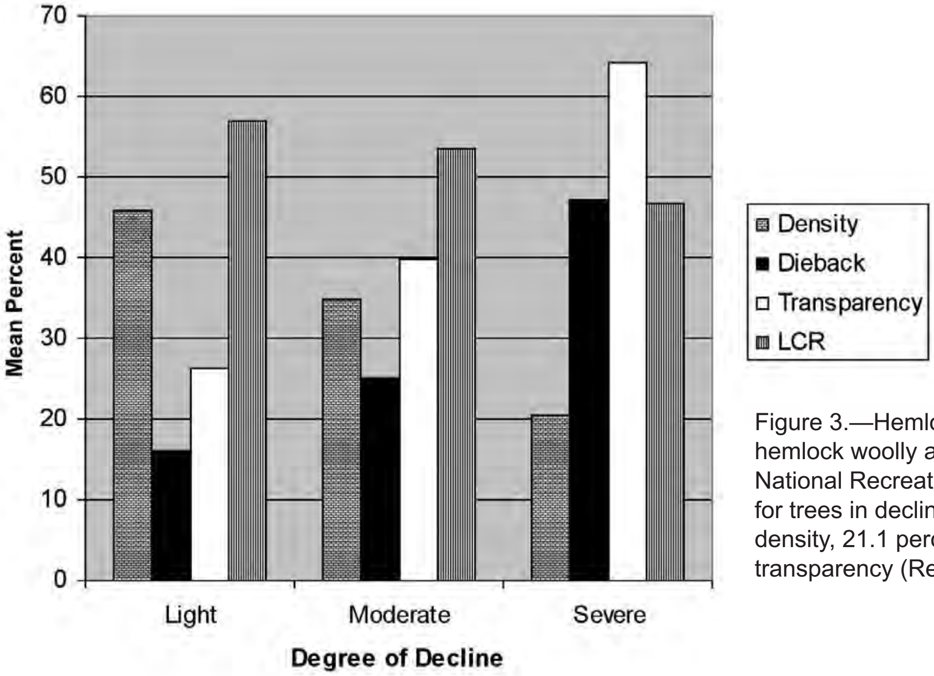

Figure 3.—Hemlock crown characteristics after 15+ years of hemlock woolly adelgid infestation at Delaware Water Gap National Recreation Area. Mean predicted values by the model for trees in decline was 55.6 percent for LCR, 35.8 percent for density, 21.1 percent for dieback, and 33.8 percent for transparency (Rentch et al. 2009).

decline. Trees in the moderate decline category are demonstrating crown vigor changes that are in transition between healthy and severe. Perhaps a temporal evaluation of the data would indicate whether hemlocks with lower vigor than the model values had been infested longer than those with crown features higher than the model mean.

Crown condition has been linked to tree survival and mortality (Dobbertin 2005). LCR is a measurement that is consistently repeatable among annual observers and is dependent only on foliage presence. Low to moderate HWA populations early in an outbreak have the least impact on LCR (Rentch et al. 2009), a relationship supported by our West Virginia data. After 4 years of infestation, all vigor categories still had mean LCRs at or above the model prediction (Fig. 2). In contrast, after 16 years at DEWA, 46 percent of the trees in moderate decline and 34 percent of those rated severe had LCRs above the model mean, which may be a factor in their continued survival. All of the 65 trees rated severe had transparency values above the model mean.

For all 36 sampling plots in West Virginia, songbird richness per plot was not correlated with vigor class ($P = 0.50$) or with LCR ($P = 0.47$). However, mean annual songbird richness increased slightly over time with 8.8 species/plot in 2004, 9.1 in 2006, and 9.5 in 2008. Mean vigor rank was 1.9 in 2004 and 2006 and 2.2 in 2008, while mean LCR was 70 percent in 2004 and 67 percent in 2006 and 2008. Although changes were slight, richness increased over time while LCR decreased, suggesting that some reduction in canopy cover benefitted songbird richness. Canopy reduction through silvicultural thinning might have a similar effect but needs to be investigated before drawing firm conclusions.

Both study areas are located in the northern climatic range for HWA, where cold winters are believed to cause slower spread rates and may help explain the longer survival of infested hemlocks (Evans and Gregoire 2007) compared to areas further south. In the northern region, silvicultural thinnings are also being tested as a means to increase hemlock vigor in overstocked stands prior to HWA infestation (Fajvan 2008). Current management guidelines recommend that thinning operations remove at least 20 percent of the basal area; however, if stands are very dense (> 46 m^2/ha), basal area removal should not exceed more than one-third of the total in any given operation (Lancaster 1985). While healthy hemlocks are no less susceptible to attack, our findings support longer survivability during infestation. Increased survivorship may improve hemlock's chances for recovery, especially if HWA populations crash and/or effective biocontrols are developed.

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AREA OCCUPANCY AND DETECTION PROBABILITIES OF THE VIRGINIA NORTHERN FLYING SQUIRREL (*GLAUCOMYS SABRINUS FUSCUS*) USING NEST-BOX SURVEYS

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Abstract.—Concomitant with the delisting of the endangered Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) in 2008, the U.S. Fish and Wildlife Service mandated a 10-year post-delisting monitoring effort to ensure that subspecies population and distribution stability will persist following a changed regulatory status. Although criticized for the inability to generate detailed population parameters, most distribution and demographic data for the Virginia northern flying squirrel have come from long-term nest-box monitoring. Because live-trapping efforts to generate mark-recapture census data largely have failed due to low trap susceptibility, post-delisting monitoring will continue to rely on nest-box surveys. However, managers will need a better understanding of actual Virginia northern flying squirrel occupancy and detection probabilities to fully use these data. Using the program PRESENCE, we analyzed 16 variants of the $\psi(.),\gamma(.),\varepsilon(.),\rho(.)$ (initial occupancy, local colonization, extinction, and detection) model with habitats ranked by probability of occurrence as a covariate for 72 nest-box lines surveyed for variable periods from 1985-2008. We defined overall presence as at least one capture per nest-box line per year of either sex or age class and persistence as the capture of either a female or juvenile per nest-box line per year. We observed an average of 4.48 ± 0.64 and 3.56 ± 0.48 years per nest-box line with a capture for overall presence and persistence, respectively. Our most parsimonious model for all Virginia northern flying squirrels was the $\psi(.),\gamma(.),\varepsilon(.),\rho(.)$ model, where ψ (occupancy) = 0.87 and ρ (detection) = 0.65. For persistence, our most parsimonious model was the $\psi(\text{Hab}),\gamma(.),\varepsilon(.),\rho(.)$ model, where habitat probability influenced occupancy with $\psi = 0.95$ for high-ranking habitat, 0.80 for medium-ranking habitat, and 0.50 for low-ranking habitat and $\rho = 0.65$. Contrary to our expectations, detection was not a function of habitat ranking in our best-approximating models for either category. However, competing models where detection was a function of habitat ranking did receive empirical support. Simulations using these parameters suggest that ≥20 nest-box lines surveyed continually over 5+ years will provide relatively robust occupancy data sufficient to meet the needs of the post-delisting monitoring effort for the Virginia northern flying squirrel.

INTRODUCTION

The Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) is a disjunct northern flying squirrel subspecies that occurs in the Allegheny Mountains portion of the central Appalachians in east-central and extreme northwestern Virginia south of the species' continuous distribution on the North American continent (Wells-Gosling and Heaney 1984). Along with the endangered Carolina northern flying squirrel (*G. s. coloratus*), which occurs in the Blue Ridge Mountains portion of the southern Appalachians, the Virginia northern flying squirrel is an arboreal, cavity-nesting, and hypogeal fungal-feeding specialist largely restricted to red spruce (*Picea rubens*) and red spruce-northern hardwood forest communities at higher elevations (>900 m) (Ford et al. 2004). The Virginia northern flying squirrel was listed as endangered by the U.S. Fish and Wildlife Service in 1985 (U.S. Fish and Wildlife Service

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1990). Factors for listing included severely altered habitat from exploitative logging of the red spruce forests at the turn of the 20th century (Stephenson and Clovis 1983), coupled with few collection records; a poorly known natural history; and ongoing perceived threats from surface mining, forest management, recreational development, and atmospheric acid deposition (Stihler et al. 1995, Schuler et al. 2002). Widespread nest-box and live-trapping surveys by state, federal, university, and industry consultants from the time of listing through the present have greatly expanded the known distribution of the Virginia northern flying squirrel within eight counties in West Virginia and one county in Virginia (Stihler et al. 1995, Reynolds et al. 1999). The current known distribution closely matches that of the approximate distribution of extant red spruce or red spruce-northern hardwood forests in the region (Menzel et al. 2006a). From these survey efforts, considerable data on reproductive characteristics, such as breeding chronology and juvenile maturation, and food habits have been quantified (Reynolds et al. 1999, Mitchell 2001). Use of radio-telemetry has allowed researchers to investigate and quantify important ecological components of the Virginia northern flying squirrel: den tree use and preference (Menzel et al. 2004) and home range and foraging habitat selection (Urban 1988, Menzel et al. 2006b, Ford et al. 2007a). In turn, predictive habitat models for assessing the likelihood of Virginia northern flying squirrel presence or absence across the Allegheny Mountains have been created with these data and capture records (Odom et al. 2001, Menzel et al. 2006a).

With more than 1,200 unique individuals handled since the late 1980s (Ford et al. 2007b) and with the realization that its habitat associations, requirements, and full geographic distribution were known (Ford et al. 2007a), the U.S. Fish and Wildlife Service moved to completely delist the Virginia northern flying squirrel in 2008 following the completion of a multi-factor status review (U.S. Department of the Interior 2008). From a regulatory perspective in West Virginia, the change in legal status at the federal level and the absence of state endangered-species statutes means that private land managers are not required to consider the Virginia northern flying squirrel in their management activities. However, the subspecies is still listed as state-endangered in Virginia; on federal ownership, primarily national forest lands in both states, the Virginia northern flying squirrel is a U.S. Forest Service Regions 8 and 9 “Sensitive Species” that still requires consideration such that agency actions do not adversely affect viability (U.S. Fish and Wildlife Service 2007). Additionally, the U.S. Fish and Wildlife Service’s post-delisting monitoring plan specifically charges that state and federal agencies in the Allegheny Mountains continue Virginia northern flying squirrel surveys to assess the subspecies’ recovery status—increasing, stable, or declining—over the next decade (U.S. Fish and Wildlife Service 2007).

Low live-trap susceptibility of the Virginia northern flying squirrel (Menzel et al. 2006b) has made it difficult for managers to assess population parameters such as density estimates among habitat types as are generated for other wildlife species. Although similarly plagued with a relatively low capture success, data taken from annual or biennial surveys of established nest-box lines with 15-25 boxes scattered over an approximately 275,000 ha area (Odom et al. 2001) have been the most reliable for naïve estimates of presence or absence and persistence and occupancy (Stihler et al. 1995, Reynolds et al. 1999). Numerous nest-box lines have been established, maintained, and surveyed since the mid-1980s in West Virginia and Virginia. However, whether or not nest-boxes can provide relatively unbiased and robust measures of Virginia northern flying squirrel occupancy sufficient to meet post-delisting monitoring requirements is unknown. Similarly, recognizing that the predicted probability of Virginia northern flying squirrel occurrence varies by habitat quality (Menzel et al. 2006a), we do not know whether detection probability is constant or variable by habitat as is routinely observed for other wildlife (Royle et al. 2005). Using the program PRESENCE, we used the aforementioned historic Virginia northern flying squirrel nest-box data from West Virginia to examine occupancy and detection probability measures to provide survey guidance for post-delisting monitoring.

METHODS

Detailed descriptions of the high-elevation red spruce and red spruce-northern hardwood habitats occupied by the Virginia northern flying squirrel in the Allegheny Mountains of eastern West Virginia and northwest Virginia are provided by Ford and others (2004, 2007a) and Menzel and others (2006b). We summarized nest-box survey data from records maintained by the West Virginia Division of Natural Resources to generate annual presence or absence values for each survey line for each year a line was visited between 1985 and 2008. Nest-boxes (33.3 x 12.1 x 12.5 cm with a 4.8 cm opening) typically were constructed using white cedar (*Thuja* sp.) or cypress (*Taxodium* spp.) and hung > 3 m on trees (Terry 2004). Nest-box lines, each consisting of 15-25 nest boxes typically arranged along a linear transect, occurred from approximately 800 m to 1,500 m in elevation, although most occurred at elevations >1,000 m (Odom et al. 2001, Menzel et al. 2006a). Although some nest-box lines were located on state-owned lands or private properties, most data were from those nest-box lines located on the Monongahela National Forest. Nest-boxes usually were surveyed once a year, most often in late spring to early summer, though some surveys occurred in summer or fall. Individual nest-box lines were surveyed an average of 9.34 ± 1.35 years. We limited our analyses to those nest-box lines that had been located with geographic positioning systems or were mapped previously (Odom et al. 2001). Within a geographic information system (GIS) (ArcMap 9.1, Environmental Systems Research Institute, Redlands, CA), we assigned each nest-box line a ranking of high, medium, or low according to a simple, yet relatively robust, Virginia northern flying squirrel habitat probability-of-occurrence model developed for the area (Menzel et al. 2006a). For nest-box lines that crossed habitat type polygons within the GIS, we visually assessed lines and made an assignment based on the habitat ranking into which the majority of boxes within an individual line fell, along with our expert assessment of adjacent habitat type.

From capture records, we created two datasets. First, we created a presence or absence dataset for overall Virginia northern flying squirrel captures regardless of actual number of individuals encountered, sex, or age class to examine overall detection and occupancy. Secondly, to examine detection and occupancy from a persistence perspective, we created a dataset whereby presence was assigned only if an individual nest-box line produced either a female or juvenile capture during the annual survey (adult males excluded).

We considered any Virginia northern flying squirrel <75 g as a juvenile (Wells-Gosling and Heaney 1984) and decided that individuals captured in spring would represent local production rather than immigration. In this dataset, the presence of an adult male without the additional capture of an adult or juvenile female or juvenile male on a nest-box line was considered an absence. Using program PRESENCE (McKenzie et al. 2005, Hines and McKenzie 2008) and habitat probability rankings (high = 2, medium = 1, and low = 0) (Menzel et al. 2006a) as a covariate, we calculated detection probabilities and occupancy values for all 16 combinations of the $\psi(.),\gamma(.),\varepsilon(.),\rho(.)$ (initial occupancy, local colonization, extinction, and detection) model for both datasets. Although not expressly interested in local colonization and extinction, we used this "open" model because of the survey duration at many of the nest-box lines.

We used Akaike's Information Criterion (AIC) corrected for small sample size to rank models (Burnham and Anderson 2002). We drew our primary inference from the best-approximating model for each dataset. We considered those models within two units ΔAIC_c as competing models with the most empirical support. We discarded all models for which the program PRESENCE failed to find convergence. To assess efficacious post-delisting monitoring designs using nest-boxes, i.e., number of lines and number of years monitored, we input the detection probabilities and occupancy values from our best-approximating models into the program PRESENCE simulation function. Using runs of 1,000 iterations each, we simulated occupancy standard errors for combinations of 5, 10, 15, 20, and 25 nest-box lines and survey durations of 3, 5, 7, 10, and 15 years.

RESULTS

We were able to analyze nest-box survey data from 72 individual nest-box survey lines that met our selection criteria. Survey effort and Virginia northern flying squirrel captures varied by habitat type, but most (88.9 percent) nest-box lines occurred in either high-ranking or medium-ranking habitat (Table 1). Effort varied by individual nest-box line with surveys occurring from only 2 successive years to as many as 24 successive years (Table 1). For all Virginia northern flying squirrels, the $\psi(.),\gamma(.),\varepsilon(.),\rho(.)$ model without habitat ranking as a covariate for any parameter was the highest weighted (Table 2) with ψ = 0.87 ± 0.28 (SE) and ρ = 0.65 ± 0.10. The $\psi(\text{Hab}),\gamma(.),\varepsilon(.),\rho(.)$ model had almost equal empirical support relative to model weighting (Table 2). For this model, increasing habitat ranking positively influenced occupancy. For our persistence models, the best-approximating model was the $\psi(\text{Hab}),\gamma(.),\varepsilon(.),\rho(.)$ model (Table 2). Increasing habitat ranking positively influenced occupancy with ψ = 0.95 ± 0.17 for high-ranking habitat, ψ = 0.80 ± 0.29 for medium-ranking habitat, and ψ = 0.50 ± 0.00 for low-ranking habitat and ρ = 0.65 ± 0.10. For the remaining models that showed some empirical support but were not within 2 units of ΔAIC_c in both datasets, the habitat-ranking covariate positively influenced detection probability and habitat ranking and had an inverse relationship to colonization. Simulations using ψ = 0.87 and ρ = 0.65 over a range of years and nest-box lines suggested that ≥20 nest-box lines surveyed annually for 5+ years should provide suitable estimates of precision in occupancy estimates for Virginia northern flying squirrels for post-delisting monitoring purposes as set forth by the U.S. Fish and Wildlife Service (Fig. 1).

Table 1.—Summary of mean (± SE) years of Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) monitoring and percent captures using nest-box survey lines in West Virginia, 1985-2008, by habitat ranking of probability of occurrence (see text).

Quality	*n*	Year range	Mean years surveyed	Percent years with capture	Percent years with females/juveniles
All	72	2 - 24	9.34 ± 1.35	44.47	41.13
Low	8	2 - 19	8.75 ± 0.86	41.19	33.89
Medium	29	2 - 24	8.44 ± 1.57	47.26	41.68
High	35	2 - 23	10.22 ± 1.06	42.84	42.23

Table 2.—Akaike's Information Criterion ranking of best-approximating $\psi(.),\gamma(.),\varepsilon(.),\rho(.)$ (initial occupancy, local colonization, extinction, and detection) models and competing models with empirical support for Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) presence or absence data using nest-box survey lines in West Virginia, 1985-2008. Habitat ranking of probability of occurrence was used as a model covariate (see text). Models that failed to converge were not included in assessment.

Model	K	AIC_c	ΔAIC_c	AIC_{wt}
All squirrels				
$\psi(.),\gamma(.),\varepsilon(.),\rho(.)$	5	923.05	0.00	0.44
ψ(Hab[a]),$\gamma(.),\varepsilon(.),\rho(.)$	7	923.72	0.67	0.32
$\psi(.),\gamma(\text{Hab}),\varepsilon(.),\rho(.)$	7	925.91	2.86	0.11
$\psi(\text{Hab}),\gamma(.),\varepsilon(.),\rho(\text{Hab})$	9	926.30	3.25	0.09
$\psi(.),\gamma(\text{Hab}),\varepsilon(.),\rho(\text{Hab})$	9	927.69	4.64	0.04
Female or juvenile squirrels				
$\psi(\text{Hab}),\gamma(.),\varepsilon(.),\rho(.)$	7	923.72	0.00	0.68
$\psi(.),\gamma(\text{Hab}),\varepsilon(.),\rho(.)$	7	925.91	2.19	0.23
$\psi(.),\gamma(\text{Hab}),\varepsilon(.),\rho(\text{Hab})$	9	927.69	3.97	0.09

[a] habitat ranking of probability of occurrence (high, medium, or low)

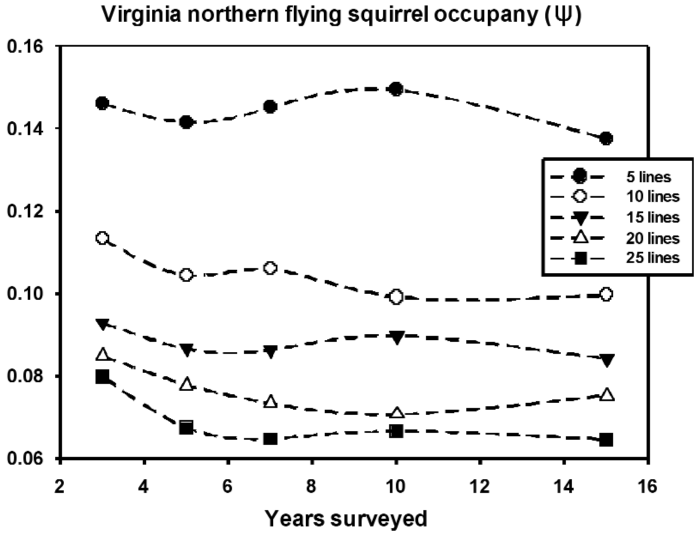

Figure 1.—Simulated standard errors for Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) occupancy values over combinations of increasing survey effort (box-lines) and increasing survey time (years). Monitoring efforts using ≥20 nest-box lines surveyed for 5+ years satisfy requirements of the U.S. Fish and Wildlife Service post-delisting monitoring plan.

DISCUSSION

The positive link between habitat ranking and occupancy in the best-approximating model for persistence (females and juveniles) and the strongly supported competing model for all Virginia northern flying squirrels confirms the utility of recent predictive habitat modeling efforts at stand levels (Ford et al. 2004) and landscape levels (Menzel et al. 2006a). Anecdotal evidence and current opinion among managers and researchers working with the Virginia northern flying squirrel have suggested that detection probability might be lower; that is, individuals might be less likely to be detected when present in good habitat conditions where an abundance of natural den sites exist or conditions are suitable for drey-nest formation in red spruce. Similarly, it is possible that detection probability was biased upward in lesser-quality habitat or younger stands, where dens could be less abundant and nest-boxes were functioning as a supplement to a limiting factor. Our best-approximating models and those with the strongest empirical support do not support this assertion. Rather, detection probability was constant among high-, medium-, and low-ranking habitat designations in the Allegheny Mountains. For the models with some empirical support that were not within two units of ΔAIC_c in both datasets, colonization probabilities inverse to habitat ranking could be indicative of greater year-to-year population stability and higher overall population densities per unit area.

Managers in other systems with other wildlife species have recognized that artificial structures such as nest-boxes can help overcome habitat inadequacies, such as an obvious lack of snags and cavities in younger or intensively managed forests (Lindenmayer et al. 2009). In the Pacific Northwest, Carey (2002) reported that the proportion of breeding female northern flying squirrels increased with the addition of supplemental nest-boxes although actual population productivity remained constant. In the Allegheny Mountains, however, Menzel and others (2004) demonstrated that natural den use and availability and den-switching were high across a wide variety of red spruce and red spruce-northern hardwood stands that also contained nest-box survey lines in most instances. In turn, we believe the results of our modeling along with the findings of Menzel and others (2004) relative to denning ecology would suggest that detection probabilities are unbiased across habitat conditions. Therefore occupancy measures probably are accurate reflections of Virginia northern flying squirrel presence or absence.

Nonetheless, we are aware of two caveats in our data that might contribute bias to our occupancy and detection probability measures. First, as has been observed generally with Sciurids and other cavity-dependent species monitored with nest-box surveys, captures tend to be low after the initial placement of nest-boxes before they become "weathered" (Carey 2002, Shuttleworth 2004, Lindenmayer et al. 2009). Accordingly, a small number of sites with only 2 years of recorded survey effort and hence, new nest-boxes, may have been misclassified as unoccupied. Secondly, a small proportion of sites occasionally were surveyed twice a year (C. Stihler, West Virginia Division of Natural Resources, unpubl. data), inflating detection probabilities slightly. Future detection probability and occupancy analyses should include a cumulative covariate of time since nest-box placement site/sampling.

Using our post-hoc examination of presence or absence data from Virginia northern flying squirrel nest-box survey lines, we believe this survey technique successfully can meet the post-delisting monitoring requirements over the next decade. Although nest-box lines as configured in our study would not provide detailed relative abundance or density estimates to allow a full understanding of Virginia northern flying squirrel habitat relationships, i.e., productivity by habitat condition, data from these nest-box lines would still be sufficient to assess persistence or changes in occupancy over the Allegheny Mountain landscape. Indeed, measures of occupancy and incidental collection of sex, age, and condition of captured individuals may be the only readily or practically obtainable data to assess population status for Virginia northern flying squirrels – a situation similar to many other cryptic wildlife species that are difficult to observe and/or capture and re-capture (Weller 2008). Monitoring the southern flying squirrel (*Glaucomys volans*) in Ohio, Althoff and Althoff (2001) concluded that occupancy measures derived from nest-box captures are a suitable surrogate for understanding habitat trends if measured over a long enough period and with enough sampling effort. Our simulation efforts would indicate that approximately 20 nest-box survey lines monitored for >5 years would provide a satisfactory level of precision to assess changes or the lack thereof in occupancy for the Virginia northern flying squirrel. Ongoing survey efforts range-wide by West Virginia Division of Natural Resources combined with additional surveys on the Monongahela National Forest, Canaan Valley National Wildlife Refuge, and Kumbrabow State Forest should easily exceed the 20 nest-box survey-line threshold (S. Jones, U.S. Forest Service, pers. comm.). Additionally, these surveys will occur across a wide gradient of Virginia northern flying squirrel habitat conditions.

From an economic and efficiency standpoint, much of the costs of monitoring using nest-boxes are the initial investment of constructing boxes and the time required to place nest-boxes in the forest. Depending on travel-time and nest-box survey-line location, our experience would suggest that two individuals can check two to three lines in a day. On the other hand, live-trapping requires significant effort, often requiring multiple visits to a single site over 3-7 consecutive days, thus making multiple individual site visits logistically difficult unless within very close proximity. Though less of an issue now that the Virginia northern flying squirrel has been de-listed, trap mortality from exposure, capture myopathy, or predation is a concern when working with northern flying squirrels (Rosenberg and Anthony 1993). Moreover, if live-trapping produces capture rates too low to generate usable mark-recapture or even minimum-number-known-alive types of data, then arguments against the selection of nest-box survey lines for monitoring Virginia northern flying squirrels are unpersuasive at best.

Although much remains unknown about the Virginia northern flying squirrel subspecies in particular and the species in general, an important aspect of future work should be to examine the relationships between persistence and/or more detailed demographics with habitat that have spatially explicit linkages (Smith 2007). For the Siberian flying squirrel (*Pteromys volans*) in Finland, Hurme and others (2008) observed that habitat patch occupancy was temporally dynamic and linked to habitat patch quality, size, and proximity or connectivity to other patches within the landscape matrix. Smith and Person (2007) hypothesized that Alaska northern flying squirrel populations might not be viable within optimal, but small, spatially isolated habitat patches or with reduced "rescue" immigration from nearby large, high-quality habitat patches. Relative to large conifer-dominated landscapes such as in Alaska or other parts of the northern flying squirrel's range, red spruce and red spruce-northern hardwood forests in the central and southern Appalachians are substantially fragmented and degraded from past anthropogenic disturbance (Stephenson and Clovis 1983, Weigl 2007). Therefore, the incorporation of additional habitat parameters beyond the recognition of simple habitat ranking, such as better measures of forest structure and the presence of folistic epipedons at the stand level, in ongoing and future nest-box monitoring would seem prudent. Such data could be an invaluable contribution for the design and implementation of red spruce forest enhancement and restoration efforts in the Allegheny Mountains in the coming years (Rentch et al. 2007).

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PENNSYLVANIA BOREAL CONIFER FORESTS AND THEIR BIRD COMMUNITIES: PAST, PRESENT, AND POTENTIAL

Douglas A. Gross[1]

Abstract.—Pennsylvania spruce (*Picea* spp.)- and eastern hemlock (*Tsuga canadensis*)-dominated forests, found primarily on glaciated parts of the Allegheny Plateau, are relicts of boreal forest that covered the region following glacial retreat. The timber era of the late 1800s and early 1900s (as late as 1942) destroyed most of the boreal forest on a large scale, but there has been some recovery of vegetation and delayed recovery of the accompanying avian communities. Important locally from a biodiversity standpoint, these forests support the most southerly extent of the current breeding range of yellow-bellied flycatcher and blackpoll warbler. Now persistent at a few sites, yellow-bellied flycatcher was documented nesting in the 1980s after 50 years of being absent or overlooked. Blackpoll warblers were not documented as a breeding species in Pennsylvania until 1993 but have been confirmed nesting most years since. These boreal forest relicts also host numerous other species of more northerly distribution, sometimes in high densities. Historically, olive-sided flycatcher was widespread and locally common in the high elevations as late as the 1890s, but has not been documented nesting since the 1930s. Many of these boreal bird species such as the yellow-bellied flycatcher and red crossbill are not easily detected and need specialized surveys for adequate monitoring. Diversity of habitat and plant species structure are important elements of locations that support the rarest and most diverse species assemblage. Populations of some species seem to be increasing over time, but problems with wintering grounds or migration stopover sites may be limiting some species as much as nesting habitat. The best boreal conifer sites have some level of protection, but their isolation and a general lack of appreciation present challenges for conservation of this ecosystem.

> *On North Mountain the forest is truly primeval; the Hemlock, the Yellow Birch, and the Maple are the characteristic trees and attain great size. The Hemlocks are scattered in considerable numbers through the forest and tower above it, their huge trunks often four or five feet in diameter marking them out as giants among their lesser brethren. The underbrush is often dense and everywhere great logs, covered with green moss, lie moldering. Here and there you hear clear cold brooks that seem to imitate the song of the Winter Wren that is almost constantly heard along them. The drawling song of the Black-throated Blue Warbler is heard on every hand. High up in the Hemlocks the drowsy sound of the Black-throated Green Warbler is heard, and the lively chatter of the Blackburnian Warbler catch the ear. Is not this a bit of northern Maine? Here it was that for the first time I heard the Wood Thrush, the Hermit, and the Olive-backed all singing at the same time. The three species were abundant and the music at sundown was a concert which for sweetness would be hard to excel.*
>
> Jonathan Dwight, writing of North Mountain in 1892 (Dwight 1892).

INTRODUCTION

Size and geographical position give Pennsylvania an important role in the Appalachian Mountain forest ecosystems. Most of the state lies within the Appalachian Mountain Bird Conservation Region. Although most of the state's forests are deciduous or mixed deciduous–conifer, some areas in the state contain boreal or conifer forests. Extant boreal conifer forests are found primarily on glaciated parts of the Allegheny Plateau and are relicts of former boreal forests that were once more extensive. Most are associated with

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forested wetlands/peatlands or are part of wetland complexes at headwaters of high-quality cold water streams (Gross 2002a). Much of the current spruce (*Picea* spp.) forest areas are located in northeastern counties, but some stands also are found in northern Pennsylvania as far west as the Ohio border, along with a few stands south of the State College area in the central portion of the state (Fig. 1).

The map of current distribution of possible spruce forest is estimated and subject to further research (Fig. 1). In particular, the Pocono Mountains, especially the High Poconos near Blakeslee in the northeast; North Mountain, the eastern part of the Allegheny Plateau in the northwest; and the Northcentral Highlands all have tracts of conifer forests that sustain populations of birds generally associated with northern forests. These conifer swamps and bogs were formed from glacial kettle lakes and filled in with peat from accumulation of organic matter (Johnson 1985; Davis et al. 1991; Davis et al. 1995a, 1995b, 2002). In older texts, these areas would have been considered to be in the "Canadian" life zone (Merrium 1894, Poole 1964).

In these conifer forests, eastern hemlock (*Tsuga canadensis*) often is dominant or is a cohort associate with red spruce (*Picea rubens*). Balsam fir (*Abies balsamea*) is much rarer than red spruce and also is scattered across the highlands of Pennsylvania, but occurs most commonly in the Pocono Mountains (Rhoads and Klein 1993). Bear Meadows Natural Area of Rothrock State Forest is an outlying location for balsam fir and several other boreal conifers (Rhoads and Klein 1993, Abrams et al. 2001). Black spruce (*Picea marina*) is less common than red spruce and confined solely to wetlands, especially sphagnum bogs and peatlands with American larch or tamarack (*Larix laricina*) (Donahoe 1954; Rhoads and Block 2000, 2005). Eastern white pine (*Pinus strobus*) also is a component of boreal conifer swamps. Even when spruces are dominant, large black gums (*Nyssa sylvatica*) are often a prominent feature of the forested wetlands where some of the birds featured in this report are found.

History and Extent of Pennsylvania Boreal Forests

Pre-settlement Pennsylvania was approximately 90- to 95-percent forested (DeCoster 1995). Glaciation and European settlement have created a more patchy forest in the state with fewer old forests. Most Pennsylvania forests are now in age classes between 60 and 120 years, with the largest 10-year classes in the 81- to 100-year range (Jenkins et al. 2004). The forests of the Allegheny Plateau once comprised a much larger percentage of hemlock. Many bird species are associated with hemlocks in the Northeast and the Appalachians. On a general basis, Acadian flycatcher (*Empidonax virescens*), blue-headed vireo (*Vireo solitarius*), magnolia warbler (*Dendroica magnolia*), Blackburnian

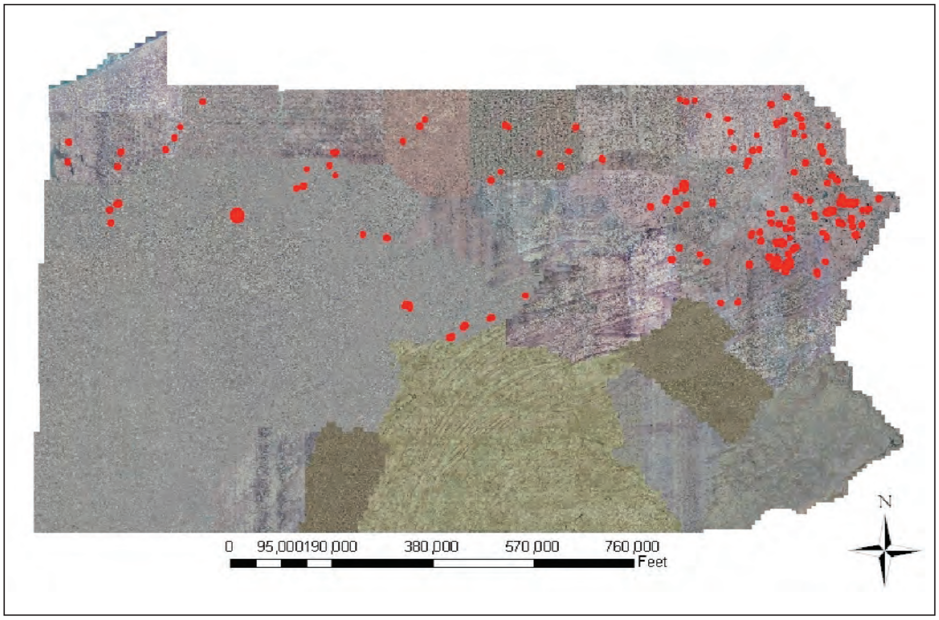

Figure 1.—Red and black spruce community distribution in Pennsylvania (red circles), PA Natural Heritage Program with The Digital Base Map of Pennsylvania and Delaware Valley Regional Planning Commission imagery as backdrop.

warbler (*D. fusca*), and black-throated green warbler (*D. virens*), are often associated with hemlock forests (Haney 1999, Ross et al. 2004, Allen et al. 2009). Conifer forests extend across Pennsylvania, and some of the most extensive and oldest are in the northwestern counties, especially in the Allegheny National Forest and in Cook Forest State Park and some public lands nearby (Haney 1999). The forests of northwestern Pennsylvania formerly had a higher component of hemlock than in present times (Lutz 1930, Whitney 1990). Only a few old-growth forests remain in the state, and most of these are dominated by conifers, particularly eastern hemlock and eastern white pine. Several bird species are broadly associated with more mature conifer forests, including red-breasted nuthatch (*Sitta canadensis*), brown creeper (*Certhia americanus*), winter wren (*Troglodytes troglodytes*), and golden-crowned kinglet (*Regulus satrapa*), as well as the Empidonax flycatcher, vireo, and Dendroica warblers just mentioned, and the hairy woodpecker (*Picoides villosus*), Swainson's thrush (*Catharus swainsoni*), and magnolia warbler (*Dendroica magnolia*) (Haney and Schaadt 1996, Haney 1999).

The loss of avifaunal elements of the "Canadian" life zone was documented and lamented by many ornithologists and ecologists in Pennsylvania (Todd 1940; Poole 1964 unpublished; Conant 1989a, b; Mellon 1989). Similar declines have been documented in West Virginia in more recent times as a result of natural forest changes (Hall 1985). The size and extent of the former boreal conifer element in Pennsylvania is often underestimated. As an example, in 1921, the amount of eastern tamarack (*Larix laricina*) in Pymatuning Swamp before timbering and subsequent flooding for reservoir creation was estimated at 800,000 board-feet (Netting and Ven Dersel 1934); virtually none remained following those disturbances (Grimm 1952). Some of the largest sawmills were active in the forests of North Mountain, where there were substantial stands of hemlock, red spruce, and white pine (Taber 1970). Fortunately, these forest communities have demonstrated some resistance to the many pressures placed upon them and have experienced some level of recovery as evidenced by the return of some yellow-bellied flycatchers and Swainson's thrushes and the occasional presence of species such as evening grosbeak and red crossbill (Conant 1994, McWilliams and Brauning 2000). Some of the characteristic birds of this diminished boreal conifer forest will be emphasized herein. One of the objectives of my paper is to share surveys and research conducted in Pennsylvania that are unpublished or have been reported in obscure reports. Findings may be relevant to similar bird conservation concerns in the Appalachians south of Pennsylvania.

The timbering era left a lasting mark on the vegetation of Pennsylvania and much of the Appalachian Mountain region. Much of the Pocono Mountain region where many of the red spruce forests occurred, was logged fairly early compared to the rest of northern Pennsylvania because of its proximity to urban areas, coal mines, and large rivers (Oplinger and Halma 1988). This region was accessible to transportation corridors, first canals and later railroads, through Stroudsburg along the Delaware River, Mauch Chunk (later Jim Thorpe) along the Lehigh River, and Wilkes-Barre along the Susquehanna River to New York, Philadelphia, and Baltimore (Oplinger and Halma 1988, Dando 1996). Large rafts of pine were floated down the Susquehanna from southern New York and northern Pennsylvania to Baltimore as early as 1794 (Harvey and Smith 1927).

The tanning industry started as early as 1822 in Stroudsburg and grew to a million-dollar industry by the 1860s. Timbering was extensive during the Civil War in the lowlands of the Poconos and culminated in the higher elevations of the Poconos in the 1870s (Mellon 1989, Dando 1996). Much of the hemlock was cut for the large tanneries, but pine was substituted by the 1880s because demand had already greatly depleted hemlock. By 1905, the area around Canadensis in Monroe County had little timber left and the Poconos were termed "a country of huckleberry barrens" (Weygandt 1905). By comparing land survey records to USDA Forest Service inventory in the 1980s, Dando (1996) determined that pines decreased in frequency from 31.5 percent to 5.7 percent, hemlock increased slightly from 9.2 to 12.4 percent, and spruces decreased from 7.3 to 1.5 percent (a nearly fivefold decrease).

In pre-settlement Pocono forests, black spruce occupied the ring immediately around wetlands and red spruce grew farther up-slope. A history of fire-adapted communities including *Pinus rigida* and scrub barrens suggests that the southern Pocono region's pre-settlement ecosystems were influenced by Amerindians' fire regime (Dando 1996, Latham et al. 1996).

To the west of the Pocono Mountains, another spruce forest, the North Mountain area, was considered wilderness in the late 19th century and was lumbered primarily in the 1890s through 1914. North Mountain is a local name given to the eastern part of the Glaciated High Plateau Section of the Appalachian Plateau Province in parts of Sullivan, Luzerne, and Wyoming counties (Pennsylvania Department of Conservation and Natural Resources [DCNR] 2000). It includes Ricketts Glen State Park, Wyoming State Forest, and parts of State Game Lands 13, 57, and 66. Much of these properties lies in the glaciated part of the state (DCNR 2005). The last logging railroad built in Pennsylvania was constructed in 1942 to harvest Tamarack Swamp, a virgin spruce forest in western Wyoming County (Taber 1970). During the height of logging on North Mountain in the late 1890's, in a radius of about 10 miles four lumber companies cut about 300,000 board feet per day. In addition, the Stony Brook Lumber Company cut 30,000-40,000 board feet of mostly spruce daily from 1911 to 1916 in nearby western Wyoming County (Taber 1970). A major beetle infection affected the spruce forest of northern Pennsylvania in 1895-96 and stimulated massive cutting to prevent loss of the timber (Petrillo 1991). More than 11 million board feet of spruce were cut on North Mountain between the Ricketts and Kasson Brook area in a short time. A devastating storm in September 1896 felled more than 200 million feet of timber that was salvaged. By the turn of the last century, most of the spruce forest of Pennsylvania was cut as a consequence of these events.

Logging continued into the 1940s, when Hicks Jennings cut the last remaining virgin spruce in Tamarack Swamp next to the Stony Brook holdings on Dutch Mountain. The characteristics of these forests are not well known, but they appear to match the description of Appalachian-Adirondack spruce forest described by Cogbill (1996), especially those associated with wetlands and pond or lake borders. Eastern white pine was prized for masts used for ship-building and many other purposes. Hemlock was cut primarily for the tanning industry; many logs were left in the woods after their bark was stripped. Spruce was not only logged, but also shredded for excelsior. Much of this forest also burned after logging, delaying natural regeneration further. The use of fire for maintaining blueberry barrens kept some high-elevation areas in the Pocono Mountains in a stage of oak-pine scrub barrens rather than forest, but these areas are returning to forest cover (Latham et al. 1996).

The remaining conifer forests of Pennsylvania support a variety of birds and other wildlife of high conservation concern in the state (Goodrich et al. 2002). These include: northern flying squirrel (*Glaucomys sabrinus*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasiurus moctivagans*), snowshoe hare (*Lepus americanus*), and fisher (*Martes pennanti*), and formerly marten (*Martes americana*) and perhaps the lynx (*Lynx canadensis*) (Stanwell-Fletcher 1936, Genoways 1985, Pennsylvania Game Commission and Pennsylvania Fish and Boat Commission 2005). Several rare plants also occur in these forests and wetlands (Davis et al. 1995, Fike 1999, Davis et al. 2002). The list of plants found in these forests is similar to that for old-growth spruce stands in New England (Cogbill 1996).

Boreal Birds of Pennsylvania of Concern as Target Species for Conservation or Indicator Species

The boreal bird community in Pennsylvania is a subset of conifer forests and of northern hardwood forests. A fairly long list of its members could be made, but this paper will emphasize a few of those species that serve as indicators for these habitats. Some of the characteristic birds of the North American boreal forest are found in the high-elevation forests of the Appalachian Mountains. Pennsylvania's boreal conifer forests serve as a link in a chain of "habitat islands" between the Central Appalachians and the Catskills and Adirondacks. Breeding populations of Bicknell's thrush (*Catharus bicknelli*), a boreal forest bird of high conservation priority, live within 100 miles of the Dutch Mountain wetlands and Pocono Mountains, only a short overnight flight for the long-distance migrants discussed in this paper (Rimmer et al. 2001, Rimmer 2008). Several of the birds discussed below have much larger populations in the plateau forests of New York State. As such, the Pennsylvania boreal forests are a link, perhaps genetically, between scattered islands of habitat and populations between these larger archipelagos of conifer forest. Many bird species are commonly associated with boreal or conifer forests (Table 1). The following is a discussion of some species of particularly high concern for their conservation interest or their value as indicator species of this threatened ecosystem.

Olive-sided flycatcher (*Contopus cooperi*). Although apparently no longer breeding in the Appalachian Mountains, the olive-sided flycatcher is a priority species for conservation in Bird Conservation Region (BCR) #28 and other BCRs (U.S. Fish and Wildlife Service 2002). Before the turn of the 20th century, the big boreal pewee (as it was once called) was fairly widespread in swamps, mature forests, edges, and near ponds and lakes in Pennsylvania mountains, usually those with elevations greater that 600 m (Gross 1992b, McWilliams and Brauning 2000). It was associated with old-growth forests on North Mountain and in Tionesta forest areas (McKean and Warren counties) (Cope 1936). It was an uncommon and locally distributed breeding species in northern and mountainous parts of the state and was often associated with headwaters (Warren 1890, Todd 1940, Poole unpublished manuscript). Now, however, it is considered extirpated as a nesting species with no evidence of nesting since the 1930s (Poole 1964, Gross 1992a, McWilliams and Brauning 2000). It formerly was found principally on the Allegheny Plateau but also in the Ridge and Valley Province's higher elevations. It was not confined to the far north but was scattered throughout the highlands. This species occupied the northern corners of the state, including the Pocono Mountains and the northwestern wetlands and forests (Carter 1904, Simpson 1909, Harlow 1913, Todd 1940, Street 1954). Stone (1900) stated of this species on North Mountain of Sullivan, Wyoming, and Luzerne counties: *"Rather common; scattered at intervals over the mountains. Its penetrating call heard continually."* The loud *"Whip! Three beers!"* whistled song was also commonly heard in Pymatuning Swamp as late as 1932, which may be the last documented nesting in Pennsylvania or Ohio (Todd 1940). The Pymatuning Swamp (now Lake) was flooded and no longer has significant habitat for this or other conifer forest birds. It is notable that Hazleton, Luzerne County, was the site of the first documented nesting in Pennsylvania (Young 1898), but this forest was replaced by open pit mines that now dominate the local landscape. This location is not on the "northern tier" of counties but closer to the middle latitude near U.S. Route I-80.

Several survey challenges face managers interested in documenting nesting of this species in the Appalachians. One such challenge is that many north-bound migrants are still present in June and south-bound migrants may be moving through the state as early as July when a possible breeding bird might still be present. The few locations where summer birds have been reported are often remote locations. Persistence may be necessary to document any olive-sided flycatcher nesting in the state. Although there have been summer reports in recent decades, no nesting of the species has been confirmed since the 1930s (Gross 1992b, Pennsylvania Society for Ornithology 2006.) Singing olive-sided flycatchers have been observed in the summer in a blow-down in an old-growth forest, burned-over mountain forests, and black spruce swamps (Gross 1992b, Haney and Schaadt 1996). Recently occupied locations are consistent with the former breeding range in the state, including Lackawanna, Wyoming, Tioga, and Cameron counties. A particularly intriguing report of a territorial olive-sided flycatcher came from the old growth hemlock-beech forest in Tionesta Scenic Area of Allegheny National Forest in 1993 (Haney and Schaadt 1994). The mature forest was more open than usual because of an outbreak of the defoliating caterpillar, elm spanworm (*Ennomos subsignarius*). Territorial birds were also seen in the old tornado blowdown area nearby, where many snags provided foraging opportunities for this flycatcher. There appears to be adequate habitat in Pennsylvania for some nesting to occur. The closest location where this species has nested recently is about 100 miles northeast of the border in the Catskill Mountains (Altman and Sallabanks 2000). It also nests in New York's Taconic and Adirondack mountains (Peterson 2008a).

The olive-sided flycatcher is a paradox for bird conservation because it occurs in both mature conifer forests and disturbed forests, especially at wetland edges or in fire-

Table 1.—Bird species generally associated with boreal conifer forests and wetlands in Pennsylvania.

Bird species - common name *Scientific name*	Habitat Specifications, Distribution Notes, Limiting Factors, and Conservation Challenges.
Ruffed grouse *Bonasa umbellus*	Young and low growth of conifers and heaths; edges of forested wetlands; forest gaps. Harsh winters, lack of regeneration, and forest age are limits to population.
Sharp-shinned hawk *Accipiter striatus*	Variety of mixed and conifer forest, often nesting in conifers including exotics. Forest size and fragmentation are limiting.
Northern goshawk *Accipiter gentilis*	Extensive forest, especially where conifers are dominant and at higher elevations. Often nests in conifers, usually large-scale forests. Declining in state and region, productivity low recently. Nest predation by mammals, West Nile virus, and spring weather may be limiting factors.
Red-shouldered hawk *Buteo lineatus*	Riparian forests and forested swamps, including high-elevation forested wetlands, beaver-altered wetlands, hemlock-dominated riparian forests.
Merlin *Falco columbarius*	Expanding south into state from north, often nesting in conifers. It is not associated with extensive forests but nests in towns, cemeteries, parks near lakes.
American woodcock *Scolapax minor*	Shrubby wetlands and meadows, including bogs and swamps, and along streams in forests, as well as early-succession forest. Threatened by loss of wetlands and early-succession habitat.
Barred owl *Strix varia*	Extensive mixed or conifer forests, including riparian forests and forested wetlands. Fairly common but may be limited by competition with larger Great Horned Owl (*Bubo virginianus)* where forest is fragmented.
Long-eared owl *Asio otus*	Conifer stands in mosaic of fields and forest, sometimes in agricultural landscape and sometimes in extensive forest. Reported to have inhabited old-growth hemlocks. Poorly studied and understood in state.
Northern saw-whet owl *Aegolius acadicus*	Extensive mixed and conifer forests, especially higher than 1,500 ft and where there is dense understory of saplings and shrubs. Needs species-specific protocol for monitoring. Preyed on by larger owls.
Yellow-breasted sapsucker *Sphyrapicus varius*	Northern hardwood and mixed conifer-hardwood forests, especially where moist. Prefers foraging on softwoods. Common and widespread on plateaus, especially over 1,500 ft, increasing over the last 3 decades.
Olive-sided flycatcher *Contopus cooperi*	Formerly conifer forests, conifer and mixed forests, burned-over forest, edges of lakes and ponds. Good habitat not occupied. No confirmed nesting since the 1930s.
Yellow-bellied flycatcher *Empidonax flaviventris*	High-elevation forested conifer wetlands. Habitat is fragmented and scattered. Spruce forest and peatlands reduced by resource extraction. Population small and scattered. Good habitat unoccupied. (See text for more details.)
Alder flycatcher *Empidonax alnorum*	Shrub-scrub wetlands, riparian scrub, open sections of forested wetlands.
Blue-headed vireo *Vireo solitarius*	Conifer and mixed forests, especially riparian and swamp forests. Threatened by conifer pests and subsequent loss of hemlocks.
Common raven *Corvus corax*	Formerly confined to remote mountainous forests, now widespread in a variety of forests and mosaic of forest and fields, including some towns and agricultural areas.
Black-capped chickadee *Poecile atricapillus*	Variety of forests and forested wetlands dominated by conifers or deciduous species, or mixed.
Red-breasted nuthatch *Sitta canadensis*	Spruce, hemlock, and pine forests, including native conifers and exotic plantings. Inconsistent in occupation of many locations. Threatened by hemlock loss from pests.
Brown creeper *Certhia americana*	Mature forests and forested wetlands, primarily larger tracts of forest. Threatened by loss of large trees to diseases and pests.
Winter wren *Troglodytes troglodytes*	Cool, moist forests with downed timber and foliage diversity. Tends to be associated with conifers, especially hemlock and spruce.

(Table 1 continued on next page)

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Golden-crowned kinglet *Regulus satrapa*	Native and exotic conifers, including red spruce, Norway spruce, hemlock stands; generally mature trees. Threatened by hemlock loss from pests.
Veery *Catharus fuscescens*	Not only in well-stratified forest with shrubs, but also in forested wetlands and shrubby thickets, including heaths.
Swainson's thrush *Catharus ustulatus*	High-elevation conifer forests and wetlands, including riparian hemlock and spruce woods; seeps and springs. Seems to adjust to silvicultural treatments, nesting at edges of clear cuts. Forages in blueberry shrub thickets within forests. Threatened by forest fragmentation and decrease in understory structure.
Hermit thrush *Catharus guttatus*	Mixed forest and conifers, generally at higher elevations and cooler micro-climate than Wood Thrush (*Hylocichla mustelina*). Increasing in state while Wood Thrush is decreasing.
Golden-winged warbler *Vermivora chryoptera*	Found locally in tamarack swamps, thickets, and forest edge in the Pocono region. Not found in most boreal forests or forested wetlands except at edges of beaver dam meadows, and scrub near spruce-dominated forest. Threatened primarily by lack of disturbance regime that creates desired habitat mosaic.
Nashville warbler *Vermivora ruficapilla*	Forest edges and gaps in higher elevations (>1,500 ft), including bogs, swamps, old orchards, pond and stream edges, meadows with scattered trees and bushes.
Magnolia warbler *Dendroica magnolia*	Conifer forests of various ages, including young, close-growing conifers, mixed forest, and old-growth conifers. Can have high densities in spruce and hemlock. Loss of conifers through disease and pests is a threat.
Black-throated blue warbler *Dendroica caerulescens*	Northern hardwood/hemlock and spruce forests with well-stratified woody vegetation. Forest simplification and fragmentation are major threats.
Yellow-rumped warbler *Dendroica coronata*	Conifer forests, both natural and planted,including pine plantations. Expansion in state has been documented since 1980s.
Black-throated green warbler *Dendroica virens*	Mixed and conifer-dominated forests. Higher densities in older forests.
Blackburnian warbler *Dendroica fusca*	Tall conifers and sometimes deciduous trees. Strongly associated with hemlock and spruce, but also found in oaks. Benefits from old growth attributes. Greatest threat is loss of large conifers, especially hemlocks, from pests.
Northern waterthrush *Seiurus noveborecensis*	Boreal forested wetlands, and edges of slow-moving streams and ponds with dense understory. Limited by forest fragmentation and simplification at higher elevations and by the health and size of peatlands with shrub cover.
Canada warbler *Wilsonia canadensis*	Forest interior species usually found at higher elevations and where there is cool, moist forest with high foliage density in understory and shrub layer. Found in peatlands and in mixed habitat dominated by large hemlocks at elevations below 1,000 ft. Threatened by loss of shrub layer, simplification of vegetative structure, forest fragmentation, and pests of hemlock.
White-throated sparrow *Zonotrichia albicola*	Forest and wetland with cool microclimate and strong shrub component. Often in peatlands. Also found in rights-of-way, stream and lake edges at higher elevations (generally >2,000 ft).
Purple finch *Carpodacus purpureus*	Edge of conifer and mixed forests, including forested wetlands. Increasing on Pennsylvania BBS routes.
Red crossbill *Loxia curvirostra*	Nests occasionally in native conifer forests and swamps, including lower-elevation riparian conifers and pine barrens. Limited by the size, health, diversity, and distribution of conifer forests. Nests in Norway spruce in New York.
White-winged crossbill *Loxia leucoptera*	Possibly nests in eastern and northern Pennsylvania. Forages on small-coned conifers, including exotics.
Pine siskin *Carduelis (Spinus) pinus*	Erratic nester throughout the State including towns. Not associated with native spruce or fir forests in Pennsylvania. Can nest in backyards and towns. Feeds not only on conifer seeds but also on annual and perennial herbs and grasses.
Evening grosbeak *Coccothraustes vespertinus*	Occasionally nests in high-elevation mixed forests, including edges, backyards with trees, and conifer swamps. Responds to caterpillar outbreaks (elm spanworm).

disturbed forests. It is among those species associated with "disturbance maintained woodlands" (Hunter et al. 2001). Suppression of forest fires in some areas and lack of support for conifer forests in others are two of the limiting factors for this species in its breeding range (Altman and Sallabanks 2000, Wells 2007). Like other migrant songbirds that winter primarily in southern Central America and northwestern South America, the olive-sided flycatcher has declined in recent decades. The highest known winter densities occur in the Colombian Andes (Altman and Sallabanks 2000). Other similarly declining species that winter in the same region include golden-winged warbler (*Vermivora chrysoptera*), cerulean warbler (*Dendroica cerulea*), and Canada warbler (*Wilsonia canadensis*) (DeGraaf and Rappole 1995, Stotz et al. 1996, Wells 2007). The decline of olive-sided flycatcher even where the nesting habitat has not changed or has been restored is an obvious reason for concern and suggests that limiting factors on the wintering grounds or in migration may also be important (Marshall 1988, Wells 2007).

Yellow-bellied flycatcher (*Empidonax flaviventris*). Emphasis has been placed on the yellow-bellied flycatcher because some research has been conducted on it in the state, and it illustrates many of the challenges facing ornithologists who are attempting to conduct monitoring or advance conservation on behalf of the wildlife that depends on this habitat.

The yellow-bellied flycatcher often occurs with other species associated with conifer forests. In particular, almost all territories overlap with active nesting territories of northern waterthrush (*Seiurus noveboracensis*), Canada warbler (*Wilsonia canadensis*), white-throated sparrow (*Zonotrichia albicolla*), and purple finch (*Carpodacus purpurea*). All of these species benefit not only from the conifer component of the forest, but also from canopy gaps. White-throated sparrow was not a common bird in the region before deforestation, and subsequently its population increased in shrubby areas (Dwight 1892). Concern has been raised in the last two decades for this suite of birds, but even in the 1980s the boreal forest element in the Pennsylvania avifauna was generally neglected (Gill 1985).

The yellow-bellied flycatcher is one of the most characteristic breeding birds of the boreal conifer forest ecosystem (Gross and Lowther 2001, Dunn and Blancher 2004). This species reaches the southern extent of its current breeding range in Pennsylvania, but formerly nested occasionally at isolated high-elevation forests of the southern and central Appalachians as far south as Grandfather Mountain, NC (Gross and Lowther 2001). These Appalachian Mountain sites tend to be characterized by old-growth structure or elements within large core forest matrices. The few locations where yellow-bellied flycatchers have nested in recent decades are in the highlands of the Allegheny Plateau west of the Susquehanna River from North Mountain to the Allegheny National Forest (Gross 2002a, 2002b; Second Pennsylvania Breeding Bird Atlas 2009). Pennsylvania locations have not had major human disturbance for over 70 years (Mellon 1990, Gross 2002b).

Contrary to previous reports (Bent 1942, American Ornithologists' Union 1953), yellow-bellied flycatchers have not nested in the Pocono Mountain region for several decades (Gross 1992a, 2002b), but some suitable habitat does exist in that region. Most Pocono bogs and swamps supporting yellow-bellied flycatcher were destroyed, some in the late 1930s (Street 1954), for peat bog excavation, dam building for recreational lakes, vacation home development, and road-building (P. Street, personal communications at Pocono Lake Preserve, Berwyn, PA, 2001). The yellow-bellied flycatcher is designated as a stewardship species for the Northern Forest (Dunn and Blancher 2004). Although Breeding Bird Survey (BBS) routes have not indicated a decline in this species, it is poorly served by a roadside survey such as BBS because much of its range either is in the mountains and wetlands of the northern United States or lies north of the road network in Canada (Gross and Lowther 2001). This species has increased in New York State, especially in the Adirondacks (Peterson 2008b) and in Ontario (Bird Studies Canada et al. 2006), but seems to have declined in the White Mountains of New Hampshire (King et al. 2008). Yellow-bellied flycatcher has the deserved reputation to be quiet and unobtrusive, so it is easy to overlook in surveys and, as a result, some breeding locations may be unidentified or the extent of use underestimated.

Locations where yellow-bellied flycatchers have nested in Pennsylvania have certain macrosite characteristics. They have been found nesting only in large, unfragmented forests above 1,600 feet and generally above 600 feet. Almost all occupied nesting sites are in the glaciated section of the Allegheny Plateau. The largest and most regular population of yellow-bellied flycatcher is in a boreal conifer wetland complex (Dutch Mountain wetlands of western Wyoming County), and most other sites are some kind of conifer-forested wetland (Fike 1999; Gross 2002a, b). Most regular sites are headwater wetlands surrounded by contiguous forest in all directions for at least 1 mile. Conifer forests that support this species are sometimes still in "recovery" from timbering >70 years previously. Peatlands were removed for the commercial production of peat and also flooded to create recreational water bodies. Flooding by beavers and subsequent reforesting and moss reestablishment may also be a factor in the increasing suitability of sites for yellow-bellied flycatcher (Mellon 1989). Spatially, many of these breeding locations appear quite isolated and dispersed even within a localized area.

The yellow-bellied flycatcher was rediscovered nesting in Pennsylvania during the first Pennsylvania Breeding Bird Atlas after 60 years without nesting evidence (Gross 2002a, 2002b). Microsite characteristics are cool, shady, moist forest usually with a high percentage of moss as ground cover, giving the species a nickname of "moss tyrant." The only regular nesting grounds in recent decades are in conifer swamps, but this species also may nest along cool, shaded streams with moss and downed timber. Yellow-bellied flycatcher territories often have attributes of old-growth conifer forest with a diverse age and size structure of trees, a pit and mound microtopography, diverse herbaceous and small woody plants, and large volumes of standing and fallen dead timber (Tyrrell and Crow 1994). Territories occur in gaps in the canopy produced by soil characteristics or windfalls. Territories always have conifer trees as dominants in the overstory, but also contain nearly equal amount of coverage by deciduous trees, generally those associated with northern hardwood forests. Pennsylvania sites are usually dominated by conifers such as red spruce, eastern hemlock, eastern white pine, and sometimes American tamarack or black spruce. Red spruce typically are dominant, some reaching or exceeding 100 years old (Davis et al. 1995). Mixed in with the conifers are usually red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), and black tupelo and, more marginally, American mountain ash (*Sorbus americanus*) and American beech (*Fagus grandifolia*). Some Pennsylvania sites are dominated by eastern hemlock, including older specimens of each. Sites also tend to have a diversity of shrubs, especially blueberries (*Vaccinium* spp.), swamp azalea (*Rhododendron viscosum*), sheep laurel (*Kalmia angustifolia*), Labrador tea (*Ledum groenlandicum*), wild raisin (*Viburnum cassinoides*), leatherleaf (*Chaemaedaphne calcyculata*), bog rosemary (*Andromeda glaucophylla*), and mountain holly (*Nemopanthus mucronatus*).

The ground cover usually includes diverse broad-leafed herbs, sedges (*Carex* spp.), and mosses. Some forest floor plant species characteristic of boreal forests are usually associated with yellow-bellied flycatcher territories, including goldthread (*Coptis trifida*), starflower (*Trientalis borealis*), bunchberry (*Cornus canadensis*), creeping snowberry (*Gaultheria hispidula*), blue bead-lily (*Clintonia borealis*), twinflower (*Linnaea borealis*), and cinnamon fern (*Osmunda cinnamomea*). Cinnamon fern can be dominant in yellow-bellied flycatcher territories, providing extensive cover. Most nests have been found where sphagnum moss is prevalent ground cover; some nests are well-concealed in deep moss or tree roots. This species can respond to large-scale natural disturbances of mature forests as long as certain attributes of its micro-habitat are retained. A massive tornado hit the Tionesta area of the Allegheny National Forest in May 1985, flattening about 400 hectares of old-growth forest and toppling almost all canopy trees (Peterson and Pickett 1991). Yellow-bellied flycatchers nested along a small stream in this blowdown area in the early 1990s, where blowdowns of large trees created shady areas and regenerating seedings and saplings were abundant. Yellow-bellied flycatchers tend not to nest in unbroken spruce stands, preferring openings in the spruce canopy caused by soil conditions, wind-throw, or other disturbances. Family groups (fledglings) use not only the forested wetland but also adjacent conifer forest during post-nesting dispersal, when young are still dependent on parents. Some measurements of yellow-bellied flycatcher nesting habitat allow inferences of the preferred characteristics, but these data are incomplete and subject to change as more territories are measured. Of three occupied locations, vegetation samples were taken from 11 sample circles. In these sites, there was approximately 46-percent canopy cover with 29 percent by evergreen conifer trees. Within the territory, shrub cover was about 50 percent, fern cover 80 percent, and moss cover 88 percent. Litter cover also was very high at 96 percent. The profile of vegetation cover is presented in Table 2.

The yellow-bellied flycatcher's behavioral ecology promotes its persistence in the Appalachian Mountain landscape. Like other tyrant flycatchers, the yellow-bellied flycatcher demonstrates strong anti-predator behavior. Its nest is notoriously difficult to find, usually well hidden under vegetation, a leaning tree, or a log, or tucked in among roots of a tree or a tip-up blow-down (Gross and Lowther 2001; Fig. 2). The female tends to sit very tight, confident in the concealment provided by its mossy nest. She also protects the nest location by furtively travelling to and from the nest through dense vegetation. Pairs readily defend their nest areas from other songbirds, including blue jay (*Cyanocitta cristata*), a potential nest predator, as well as warblers and sparrows of a similar size. Like other *Empidonax* flycatchers and unlike other forest flycatchers, yellow-bellied flycatchers forage with sally gleans and upstrikes on leaves and stems within the dense vegetation of their nesting area (Fitzpatrick 1980, Remsen and Robinson 1990, Gross and Lowther 2001). This far south, pairs of this species will double-brood; the female builds a new nest as the male tends young of the first nest. The tendency for double-broods seems correlated with early arrival of the female in a territory (and perhaps philopatry), allowing time for the second nest. However, males can remain unpaired as late as mid-June before successfully pairing with a mate. Territories tend to be clustered in likely habitat with unmated males near pairs.

Table 2.—Vegetation present at various heights in yellow-bellied flycatcher territories.

Height in Feet (m)	Percent Cover (%)	Standard Deviation
2 (0.6 m)	87	12.2
4 (1.2 m)	63.6	21.8
6 (1.8 m)	35.1	17.6
8 (2.4 m)	22.1	11
10 (3.0 m)	26.4	5.9
12 (3.7 m)	23.4	13.2

The breeding population in Pennsylvania is quite small and varies yearly. Some locations are occupied only intermittently or abandoned after a year or two of occupation. The population of yellow-bellied flycatcher is difficult to track because site occupancy is variable and some singing males are not paired. The population in the Dutch Mountain wetlands of Wyoming and eastern Sullivan counties has ranged from three to 13 territories (Gross 1992c; D.A. Gross, unpublished data). Five other sites in the Northeast counties have produced young in at least one year, but unevenly through the years. Only one site has been occupied for at least 19 consecutive years and it is not always productive. Only one site in western Pennsylvania, the Tionesta Scenic and Research Area of Allegheny National Forest, is known to have produced young in each of the last 20 years. In some cases, alder flycatcher (*Empidonax alnorum*) occupies the same territories as yellow-bellied flycatcher previously occupied, implying some intra-generic competition in which the larger species dominated and replaced the other. Here is a summary of populations in Pennsylvania, acknowledging that site occupancy is variable:

- Dutch Mountain wetlands: 3-13
- Loyalsock State Forest: 1-3
- Other northeastern Pennsylvania sites: 8 (1-3 populations each)
- Northwest county sites: 2-4 sites (1-2 populations each)

Total: less than 25 known in any year (more sites than blackpoll warbler).

Blackpoll warbler (*Dendroica striata*). The first recent breeding evidence for blackpoll warbler was in 1993, when a male was heard on territory in Coalbed Swamp, Wyoming County (Davis et al. 1994, Gross 1994). The following year, a nesting pair was located and the first nest found (Gross 1994). Another nest was found in 1995 and breeding was confirmed during each of the next 10 years, 1994-2003 (Gross 2002, unpublished data). In 2005, blackpoll warbler was added to the state's list of endangered species on the recommendation of the Ornithological Technical Committee of the Pennsylvania Biological Survey after 10 consecutive years of breeding in the state. This population extends its breeding range south from the Catskill Mountains of New York (Hunt and Eliason 1999). Similar to other blackpoll warbler populations in the northeastern United States, the Pennsylvania population lives is an isolated island of boreal conifer habitat. The closest nesting population is about 100 miles northeast in the Catskills (Hunt and Eliason 1999).

In Pennsylvania, blackpoll warblers are found breeding only in spruce-dominated parts of forested wetlands. They often are found in the territories of yellow-bellied flycatchers but can also be found where spruces and other conifers are more dominant and few deciduous trees or other vegetation is present. Blackpoll territories may include upland conifer forest with its characteristically tall and large red spruce and eastern hemlock. Thus far, this species has been confirmed in only two conifer wetlands, but it may be found elsewhere. Singing males have been reported in various locations in the Pocono Mountains and the north-central highland forests. The history of this species is not well-understood in the state because much of the conifer forest of northeastern counties was cut before ornithologists visited and inventoried it. Blackpoll warblers could easily have nested in pre-timbered Pocono spruce forests without detection. Their territories often overlap with those of con-generic magnolia (*D.magnolia*), blackburnian (*D. fusca*), and yellow-rumped (*D. coronata*) warblers. The blackpoll warbler has one of the most restricted ranges and one of the smallest populations of any breeding species in the state. The last thorough survey, conducted in 2002 (Gross 2002), found 14 breeding territories and an additional four unattached but singing males. All of these blackpolls were in the Dutch Mountain wetlands of western Wyoming County (State Game Lands 57) in spruce swamps and forests. Surveys of some locations since the 2002 study suggest that this species is declining in areas where it has nested recently. The current total population is probably less than 25 pairs and possibly less than 15 pairs.

<u>Northern saw-whet owl (*Aegolius acadicus*)</u>. Although not a rare breeder or migrant in Pennsylvania, the saw-whet is a priority species for the Appalachian Mountain BCR (U.S. Forest Service 2002), thus deserving mention here. One of the most enigmatic yet charismatic of the region's birds, the northern saw-whet owl has received long-overdue attention recently. For several years, this species was considered a "Candidate-Undetermined" in Pennsylvania due to the lack of documentation of its breeding population. Many factors have led to consideration of the northern saw-whet owl as a rare breeding bird in Pennsylvania; it is now viewed as deserving more monitoring and inventory as part of the night bird group (Brauning et al. 1994, Gross 1998a).

The northern saw-whet owl has posed challenges to ornithologists for several reasons. Saw-whets are diminutive, nocturnal, and well hidden in the dense vegetation they inhabit. Although notoriously tame when found, they are easily overlooked. Individuals freeze in place when discovered, apparently as a means of concealment (Swengel and Swengel 1992). The saw-whet vocalization period is fairly short and confined to early spring (although they respond to imitations of their calls much later) (Palmer 1987, Swengel and Swengel 1987). During night hours when saw-whet owls are vocally active, birders do not visit the forested areas they inhabit. Until only recently, most vocalizations were not available in commercial products or at free websites that allowed interested observers to learn identification by recognizing these sounds. Because the saw-whet is migratory, it is important to avoid confusing migrating individuals with breeding birds. Northbound saw-whets are still migrating when some pairs have begun nesting in Pennsylvania. According to some observers, migrants do not respond vocally to taped song, so an audio-lure (tape/CD/MP3 playback) method may not sample many nonbreeders (D. Brinker, Maryland DNR, personal communication). Observers may find it difficult, however, to separate migrants from breeders in single short-term visits.

Recent studies have shed more light on this diminutive nocturnal bird. In a statewide breeding survey project (known as "Project Toot Route"), volunteers conducted eight-point road routes with an audio-lure protocol that changed our impression of its nesting range and abundance in Pennsylvania (Gross 2000, 2001). Project Toot Route and the subsequent Second PBBA have revealed that the number and distribution of saw-whets is larger than previously documented (Stone 1894, Sutton 1932, Todd 1940, Poole 1964, Gross 1992a, Cannings 1993, Milling et al. 1997, Second Pennsylvania Breeding Bird Atlas 2009). At least three singing saw-whets were found within 20 miles of the Mason-Dixon Line in Pennsylvania mountains, including the Allegheny Plateau and South Mountain (perhaps continuing south to the Catoctin Mountains, MD). The perceived gap in breeding range in southwestern Pennsylvania and east-central West Virginia probably reflects lack of coverage in surveys rather than a paucity of owls.

Routes with the larger number of saw-whets were primarily on North Mountain or in the northwest counties, especially in and near Allegheny National Forest (Gross 2000, 2001). Most northern saw-whet owls live up to their reputation for breeding in cool, higher-elevation forests with a well-diversified foliage structure. The higher vegetative cover enables saw-whets to forage low near their rodent prey without detection and also to avoid predation from larger owls (Cannings 1993). Virtually all saw-whets found on "toot routes" were in large patches of forest, but some have been reported at the edges of forests. They can be fairly common in forested wetlands with a healthy shrub and sapling layer. Good vegetative structure and conifer cover seem to be components important to its breeding habitat. Cool summer temperatures may also be necessary for saw-whets.

Brief Mention of Other Avian Members of the Boreal Forest Community

Yellow-bellied sapsucker (*Sphyrapicus varius*). This medium-sized woodpecker is one of the characteristic breeding birds of the Pennsylvania mountains (Gross 1992d). It is widespread and common across the Allegheny Plateau and higher elevations of the Ridge and Valley section. Sapsuckers may be the most common breeding woodpecker of the North Mountain region and the Allegheny National Forest. It is found not only in large forest tracts but also in yards and orchards of the plateau. It is one of the most common birds in boreal conifer forests and wetlands and is also found in northern hardwoods and mixed hardwoods and eastern hemlock forests. South of Pennsylvania, this medium-sized woodpecker is declining.

Swainson's thrush (*Catharus ustulatus*). The rarest of the thrushes in Pennsylvania is associated with conifer and mixed conifer-deciduous forests at higher elevations (Brauning 1992). It is found most commonly in northwestern counties, where there are extensive forests at higher elevations. It seems to be increasing in northeastern Pennsylvania, although not always occupying locations where it was found prior to the exploitative logging period (Cope 1936, Brauning 1992). Some ornithologists consider the Appalachian Mountain population as a distinctive subspecies in the olive-backed group of Swainson's thrush (*Catharus ustulatus appalachiensis*) (Ramos and Warner 1980, Pyle 1997, Mack and Yong 2000), The Appalachian subspecies spends the winter in Colombia and northeastern Peru, where bird conservation is considered problematic due to loss of habitat (Ramos and Warner 1980, Mack and Yong 2000). Its breeding distribution is rather localized but much more widespread in the northwestern Pennsylvania counties than elsewhere. The old-growth eastern hemlock-white pine forest of the Tionesta Natural and Scenic Area in the Allegheny National Forest probably has the largest population in the state (Haney and Schaadt 1994a, 1994b, 1996). Formerly, it was common in Tamarack Swamp, Clinton County (Cope 1901), but has not been found in return visits for several decades (Reimann 1941, Pennsylvania Society for Ornithology 2006). It formerly was fairly common on North Mountain, Sullivan County, especially in the "virgin forests" (Dwight 1892, Cope 1936), but now it is only scattered and local (Gross 2003, Sauer et al. 2005, Pennsylvania Society for Ornithology 2006). Not only is Swainson's thrush rare, but it is also secretive and easily overlooked by observers.

At one time, Swainson's thrush was reportedly locally common to abundant in Pennsylvania's northern counties (Poole unpublished manuscript; Brauning 1992). It was rare and local in Warren County where it was found nesting to "deepest parts of the virgin forest" in Tionesta (Cope 1936). This species also once was more common in the Appalachians south of the Mason-Dixon Line. It was locally common in red spruce forests in West Virginia before timbering (Bent 1949, Hall 1984). It certainly is more common and widespread in the extensive mixed forests of northwestern Pennsylvania than in the Northeast, where many of the reports of this species singing in forests turn out to be unmated males (personal observation).

Recent surveys suggest that this species is gradually reclaiming parts of its breeding range. Although it is common in Pennsylvania's largest old-growth conifer forest, the Tionesta Scenic Area of Allegheny National Forest (Haney and Schaadt 1994a, 1994b, 1996), it also is found at edges of clearcuts, in openings caused by windthrow or forest roads, and in blueberry glades within forests. It is another paradoxical species that responds to attributes of both old-growth forest and disturbed forests (Mack and Yong 2000, Hunter et al. 2001). It also forages for insects on the wing and by up-striking more than do other forest thrushes, giving it the "mosquito thrush" nickname in the past (Bent 1949, Mack and Yong 2000). No matter what the micro-habitat features, this thrush is found almost exclusively in large-scale forests at higher elevations in the Appalachians.

Canada warbler (*Wilsonia canadensis*). This priority species for the Appalachian Mountain region has been declining in the Northeast for several years, apparently as a result of habitat changes (Conway 1999, U.S. Fish and Wildlife Service 2002, Lambert and Facchio 2005, Wells 2007). Although declining in Pennsylvania as well, the Canada warbler can still be locally abundant in boreal forested wetlands. In Pennsylvania, the Canada warbler breeds in cool, moist forests and forested wetlands, especially where conifers and heaths are dominant. It particularly favors eastern hemlock and spruce. Canada warblers are notorious for their preference for dense growth of rhododendron and other heaths along mountain streams and moist forests. It tolerates minor disturbances, responds well to gaps in canopy cover, and is not particularly area-sensitive within a forested landscape, but it is generally found in large-scale forests. Like other species discussed here, the Canada warbler benefits from greater vegetative structural diversity found in naturally occurring and manmade canopy gaps of forests and forested wetlands. It can be locally abundant in boreal conifer swamps of North Mountain and the Pocono region (Gross 2002a; D. Speicher, Pocono Avian Research Center, personal communications, 2009).

Red crossbill (*Loxia curvirostris*). One of the most enigmatic conifer-obligate bird species that has merited recent conservation concern is the red crossbill. Red crossbills are very rare and erratic in Pennsylvania and most of the northeastern United States (Fingerhood 1992, Atkisson 1996). Historically, this species has nested (or attempted to nest) in several counties of Pennsylvania ranging from the northern tier to the Philadelphia area (Fingerhood 1992, personal observation). In the last two decades, red crossbills have apparently nested or attempted to nest near Lopez, Sullivan County; near Pine Creek Gorge, Tioga County; and in Sproul State Forest, Clinton County. The Second PBBA results may reveal more locations. The red crossbill may actually be a group of very similar-looking bird taxa that could be considered species (Groth 1993a, Parchman et al. 2006). These proposed "cryptic species" are at least nine distinct "types" that vary by size of bill and body, as well as by vocalizations (Groth 1993a, 1996; Benkman et al. 2009). Each type of crossbill is best adapted to certain species of conifer for which its bill is especially efficient in opening the cone (Benkman 1987). Red crossbill types 1 and 2 have been confirmed nesting in the Appalachians (Groth 1988). These types are best identified by subtle differences in their call notes, which allow them to sort out with little mixing between ecotypes (Groth 1993a, 1996). Several types probably nested in New York during the latest PBBA, between 2000 and 2005 (Young 2008a).

In Pennsylvania, red crossbills of Type 1 have been observed feeding on eastern hemlock, eastern white pine, and white spruce (*Picea glauca*) (personal observation). The "old Northeastern" red crossbill (Dickerman 1987) is probably the Type 1 red crossbill, a medium-sized form with an upward inflected flight note that also is found in the southern Appalachians and the Pacific Northwest (Groth 1993a, 1996; personal communication). In New York, red crossbills have been feeding and nesting in Norway spruce (*Picea abies*) and feeding in red pine (*Pinus resinosa*) and white spruce (*Picea glauca*) (Young 2008a). White-winged crossbills also have been reported breeding in Pennsylvania. This more northerly crossbill nests in New York within 50 miles of the Pennsylvania border and feeds primarily on soft-bracted conifers, including both Norway and white spruces (Young 2008b). Both crossbills possibly occur in native as well as planted conifer forests. Current distribution of the red crossbill may not include its historic range.

Historically, they have been found nesting at a variety of sites, including riparian pines at various locations along the Susquehanna River and pine barrens near the Philadelphia area (Fingerhood 1992, Brauning et al. 1994).

Other conifer specialists, such as evening grosbeak, have a history of nesting in Pennsylvania. The evening grosbeaks were responding to an outbreak of elm spanworm (Conant 1994, personal observation). Infestations and then declines of spruce budworm (*Choristoneura fumiferans* Clem.) in southern Canada are possible cause of increases, subsequent declines, and consequent irruptions of many boreal songbird species, including crossbills, chickadees, and purple finches, into the northeastern United States (Bolgiano 2005). Opportunities may arise for both the birds to colonize new locations and for researchers to study these distribution changes. As conifer specialists, crossbills are particularly sensitive to the availability of conifers on a large scale (Benkman 1993). Older conifers produce more cones, and management for older conifers would probably result in an increase in these species. More crossbills breed where there are larger cone crops (Benkman 1990; Young 2008a, b).

CHALLENGES AND FUTURE DIRECTIONS

Inventory and Monitoring Challenges

One of the most obvious challenges for management and conservation of boreal conifer bird species is the inventory and monitoring of populations. The size and regularity of these populations are not well understood, so it is difficult to develop and implement management plans. The difficulties are raised because these species:

1. Occupy remote locations, often without convenient trail or road systems for survey access.
2. Need specialized survey protocols, including audio–lure and mapping of territories, and a need to regularly conduct surveys to determine persistence and trends.
3. Require multiple survey visits, including early and late seasons, within one nesting season. (Some species nest fairly early and others nest late.)
4. Tend to be more difficult to detect and, when present, easily overlooked, even by accomplished observers.
5. Occur in biologically sensitive sites incompatible with repeated or high human visitation.
6. Occupy locations rather irregularly due to uneven environmental conditions or other constraints, such as cone crop size and varying rain amounts that affect swamp conditions.
7. May be somewhat nomadic, depending on species, and do not regularly occupy locations even under the best conditions.
8. May have uneven sex ratios in some species, requiring extra effort to determine occupancy of pairs, not only singing males, and viability of the breeding population.
9. May not occupy locations every year as a breeding pair. Some locations nevertheless are occupied persistently if not annually, so multiple-year studies are necessary to determine population status.

Challenges for monitoring and inventory of these rare boreal birds include basic identification issues that are important to address for the credibility of the methods and results. The yellow-bellied flycatcher is a member of the *Empidonax* genus of tyrant flycatchers, one of the most challenging groups of birds to identify (Kaufman 1990, Kaufman and Sibley 2002). It serves well as an example of this challenge.

Despite perceived advances in birding skills, knowledge of the avifauna, and bird identification products, some difficulties remain in coverage of yellow-bellied flycatcher, including confusion with other species, and identification challenges presented to the observer. For many decades, the genus *Empidonax* has posed difficulties with visual identification, to the point where some texts used the same illustration for multiple species.

Few observers have much experience with this species on the nesting grounds. Its vocalizations still can be confused with other birds, especially eastern wood-pewee (*Contopus virens*) and least flycatcher (*Empidonax minimus*). Most commercial products of bird vocalizations condense in the same track sounds that are rarely given in the wild together as a short sequence. These audio products also compress the vocalizations, decreasing the time between calls and giving the illusion of a faster pace than the actual frequency of the advertising song (*che-bunk*). The *"che-bunk"* advertising song (also an abrupt, hoarse *killink* or *killik*) is similar to least flycatcher's but given at a more leisurely pace of 6-8 times per minute, compared to the frenetic pace of about 60 times per minute by a male least flycatcher. In fact, this is a diagnostic identification feature of a yellow-bellied flycatcher's advertising song. Males tend to switch to a single-syllable song, perhaps as a demonstration of status—*schleck!*, *psek!*, or *kik!*—similar to the call of downy woodpecker (*Picoides pubescens*) or hairy woodpecker (*P. villosus*) when they become paired. This switch from an advertising song to another song is similar to the pattern found in Pacific-coast flycatchers, *Empidonax difficilis* (Lowther 2000), and many wood-warblers (Spector 1992). Migrating males also will sing the advertising song in early June, confusing the situation for observers. Many males that sing the advertising song after early June are unmated males attempting to find a mate, which they sometimes do successfully. If they wander widely (more than 90 m from a center point), they also are likely to be unmated males. Individual males are sometimes rewarded for their persistence on territory. On the other hand, once pairs have young in nests, they are generally quiet and males often do not respond to audio-lure at this stage.

Other identification challenges include the red crossbill types, which are most easily verified by their call notes (Groth 1993a). If possible, aural recordings should be made of questionable records to review and verify an identification.

Possible Solutions for Inventory and Monitoring

Concerted efforts will be needed to inventory and assess bird species populations in the boreal community. Some individuals may occupy territories but not reproduce for lack of a mate. It may be necessary to design and implement surveys that include an assessment of territory occupancy as well as breeding status and success. Off-road bird surveys will need to be devised and maintained to assess population sizes and persistence of the indicator species of this ecological suite. Some surveys may require special audio-lure (tape playback) protocols as part of their design. Some standardized bird monitoring techniques such as point counts have their place in such habitats, but more focused procedures such as the mountain bird monitoring protocol (Hart 2007) or Monitoring of Avian Productivity and Survivorship (MAPS) (DeSante et al. 2009) might be more appropriate and successful in some locations. These approaches, however, require extensive commitment and resources from individuals or organizations. An older technique known as "spot-mapping" or "territory mapping" has been successfully implemented in monitoring trends in spruce forests (Robbins 1970; Hall 1983, 1984). Although time-consuming, this technique could be useful with geo-referencing and other improvements for monitoring a bird community of particular concern.

Some solutions proposed for surveying this suite of birds could act as a monitor of these threatened ecosystems' health (Pennsylvania Game Commission and Pennsylvania Fish and Boat Commission 2005):

1. Involve the public in "citizen science" projects that inventory and monitor areas of greatest interest (e.g., eBird, BBS routes, Important Bird Areas (IBA) monitoring, Breeding Bird Censuses, Breeding Bird Atlases).
2. Adopt off-road point counts in high-elevation forests and wetlands, especially in IBAs and locations that support the most rare and sensitive species.
3. Initiate or support specialized surveys of this habitat, particularly the Mountain Bird Monitoring Protocol (Hart 2007) and MAPS (DeSante et al. 2009).
4. In addition to completing standardized surveys, conduct species-specific surveys that target habitat associated with the species; use geo-referencing and audio-lure when appropriate.
5. Track territory-occupancy and the breeding status and success of selected species by mapping (digital geo-referencing).
6. Synthesize various bird surveys with geo-referenced appropriate measurements of habitat health (e.g., vegetation measures and tree pests).
7. Use banding and other methods of tracking individuals to better determine philopatry, nest success, and habitat use,

including post-nesting dispersal; follow MAPS protocol in selected locations.

8. For diurnal forest raptors and nocturnal bird species in this landscape, adopt special surveys, which may be part of or complement statewide standardized surveys.
9. Track changes in bird populations in areas where treatments are implemented or natural changes in the habitat have occurred (a fire, for example) to better understand how these changes in habitat affect bird species of conservation concern.

Promise and Potential for Boreal Conifer Forests

Threats to boreal forests and wetlands: One of the most pervasive threats to the boreal forests and forested wetlands of Pennsylvania originates from the lack of awareness that these ecosystems are part of the state's natural communities and therefore merit protection and management on their behalf. There also are competing values even among the wildlife community, which places more emphasis on flooding wetlands to create standing water that support waterfowl and sport fisheries. The cool, comfortable highlands of Pennsylvania have been a recreation and second-home destination for many decades. Conifer forests and wetlands often suffer in competition with recreational space and housing. In addition, wind energy and gas exploration promise to compete for resources in the Pennsylvania highlands, potentially replacing conifer forest permanently, severely fragmenting the remaining tracts of forests, and threatening to pollute boreal conifer wetlands.

Ornithologists and conservationists have long lamented the loss of forested wetlands and conifer forests, often to peat excavation, reservoir creation, and the long-term effects of logging on a grand scale in Pennsylvania and elsewhere in the Northeast and mid-Atlantic. Past widespread land alterations have had long-time negative impacts on both the avian populations and the potential for recovery. Draining, diking, damming, and other hydrological disruptions have irrevocably changed habitat with potential for these rare species. The recreational industry has caused the loss of many wetlands, including peatlands, through flooding to create recreational water bodies. Since yellow-bellied flycatcher and other ground-nesting birds often use sphagnum moss or dense ground cover, mosses must be protected by preventing desiccation and excessive trampling.

Another threat to these habitats is forest fragmentation, especially from road construction. Wind energy development is a looming threat to any high-elevation natural community because of its infrastructure development and consequential fragmentation (U.S. Fish and Wildlife Service 2003, National Research Council 2007). As a result of these concerns, the Pennsylvania Game Commission has instituted a cooperative agreement with wind-power development companies with a bird population and mortality protocol (Pennyslvania Game Commission 2007). Forest would be replaced by grassy and weedy areas most likely dominated by invasive plant species and at a scale not helpful to species of conservation priority. Acidic atmospheric deposition is another threat to the forests of highland Pennsylvania, but that subject has been covered by other presenters at this conference and other authors and so will not be covered thoroughly here. Atmospheric acid deposition is a possible concern for reproductive capacity of many forest songbirds, including common species (Hames et al. 2002). Global climate change also has potential for a significant impact on this group of species (Rotenhouse et al. 2008). Concern for effects of this change on bird and wildlife populations could stimulate more specific monitoring of species and habitats most sensitive to possible habitat changes.

Conifer forests do not seem to have recovered as quickly as have the deciduous forests from the lumbering era. The remaining boreal conifer forests and wetlands are isolated and fragmented, often with dissimilar habitat bordering them. Conifer stands tend to be dense and without interruption in the canopy. Gaps that imitate the effect of wind-throw would imitate conditions conducive to several species discussed in this paper. These forests tend to be either destroyed or ignored. Some management of the forests for characteristics that favor priority species is possible with proper planning and commitment of resources.

The quality of forests also suffers from various tree pests and diseases. Among these are the hemlock woolly adelgid

(*Adelgis tsugae*) and the elongate hemlock scale (*Fiorinia externa*). Forest pests such as hemlock woolly adelgid and spruce beetles are significant threats to the state's conifer forests. Hemlock woolly adelgid infestations can be severe in the Appalachians, where high tree mortality dramatically changes the forest canopy and understory. Drought exacerbates these pests' effects on eastern hemlock. Excessive white-tailed deer (*Odocoileus virginianus*) herbivory is a constant threat to forest health in Pennsylvania (Latham et al. 2005). The forest vegetation structure is simplified and plant diversity diminished by excessive deer browsing. Some of the species discussed in this paper benefit from a rich and diverse understory that excessive deer browse can destroy. Many of the boreal conifer forests are in extensive forest tracts, generally in their favor, but these areas sometimes do not receive the hunting pressure on the deer herd necessary for good forest health.

Unoccupied habitat remains available for some of our target conservation bird species. In some cases, males declare territory but cannot attract females. This pattern suggests that there are some population limits on the wintering ground and migration route. It will be a challenge to address limitations that may be occurring on the wintering grounds for these species and partner with organizations to find solutions to these challenges (Pashley et al. 2000, Wells 2007). Global climate change also is a threat to these conifer forests (Rotenhouse et al. 2008). Species with narrower elevational ranges are particularly vulnerable to rapid climate change, and isolated populations will be challenged by shrinking size and connectivity of these habitat islands. Many of the higher-elevation and northern species of Pennsylvania are probably at greatest risk to state extirpation by rapid changes in climate, especially warming. On the other hand, possible increases in precipitation may create some conditions conducive to spruce in areas now too dry for propagation and growth.

Potential for boreal forest conservation and management: In recent years people have increasingly recognized and appreciated these forests in recent years. Several sites are listed in the Pennsylvania Important Bird Area Program (Crossley 1999, Audubon Pennsylvania 2009). Most sites with significant boreal conifer forest are owned by public entities, particularly the Pennsylvania Game Commission, the U.S. Forest Service (Allegheny National Forest), and DCNR Bureau of Forestry. Several species are listed in the Pennsylvania Wildlife Action Plan (Pennsylvania Game Commission and Pennsylvania Fish Boat Commission 2005). The bird species are not alone in this regard. Among those species given priority for conservation is the Northern Flying Squirrel, which has endangered status in Pennsylvania. Planning and management for wildlife lands have incorporated protections for those species listed by the Pennsylvania Natural Heritage Program.

Planning for the restoration of older forests is critical for the future of conifer forests and wetlands. An old-growth forest system is being planned for Pennsylvania, with most projected old growth in the central part of the state (Jenkins et al. 2004). Such forests would primarily be northern hardwood, hemlock, pine, and mixed forests. These forest types would not be optimal for many of the boreal conifer forest bird species but certainly would benefit many. Increasing the area of older conifer forest would be particularly beneficial to crossbills (Benkman 1993). Planning for older forests does not preclude planning for early-succession forests and disturbance regimes necessary to create gaps sufficient to support a suite of species that depend upon that habitat (Hunter et al. 2001). Indeed, a matrix of forest types will benefit forest bird species that now are not flourishing where most forests are middle-aged and lacking the foliage and spatial heterogeneity necessary to support them.

The Pennsylvania Important Bird Area program is a key bird conservation initiative that prioritizes areas for conservation, inventory, and research. Some locations designated as Pennsylvania Important Bird Areas that include boreal forest are: Heart's Content and Tionesta Scenic and Research Natural Area of Allegheny National Forest, McKean and Warren Counties; Tamarack Swamp Natural Area, Clinton County; Black Moshannon State Park, Centre County; Rothrock State Forest, including Bear Meadows Natural Area, Center, Elk, Cameron, and Clearfield Counties; Loyalsock (formerly Wyoming) State Forest, Lycoming and Sullivan Counties; Ricketts Glen State Park/Creveling Lake area (State Game Lands 13 and 57), Sullivan, Luzerne, and Wyoming Counties; Dutch

Mountain Wetlands, State Game Lands 57, Wyoming County; Promised Lake State Park and Bruce Lake Natural Area, Pike County; Pocono Lake Preserve area, including the Thomas Darling Preserve (Two Mile Run Swamp), Monroe County (Crossley 1999, Audubon Pennsylvania 2009). Some important sites may not be designated by the IBA system; if they were given this status, they might garner more support for protection.

Concerns are not limited to birds. Several areas also are designated as Important Mammal Areas because of their importance to particular mammals of conservation concern. These kinds of conservation plans overlap in many places because of shared concerns for certain ecosystems that support priority species.

Interest in the inventory and monitoring of birds in this ecosystem has increased as the knowledge and appreciation for the bird community has grown. More birders are seeking out these areas as part of their recreational birding and as part of their participation in "citizen science" projects, such as the BBA and eBird. Active research is taking place in the format of the MAPS program and owl banding (Project OWLNET) at the Tom Darling Preserve, Monroe County, on a boreal forested wetland bird community (D. Speicher, personal communication;, www.poconoavian.org).

Silvicultural practices have been shown to increase the amount and quality of spruce in mixed forest where regeneration is occurring slowly or not at all (Rentch et al. 2007). Thinning the deciduous component in the canopy of Allegheny Plateau forests (in Pennsylvania, generally red maple and American beech) where there are regenerating spruce seedlings and saplings could be an effective ways to increase the spruce component of our forests. Reducing basal area of the canopy by 50 percent has the potential to double red spruce basal area in a mixed forest after 20-40 years. Such strategies may be helpful to replace the hemlock that will inevitably be lost to hemlock woolly adelgid and other pests and diseases. The regenerating spruce also provides benefits for species needing thermal protection in winter, such as ruffed grouse (*Bonasa umbellus*) and snowshoe hare. Partnerships between different advocacy groups and agencies taking a multi-species ecosystem approach to forest management would generate results meeting the goals of many diverse organizations.

The natural regeneration of Pennsylvania boreal conifer forests has been taking place primarily through benign neglect. Natural recovery of spruce forests has progressed slowly as spruce regeneration has fanned out from core areas of mature trees. These core areas are primarily in forested peatlands but also in isolated uplands sites. Headwater wetlands are getting increased attention through advocacy for watershed protection. The spruce- and eastern hemlock-dominated wetlands are generally in headwaters of high-quality coldwater streams, important for trout fishing and as a water source for communities and industry. The loss of eastern hemlock, the State tree, could have devastating effects on populations of several bird species, trout, and other wildlife found more commonly in its deeply shaded forest. Application of insecticides and release of *Sasajiscymnus tsugae* beetles have potential for local treatment of hemlock wooly adelgid. County conservation districts, sportsmen's groups, and watershed protection organizations support the protection of headwater wetlands and forests. Concern for the loss of deep-shaded hemlock-lined streams is a common denominator between trout fishing and conifer-related birds that would encourage partnerships for the common cause of habitat and watershed protection. Some basic silvicultural techniques could significantly increase the size of spruce forests where natural regeneration is already occurring. Such advocacy and restoration efforts would benefit many bird species as well as mammals, including the northern flying squirrel. It will not be easy, but the path is paved for some successes with conservation of the ecosystems that support this overlooked suite of birds.

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BROOK TROUT MOVEMENT WITHIN A HIGH-ELEVATION WATERSHED: CONSEQUENCES FOR WATERSHED RESTORATION

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Abstract.—We used radio-telemetry to quantify brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) movements in the Shavers Fork of the Cheat River, West Virginia, and an adjacent second-order tributary (Rocky Run). Our objectives were to quantify the overall rate of trout movement, assess spatial and temporal variation in movement behaviors, and relate movement behaviors to variation in stream flow, water temperature, and access to coldwater sources. Brook trout residing in the small tributary demonstrated extremely low movement rates in summer and fall. In contrast, main stem trout exhibited high overall movement rates in the summer but low rates in the fall. Brook trout had a strong tendency to move upstream throughout the summer followed by a final pulse into smaller tributaries to spawn in the fall. Brook trout movements during the summer were significantly related to both maximum water temperature and the distance of fish from a coldwater source. These data indicate that trout inhabiting larger streams are capable of moving considerable distances to access required habitat, such as coldwater refuges and spawning habitat. Our results underscore the importance of a watershed-scale perspective for successful conservation and management of wild trout populations in this region.

INTRODUCTION

Physical, chemical, and biological factors exist within lotic systems as a complex patchwork, rather than as the smoothly continuous gradients of conditions often seen on land (Kotliar and Weins 1990, Giller and Malmqvist 1998). These factors can change dramatically on a temporal and spatial basis (Hildrew and Giller 1994). In particular, stream flow, water temperature, and invertebrate prey densities may vary significantly on a yearly, seasonal, daily, and even hourly basis. As a consequence, stream fishes often experience optimal, suitable, and poor habitat patches within the same general area depending on the time of the year and climatic conditions. In addition, trout require a variety of non-substitutable complementary habitat types (critical refuges, foraging habitat, spawning habitat) to complete their life cycle (Schlosser 1991, Behnke 1992, Schlosser and Angermeier 1995). Anthropogenic impacts usually reduce habitat complexity and quality while increasing the linear distance between high-quality non-substitutable complementary habitat types (Albanese et al. 2004). In response, stream fishes utilize specific sites (microhabitats) that blend an acceptable suite of physical, chemical, and biological characteristics possibly at several spatial scales, depending on conditions and needs (Dolloff et al. 1994, Young 1995, Torgersen et al. 1999).

Given these complexities, the ability of stream fishes to maximize survival, reproduction, and growth depends strongly on their ability to assess habitat quality and to move between different habitat types as needed (Berman and Quinn 1991, Gibson 1996, Torgersen et al. 1999). Movement denotes motion on a small scale, allowing individuals to utilize the best habitat for feeding, reproduction, and refuges from predators and environmental extremes on a daily and seasonal basis (Schlosser 1991, Meyers et al. 1992, Schlosser and Angermeier 1995, Gowan and Fausch 1996, Burrell et al. 2000, Gowan and Fausch 2002). Migration is used to describe extended, directional movement that is an integral part of the life cycle (Behnke 1992). Migration enables fish to reach habitats required

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annually by different life-history stages and to exploit refuges from large-scale disturbances (e.g., floods). Migration also allows gene flow and demographic rescue for small populations, and colonization or recolonization of unoccupied habitats (Northcote 1997, Swanberg 1997, Roghair and Dolloff 2005). Recently Fausch et al. (2002) used the term “ranging behavior,” commonly used in landscape ecology and metapopulation biology, to describe fish movement. The main characteristic is not unidirectional movement, as the term “dispersal” implies, but long-distance movement that ceases when fish encounter patches with suitable resources (Fausch et al. 2002). For simplicity, we will use the term “movement” in general terms. Researchers have confirmed that *Salmonidae*, and brook trout (*Salvelinus fontinalis*) in particular, exhibit high levels of movement despite continued discussions over extent, timing, and duration (Curry et al. 2002, Rodriquez 2002).

A complete understanding of trout movement and habitat use is therefore critical to fisheries and resource professionals to properly manage trout fisheries in a watershed context, and to enhance or restore their functionality when needed. Nevertheless, few studies have explicitly sought to link trout movements to spatial and temporal variability in habitat quality, especially over multiple seasons within both main-stem lotic systems and smaller associated tributaries (Maki-Petays 1997, Bunnell et al. 1998, Burrell et al. 2000). The objectives of our study were to: 1) quantify the overall rate of trout movement; 2) assess spatial and temporal variation in movement behaviors; and 3) relate movement behaviors to variation in stream flow, water temperature, and access to coldwater sources (CWSs). We will briefly present our results with an emphasis on demonstrating how the data can be used as a guide for future in-stream restoration that meshes with federal (U. S. Forest Service [USFS] Monongahela National Forest Plan), state (Back the Brookie, overall conservation effort), and local goals for the watershed. This watershed is a stronghold for native brook trout in West Virginia and is recognized as such within the Eastern Brook Trout Joint Venture (EBTJV), a national multi-agency partnership established in 2004 to conserve, protect, and re-establish native brook trout through cooperative efforts.

STUDY AREA

The study area was located entirely within the Monongahela National Forest and on Snowshoe Ski Resort property in central West Virginia. We conducted fieldwork within the main stem of the upper Shavers Fork and a second-order tributary, Rocky Run. The physical and biological characteristics of the upper Shavers Fork main stem and Rocky Run study areas differ dramatically. The main stem is relatively wide and shallow, has a low gradient and an open canopy, is warmer, and is more productive than Rocky Run and other tributaries (Bopp 2002). Rocky Run is narrow and has a higher gradient, a dense canopy, and a high occurrence of large boulders and large woody debris (LWD). Although many small streams in the watershed are acidic as a result of acid deposition, both the upper main stem (currently treated with limestone fines by the West Virginia Department of Natural Resources [WVDNR]) and Rocky Run are generally circum-neutral (i.e., possess a baseflow pH between 6.6 and 7.0). Fish assemblages in the upper Shavers Fork and its tributaries are typical for Appalachian streams and include: brook trout, brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), rosyface shiner (*Notropis rubellus*), rosyside dace (*Clinostomus funduloides*), blacknose dace (*Rhinicthys atralatus*), longnose dace (*Rhinicthys cataractae*), central stoneroller (*Campostoma anomalum*), fantail darter (*Etheostoma flabellare*), mottled sculpin (*Cottus bairdii*), northern hog sucker (*Campostoma nigicans*), and creek chub (*Semotilus atromaculatus*).

METHODS

Temperature and Stream Flow Monitoring

An 8 km study reach was delineated on the Shavers Fork main stem and a 2 km reach on Rocky Run (Fig. 1). Wooden stakes with fluorescent tips were placed along the study reaches every 50 m on the main stem, and every 25 m on Rocky Run. Seven continuous temperature loggers (HOBO™, Onset Computer Corporation, Bourne, MA) were anchored within the main-stem study area, and three loggers were anchored in the tributary. Spacing of the loggers was arranged to capture spatial and temporal variation in ambient water temperature throughout the

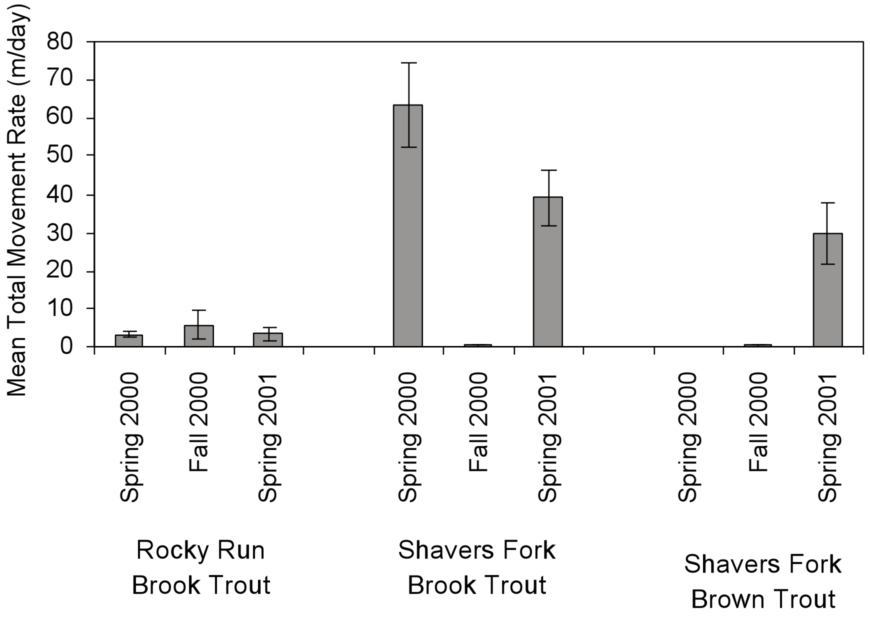

Figure 1.—Mean (+SE) total movement rate of brook trout and brown trout inhabiting Rocky Run and the main stem of the upper Shavers Fork watershed. (Total movement rate = sum of all movements upstream and downstream.)

study area. Shavers Fork stream flow was monitored at the U.S Geological Survey (USGS) gauging station located at Cheat Bridge, WV, approximately 25 km downstream from our study area.

Trout Capture and Tracking

We completed the fieldwork over a period of 60-70 days during three seasons: summer 2000, fall 2000, and summer 2001. The summer sampling season continued from June 5 until August 15 of each year. The fall season ran from September 5 until November 15. Electrofishing and angling were used to capture trout used for the study. In summer 2000, only brook trout were sampled. Brown trout were added to the study design in fall 2000 and summer 2001. All fish were captured within the study region and returned as close to their original location as possible.

Twenty-eight trout were tagged and released each season for a total of 84 trout implanted for the study. Once captured, trout were surgically implanted with Lotek™ (Lotek Wireless Inc., Newmarket, ONT) internal radio transmitters following protocols derived from multiple sources (Courtois 1981, Ross and Kleiner 1982, Winter 1983, Swanberg 1997). Trout were handled according to the guidelines of the West Virginia University Animal Care and Use Committee (Protocol #9801-12). To ensure full recovery and resumption of normal behaviors, official tracking did not begin until 7 days following the release of tagged fish. All fish at large were located using a Lotek™ SRX 600 Datalogger receiver at least twice per week each season between 0600 hours and 2100 hours, completing one "track". Tagged trout were located by use of a WVDNR railcar and walking parallel to and within 50 m of the stream bank until a signal was detected (Young 1995). An exhaustive effort was made throughout each track to locate all tagged trout throughout the watershed. All located fish were visually identified to ensure that the transmitters were still associated with a living fish (Burrell et al. 2000). Tracking continued for up to 71 days each season. Most transmitters had "died" by day 60.

Trout Movement and Microhabitat Use

Upon locating each tagged trout, we collected the following information: 1) geographic location based on the stakes placed along the experimental reaches; 2) time of day; 3) water clarity; 4) hydraulic channel unit type (e.g., pool, riffle, run) (Petty et al. 2001); and 4) physical microhabitat variables at the focal point of observed trout. Microhabitat variables included focal point temperature (°C), pH, water depth (cm), bottom current velocity (m/s), average current velocity (m/s), focal point current velocity (m/s), maximum current velocity within 60 cm (m/s) (Fausch et al. 1981), distance to cover (m), cover type used (wood, rock, combination), and distance to a known CWS (m). We identified nine CWSs to the Shavers Fork main stem distributed throughout the study area. Coldwater sources included tributary confluences as well as identified lateral groundwater seeps along the banks of the main-stem channel. Cover for this investigation consisted of undercut banks, large boulders, and LWD. Current velocities were measured with a Marsh-McBirney™ flow meter (Marsh-McBirney, Frederick, MD). Trout were observed when possible to note their general location and activity before we took microhabitat use measurements. We substituted a reading of 10 cm from the bottom for an adjusted focal point whenever in-stream turbidity prevented the determination of the exact location (Young 1995). Microhabitat data will be discussed only when needed in quantifying trout movement.

Statistical Analysis

Our first and second objectives were to quantify trout movement, and to assess spatial and temporal variation in movement behaviors. Movement was quantified as the distance, in meters, between subsequent fish locations. We arbitrarily assigned positive values to upstream movements and negative values to downstream movements. We then constructed two-tailed, frequency distributions of movement distance for each year. Because movement distance was correlated with the number of days between capture, we converted all measurements of movement to a movement rate by dividing distance by the number of days between subsequent sightings. These data were then analyzed on a track-by-track basis by examining movement rates between subsequent sightings. We also analyzed the data on the basis of overall movement rates of each fish over the course of the study. Specifically, we calculated the total net movement rate (including upstream and downstream movements) and the total absolute movement rate for each fish each season. We used t-tests to test the null hypothesis that overall net displacement by trout did not differ significantly from zero. Rejecting this hypothesis would suggest a directional tendency in trout movements. We tested for differences in movement rates among seasons, years, streams, and species by conducting either t-tests or an ANOVA on log-transformed movement rates.

Our third objective was to relate movement behaviors to variation in stream flow, water temperature, and access to CWSs. We examined the effects of daily variation in temperature, flow, and access to known CWSs on trout movements during summer months. These analyses employed simple and multiple linear regressions where the dependent variable was the log-transformed movement rate of fish on a track-to-track basis. Independent variables were the maximum ambient water temperature between subsequent sightings, the 7-day average maximum water temperature, maximum stream stage height, and the distance (in meters) a fish was to a known CWS prior to movement. Our specific objective in this analysis was to examine the degree to which water temperature and distance to CWSs interact to determine trout movement rates during summer months.

RESULTS

Movement rates of brook trout and brown trout varied as a function of season, stream, and species (Fig. 1). Brook trout residing in Rocky Run were generally sedentary, with a median movement rate ranging from 0.1 m/day in fall 2000 to 2.1 m/day in summer 2000. ANOVAs conducted on total movement rates indicated that brook trout overall movements in Rocky Run were highly consistent from season to season ($F = 1.02$, $p = 0.35$). Brook trout inhabiting Rocky Run did not exhibit significant tendencies in upstream or downstream movement in any season. We never sampled a brown trout in Rocky Run, nor did a tagged brown trout ever enter Rocky Run during the study. (A few small [<200 mm] individuals were later captured in routine surveys.) Transmitters lasted up to 71 days, with location and habitat-use data taken 2-3 times per week for each active-transmitter-equipped trout. Some trout were located up to 19 times throughout a season (summer or fall).

In contrast to Rocky Run, brook trout residing in the Shavers Fork main stem exhibited dramatic upstream movement tendencies in summer 2000 and 2001 (Fig. 1). Brook trout in the main stem were observed to move as much as 100-150 m/day and exhibited median movement rates from 40.3 m/day in summer 2001 to 57.8 m/day in summer 2000. Several individuals moved more than 6.5 km during the summer 2000 and 2001 seasons.

Brown trout in the main stem exhibited an upstream movement tendency similar to brook trout in summer 2001 (median dispersal rate = 25.5 m/day). One individual moved as much as 2.6 km upstream and many others moved 1.0-1.5 km in a 65-day period. (No data exist for brown trout in summer 2000.)

High rates of overall movement by brook and brown trout residing in the main stem were not observed in the fall 2000 season. For example, median movement rates by brook trout fell from 57.8 m/day in summer 2000 to 0.4 m/day in fall 2000. Likewise, the median movement rate by brown trout in fall 2000 was 0.3 m/day. Trout in Rocky Run moved at a significantly lower rate than trout in Shavers Fork in summer 2000 and 2001, but not in fall 2000 (Fig. 1). Furthermore, trout movement rates in Shavers Fork were significantly lower in fall 2000 than in summer of either 2000 or 2001. Finally, we observed no significant differences in the overall movement rates of brook trout and brown trout inhabiting the Shavers Fork main stem. By the fall start date of September, most large brook trout had migrated from the main stem into the extreme headwaters of smaller tributaries in preparation to spawn. Trout migrated back to the main stem sometime between sampling periods (November 1-June 5). We are unsure whether brook trout overwinter in the main stem or within tributaries. Brown trout made upstream movements to spawn but were generally confined to the main stem and were not as pronounced. Concurrent routine surveys taken throughout the watershed confirmed this movement and distribution pattern. The spawning migration and its implications for management must be taken into account even though the event was not captured in our tracking results.

Given the high rates of overall movement by brook trout in the Shavers Fork main stem, we examined the effects of temperature, stream flow, and distance to CWSs on brook trout movement for our third objective. Flow did not vary significantly over the course of the study other than what would be expected due to normal precipitation events. Kolmogrov-Smirnov tests further indicated that flows did not differ significantly between years (2000 vs. 2001: $D = 0.03$, $n = 214$, $p < 0.05$). Flow during the fall of 2000 was characteristic of coldwater systems like the upper Shavers Fork under fall conditions and had an average mean daily stage height of 4.85 m. Therefore, habitat availability was sampled at one flow representative of the system during most tracking events. Brook trout movement rates were significantly related to maximum water temperature in the summers of both 2000 and 2001. In summer 2000, movement rates decreased significantly as maximum temperature increased from 12 °C to 18 °C. In contrast, movement rates increased as a function of maximum temperature when temperatures exceeded 18 °C. Habitat use was also strongly influenced by temperature (Fig. 2). At times, trout utilized habitat that was up to 4 °C cooler than ambient temperature levels. With increasing temperature, only habitat influenced by CWSs was utilized, demonstrating a loss of available habitat during warmer periods. We observed significant relationships between brook trout movement rates and distance to a known CWS. In summer 2000 and especially in summer 2001, movement rates tended to increase with increasing distance from cold water or CWSs. Multiple regression analyses further clarified the interactive effects of water temperature and distance to CWSs on brook trout movement behavior. Inclusion of both maximum temperature and distance to a CWS in regression models produced significantly better power to predict trout movement rates ($F = 4.7$, $p = 0.001$, $R^2 = 0.26$).

DISCUSSION

Movement is an adapted behavior used by large, dominant, resident trout in the Shavers Fork to adjust to spatially and temporally varying in-stream habitat conditions and productivity, and to reach non-substitutable complementary and supplementary habitat distributed at a watershed scale (Meyers et al. 1992, Schlosser and Angermeier 1995, Fausch et al. 2002, Gowan and Fausch 2002, Petty et al. 2005). Our findings are in agreement with Gowan et al. (1994) and Albanese et al. (2004), who stated that movement may be more common in variable or harsh systems (e.g., the Shavers Fork main stem) and less common in more constant or benign ones (e.g., Rocky Run). Past land-use practices have made the upper Shavers Fork main stem habitat marginal but highly productive, with reaches of excellent habitat separated by long, shallow expanses of low in-stream complexity. Thermal constraints greatly compound the need for trout to

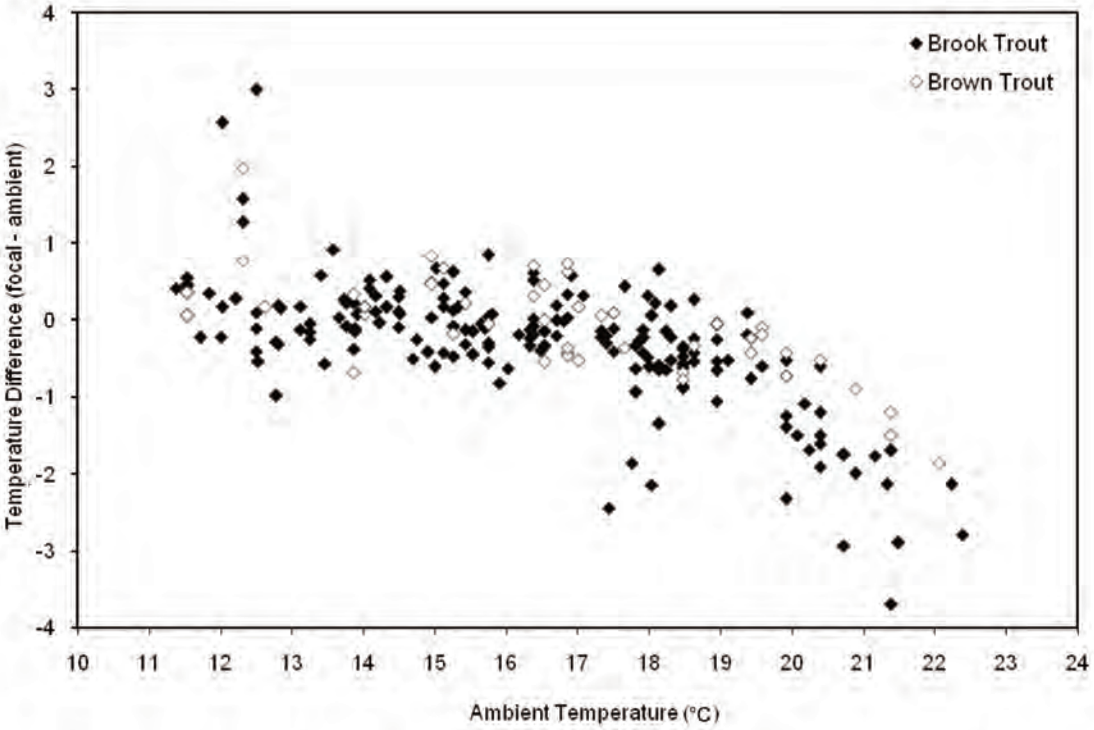

Figure 2.—Variation in the difference between focal point temperature and ambient water temperature as a function of ambient water temperature for summer 2000 and summer 2001 (N = 221). (Note brook and brown trout are separate series.)

move and seek out suitable habitat. Species that exhibit reach affinity (like trout) under ideal conditions in complex, productive habitats usually show increased movement if in-stream habitat becomes homogenized (Albanese et al. 2004), as we observed in the upper Shavers Fork.

We believe that high mobility was common when fluvial brook trout inhabited the upper Shavers Fork and other lotic systems of pre-development West Virginia. We cannot make valid comparisons between today and the past, however, because of anthropogenic effects on current movement rates/behavior and the lack of historic records of trout movement in unspoiled systems. We nonetheless feel the upper Shavers Fork was not unique in a world of similar unspoiled habitat and rivers. It is very unusual today due to the possibility of restoring the remnants of a once-common fluvial brook trout population in a remarkable Appalachian lotic system.

Our findings also highlight the issue of proper scale for ecological studies and successful management (Hildrew and Giller 1994, Cooper et al. 1998, Fausch et al. 2002, Rodriquez 2002). Findings from either water body (or one season) taken alone would be incorrect in assessing the entire trout population's habitat use and movement in the watershed. For example, our findings are applicable only to summer and fall. Potential mortality and habitat use within the upper Shavers Fork during the winter need to be researched. Further shortcomings include the short timeframe when fish were at large, and the incomplete size range of fish tracked. Improvements in transmitter technology have negated these problems for future studies.

Maximum summer water temperature is the single most important factor limiting the geographic distribution of brook trout, a coldwater fish with strict temperature requirements (Flebbe 1994, McRae and Edwards 1994). Brook and brown trout have very similar total temperature ranges and critical thermal maxima (29.8 °C and 29.9 °C, respectively); brook trout prefer a cooler range (10-12 °C) than brown trout (12-17 °C) (Wehrly et al. 2007). This preference is the main reason brown trout are rare and brook trout are abundant in the colder Shavers Fork tributary, Rocky Run. Mortality occurs quickly above 25 °C for both species, with delayed mortality at extended periods above 20 °C. Both movement and habitat selection by trout in the upper Shavers Fork are highly negatively affected by temperature (Hansbarger et al. 2005). Overall available habitat is reduced or gained depending on in-stream temperature levels in the upper Shavers Fork. During critical thermal periods, main-stem trout found and used CWS-influenced habitat that was up to 4 °C cooler than the in-stream ambient temperature. High levels of productivity in the main stem spur resident trout to stay and feed despite high in-stream temperatures during the summer months (Bopp 2002). This type of thermal regulation by salmonids is heavily documented in current literature and highlights their amazing adaptability despite strict habitat requirements (Bermann and Quinn 1991, Dolloff et al. 1994, Torgersen et al. 1999, Baird and Krueger 2003). Movement by tagged trout at times was for the sole purpose of locating and using habitat associated with CWSs, rather than for "normal" activities (i.e., feeding, avoiding avian predators). Another consequence of adaptability, however, is their susceptibility to harvest: anglers generally know the location of CWSs.

An overall reduction of in-stream temperature levels through specific restoration actions would increase habitat quality and availability year-round while reducing the distance between required habitat. The resulting reduction in the need for movement, especially during critical energy periods (i.e., summer), would benefit trout condition and fitness. Energy used for higher metabolic demand associated with increased temperature would not be diverted from other needs, and trout would not be as prone to the delayed mortality associated with secondary impacts from high temperature (pathogens, disease, winter mortality). Appalachian freestone streams are typically infertile and limited in food resources, making this possible gain in energy extremely valuable to Shavers Fork trout (Cada et al. 1987, Ensign et al. 1990, Hartman and Sweka 2001). With improved overall temperature levels, trout would also not congregate as severely during warm periods. The potential for overharvest would be limited, and delayed mortality arising from catch and release handling would decline. The main stem of the upper Shavers Fork actually benefits from additional autochthonous energy sources because its more exposed canopy makes it more productive than usual. Conversely, the more open canopy provides too much heat during the summer when coupled with in-stream geomorphology (wide, shallow debris flows; wide main channel).

The most successful method of habitat rehabilitation has been watershed protection (Meehan 1991). The higher the level of protection, the greater the likelihood that restoration efforts will be well spent and not wasted. Successful watershed restoration and enhancement requires multiple steps and planning (Roni 2006). The first step in a successful restoration plan is to construct an accurate conceptual model. Step two involves providing a biophysical and socio-political profile that identifies objectives, strategies, and targets that must be met to achieve overall goals. Step three produces a watershed plan that explains how these objectives, strategies, and goals will be met and by whom. Step four spells out actions and commitments for implementing the plan, monitoring its effectiveness, and periodically reviewing and improving it.

The scale of movement documented and information derived from other studies in the watershed show that a watershed-scale perspective is needed to adequately manage and restore the upper Shavers Fork trout fishery (Petty et al. 2001, Petty et al. 2005). A restoration plan for the upper Shavers Fork watershed should first address temperature as a limiting factor, followed by targeted structural enhancements to increase the availability of multi-factor or diverse habitats. Temperature mitigation would increase available habitat year-round. If temperature issues are not addressed first, subsequent restoration actions would prove to be ineffective or limited in effectiveness. Incorporating advanced remote sensing data along with in-stream temperature logger data would prove invaluable in determining heating zones (i.e., surface temperature mapping) to be targeted for enhancement (Fausch et al. 2002). Mitigation would be accomplished by planting trees for shading in the upper headwaters on Snowshoe property and around Spruce and other exposed "heating zones" lacking riparian cover, and through specific in-stream enhancement work covered below. Priority fish passage barriers (culverts and road crossings) could be improved or replaced to increase available habitat while promoting dispersal, genetic diversity, and system integrity and limiting population fragmentation (Wofford et al. 2005, Freeman et al. 2007, Poplar-Jeffers et al. 2008). Headwater areas could be improved by targeting specific reaches for expanded limestone treatment, increasing the overall spawning potential of resident trout in the watershed (Clayton et al. 1998, Petty and Thorne 2005).

The next step would involve specific enhancement actions directed at further reducing in-stream temperature levels, while increasing the availability of multi-factor or diverse habitats to increase overall habitat suitability (Hansbarger et al. 2008). A decrease in the residence time of water in wide, shallow "heating zones" by reducing channel width and increasing depth would lower overall in-stream temperature levels further. Reaches with adequate gradient could next be targeted for boulder and LWD placement, allowing erosion and deposition to create multi-factor habitat. A combination of appropriate cover, depth, and current velocity is needed to provide suitable habitat. If specific reaches or sections are to be set aside for special management, managers must decide whether these areas are to contain the full range of movements of resident trout and if so, how large an area to designate. Finally, successful long-term management will require cooperation from multiple landowners (i.e., USFS, Snowshoe Ski Resort, and private landholders) and continued public relations to be successful.

Issues that could further impact the upper Shavers Fork watershed must also be considered and planned for within any restoration plan. They are: 1) the placement of a wastewater treatment plant for Snowshoe Ski Resort; 2) long-term development and land use; 3) long-term thermal impacts of global warming on the upper Shavers Fork and other coldwater lotic systems in West Virginia; and 4) exotic fish and genetic concerns. Many local public meetings already have been held, and stakeholders have vigorously contested the proposed locations of the wastewater treatment plant and the choice of stream into which effluent should be discharged, the Elk or the upper Shavers Fork. Both are exceptional trout streams with high recreational value, attracting resident as well as non-resident anglers year-round. The unspoiled nature and remoteness of the upper Shavers Fork are among its most alluring qualities. We must ensure that development and other land uses do not ruin these key features.

The trout fishery in the watershed exists tenuously during the summer months (Hansbarger et al. 2008). Cold water discharged from tributaries and seeps literally sustain trout throughout the critical summer period. Predicted temperature increases from global warming could push the upper Shavers Fork to either a cool-water or warm-water stream, rendering resident trout extinct unless steps are taken to combat climate change on multiple scales. Without critical thermal refuges during summer periods and open corridors to reach them, trout would not be able to persist in the watershed (Hartman and Sweka 2001, Baird and Krueger 2003, Poplar-Jeffers et al. 2008). If the re-establishment of a fluvial native brook trout fishery is the goal of a restoration plan, the impact of exotic rainbow and brown trout needs to be examined further. These exotic species could hurt brook trout growth and ultimately survival (Fausch and White 1981, Hansbarger 2005). Eradication of exotics is usually not possible, and the benefit of these nonnative trout to anglers weighs heavily in comparison to their negative impacts on brook trout. Finally, stocking brook trout in the upper Shavers Fork should be reviewed for long-term genetic implications. Both the WVDNR and the Cheat Mountain Club, a private club located near Cheat Bridge, stock the river.

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DOES NITROGEN AND SULFUR DEPOSITION AFFECT FOREST PRODUCTIVITY?

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Abstract.—We studied the effects of atmospheric nitrogen and sulfur deposition on forest productivity in a 10-year-old, aggrading forest stand at the Fernow Experimental Forest in Tucker County, WV. Forest productivity was expressed as total aboveground wood biomass, which included stem and branch weight of standing live trees. Ten years after stand regeneration and treatment initiation, total aboveground wood biomass was compared among three treatments: whole tree harvest (WT), whole tree harvest plus annual nitrogen (N) and sulfur (S) additions at two times ambient deposition rates (WT+NS), and whole tree harvest plus N, S (two times ambient), and dolomitic lime (WT+NS+CA) additions. Furthermore, future stand productivity was estimated for a subsequent 70 years using growth projection simulator SILVAH. Total aboveground wood biomass at 10 years was not significantly different among treatments (ANOVA: F = 1.20, p = 0.33, n = 9). Mean total aboveground wood biomass values for the WT, WT+NS, and WT+NS+CA treatments were 47.5 (± 15.3) Mg ha^{-1}, 53.0 (± 14.3) Mg ha^{-1}, and 51.0 (± 15.5) Mg ha^{-1}, respectively. The dominant tree species was pin cherry (average aboveground dry weight of the three treatments was 38.2 Mg ha^{-1}). Lack of significant differences in the aboveground wood component at the stand level suggests that 10 years of three times ambient rates of nitrogen and sulfur deposition and mitigation did not impact the ability of this site to produce woody biomass. At the species level, however, yellow-poplar had significantly higher diameter at breast height and aboveground wood biomass in the WT+NS+CA stands, indicating the potential for N, S, and Ca additions to impact individual species' growth over forest succession. Projected aboveground wood biomass at stand age 80 was 230.3 Mg ha^{-1}, 229.9 Mg ha^{-1}, and 349.7 Mg ha^{-1} for the respective treatments WT, WT+NS, and WT+NS+CA. Our results suggest that although N and S additions alone do not increase stand growth, N, S, and dolomite additions increase growth of individual species within the first 10 years of stand development. Based on this early biomass increase, long-term growth in the WT+NS+CA treatment may increase 34 percent by forest age 80.

INTRODUCTION

Total global production of anthropogenic nitrogen (N) is currently 10 times greater than late 19th-century production rates (Galloway et al. 2004). During the last few decades, atmospheric N deposition to forest ecosystems has increased, especially in the northeastern United States, as a result of an increase in factory and automobile fossil fuel burning and emissions from agricultural fertilizer inputs. The increase in N deposition has led to N saturation, defined as a condition in which atmospheric inputs of N exceed the biological demand of an ecosystem (Aber et al. 1989). Nitrogen saturation can lead to nitrate leaching to stream waters, a change in species composition, decreased soil carbon (C) to N ratio, lower foliar and fine root biomass, and a potential decrease in net primary productivity (Aber et al. 1989). Increased N deposition to a forest also may result in increased losses of base elements such as calcium (Ca), magnesium (Mg), and potassium, and others such as sulfur (S) and phosphorus (Johnson 1992). Depletion of these essential nutrients may impact the productivity and health of a forest community (Yanai et al. 1999, Hamburg et al. 2003, Sullivan et al. 2006, Bigelow

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and Canham 2007). For example, Wallace et al. (2007) attributed overall decline in live basal area to an N saturation effect caused by fertilizer additions in a northern New York mixed-oak forest; tree mortality in the fertilized plots was higher even though basal area of live trees increased significantly in the fertilized plots as compared to the control plots.

Stands that receive high ambient rates of N deposition, but that have not reached N saturation, may experience an increase in productivity as N limitations are relieved. Nitrogen enrichment at the Harvard Forest in Massachusetts (Aber et al. 1993, Magill et al. 2004) resulted in increased annual net primary productivity, while an N deposition gradient in the southern Appalachians (Boggs et al. 2005) demonstrated increased basal area growth in sugar maple trees (see Appendix for list of common and scientific names for trees). Further, hardwood trees respond differently from conifers to N additions. The conifer sites at the Harvard Forest exhibited 56-percent mortality after 15 years of N additions and complete mortality was predicted for the near future; hardwood stands experienced 17 percent mortality (Magill et al. 2004). Red spruce stands in Vermont also experienced a decline (40 percent) in live basal area after 14 years and researchers suggested that high-elevation spruce forests could be converted into stands of birch and maple under continued elevated N deposition (McNulty et al. 2005).

The Fernow Experimental Forest (FEF) in Tucker County, WV, experiences some of the highest rates of N deposition in the United States, and forest stands display symptoms of N saturation (Peterjohn et al. 1996, 1999). The objective of this study was to better understand the impact of atmospheric N and S deposition on the production of total aboveground wood biomass and individual tree species' biomass response in a young, aggrading deciduous forest at this location. Further, we were interested in whether the effects can be mitigated with dolomitic lime additions. Our final objective was to estimate, by using a growth simulation model, whether early fertilization in this forest type stimulates biomass accretion during the life of a forest.

STUDY AREA

We conducted the study at the Long-Term Soil Productivity (LTSP) sites on Fork Mountain in the FEF near Parsons, WV (39°03′ N, 79°29′ W). Annual temperatures range from an average of -2 °C in January to an average of 20 °C in July (Adams et al. 2004). Precipitation averages 146 cm annually (Wallenstein et al. 2006). Dominant soil type is a Calvin channery silt loam derived from acidic sandstone and shale of the Upper Devonian Hampshire formation (Kochenderfer 2006).

In 1996, four blocks were established along a slope gradient ranging from 798 m to 847 m in elevation. Four treatments were imposed in a complete randomized block design: an unharvested and unfertilized control, unfertilized whole-tree harvested control (WT), whole-tree harvested ammonium sulfate additions (WT+NS), and whole-tree harvested ammonium sulfate additions plus dolomitic lime (WT+NS+CA). Individual treatment plots measure 0.2 hectares including treated buffer areas; plots are adjacent to each other within a block. The rate of addition for the WT+NS treatment was two times the ambient N and S throughfall deposition. Ambient deposition in early 1980 contained ~15 kg N $ha^{-1} \cdot yr^{-1}$ and 17 kg S $ha^{-1} \cdot yr^{-1}$ (Helvey and Kunkle 1986); therefore, 36 kg N $ha^{-1} \cdot yr^{-1}$ and 40 kg S $ha^{-1} \cdot yr^{-1}$ are added in fertilizer. The WT+NS+CA plots received two times ambient N and S fertilizer as well as 22.5 kg Ca $ha^{-1} \cdot yr^{-1}$ plus 11.6 kg Mg $ha^{-1} \cdot yr^{-1}$, which is equivalent to two times the rate of export of Ca and Mg to stream water (Wallenstein et al. 2006). Pre-treatment mean soil pH was 4.24 (Adams et al. 2004). Five years after treatment, soil pH was 2.96, 3.22, and 3.41 in the WT+NS, WT, and WT+NS+CA treatments, respectively (Wallenstein et al. 2006).

METHODS

Data for three of the four blocks were available for use in this study. Trees were inventoried in 2006 using either four or five 0.004 ha vegetative growth subplots in each plot. Diameter at breast height (d.b.h.) was measured for all trees greater than 2.54 cm and recorded by species. Total wood dry weight was estimated with regression equations based on d.b.h. For trees with d.b.h. 5.1 to 12.7 cm, equations were developed at the FEF (M.B. Adams, unpublished data); for trees with d.b.h. 12.8 to 50.8 cm, equations of Brenneman et al. (1978) were used (Table 1). Several tree species did not have their own equation; therefore, we used wood specific gravity to match species without an equation to species with a known equation to calculate total aboveground wood dry weight.

Analysis of variance in SAS (SAS Institute Inc., Cary, NC) was used to test for significant differences between treatments in biomass estimates for individual tree species and plot totals. Alpha level of ≤ 0.1 was used.

A growth model for the Allegheny Hardwoods (Marquis and Ernst 1992) was used to project stand growth to 80 years. Of the available growth simulation computer programs for the Allegheny hardwoods, SILVAH exhibits the least error associated with the projections (J.R. Brooks, unpublished). Data for SILVAH were plot size, tree species, and d.b.h.; growth in SILVAH is estimated by using species-specific basal area growth and mortality equations. Tree per acre (TPA) and basal area values are generated at the stand level for every 5-year period.

The SILVAH-generated values for basal area per acre and TPA for each 5-year increment were used to calculate quadratic mean diameter with Equation 1 for each of the three treatments.

$$QMD = \sqrt{\left(\frac{\frac{BA/AC}{TPA}}{k} \right)} \qquad (1)$$

Where:

QMD = quadratic mean diameter
BA/AC = basal area per acre
TPA = trees per acre
k = -0.0054542

The quadratic mean diameter for each 5-year period was then used in the species-specific biomass equations (Table 1). The biomass for each species in each treatment was multiplied by that individual species' relative density at year 10 and then by the total-stand TPA (Table 2). The sum of

Table 1.—Individual tree species dry weight equations based on d.b.h.. ($Y=ax^b$). The Fernow equations are in kilograms while Brenneman et al. (1978) equations are in pounds. Results of this study are reported in kilograms.

	Tree species	a	b	R-square
Fernow	Black birch	1.1064	2.4877	0.98
	Yellow-poplar	0.7037	2.4806	0.99
	Black cherry	0.8833	2.6047	0.98
	Red maple	0.9305	2.5922	0.99
	Pin cherry	0.8833	2.6047	0.98
	Striped maple	0.8833	2.6047	0.98
	Hercules club	0.8833	2.6047	0.98
	Sourwood	0.9305	2.5922	0.99
	Sassafras	0.8833	2.6047	0.98
	Fraser magnolia	0.8833	2.6047	0.98
Brenneman	White ash	2.3626	2.4798	0.99
	Black locust	1.5647	2.6887	0.95
	Cucumbertree	1.4359	2.5622	0.98
	Northern red oak	2.4601	2.4572	0.95
	Yellow birch	3.1042	2.3753	0.97
	Sugar maple	2.4439	2.5735	0.98
	E. hophornbeam	2.0340	2.6349	0.99

Table 2.—Species trees per hectare (TPH) used to calculate percent relative density (RD) for the dominant tree species ≥2.54 cm d.b.h. by treatment. The "other species" include striped maple, eastern hophornbeam, yellow birch, sassafras, white ash, sugar maple, black locust, northern red oak, and sourwood. The last row represents total values by treatment. Treatments are unfertilized whole tree harvest (WT), whole tree harvest plus annual nitrogen and sulfur additions (WT+NS), and whole tree harvest plus nitrogen, sulfur, and dolomitic lime (WT+NS+CA).

	WT		WT+NS		WT+NS+CA	
Tree species	TPH	RD (%)	TPH	RD (%)	TPH	RD (%)
Pin cherry	2,947	46.3	2,964	51.0	2,806	48.0
Black cherry	776	12.2	889	15.0	689	12.0
Sweet birch	1,023	16.1	477	8.0	494	9.0
Yellow-poplar	689	10.8	215	4.0	529	9.0
Red maple	247	3.9	477	8.0	566	10.0
Fraser magnolia	195	3.1	180	3.0	0	0.0
Cucumbertree	35	0.5	99	2.0	247	4.0
Other species	458	7.3	479	8.0	477	8.3
Total	6,370	100	5,780	100	5,807	100

weights for all species was used to estimate total aboveground wood biomass over the 80-year period. For the purpose of this paper, values are reported in metric units.

SILVAH does not include growth or mortality functions specific to nutrient addition treatments, such as N, S, or liming, in growth projections. Therefore, to ensure a level of validity for SILVAH estimates, basal area values from SILVAH at age 35 were compared to mean stand basal area values of 35-year-old forested watersheds at the FEF, which include a control and N and S amendments at the same levels as the LTSP treatments (Kochenderfer 2006). The treated watershed had a basal area of 36.0 m^2 ha^{-1} while the control watershed contained 28.0 m^2 ha^{-1} (DeWalle et al. 2006). Mean predicted basal area values for the LTSP sites from SILVAH at 35 years were 27.3, 28.0, and 29.1 m^2 ha^{-1}, for the WT, WT+NS, and WT+NS+CA treatments, respectively, at 35 years.

RESULTS

10-Year-Old Stands

Total Aboveground Wood Biomass and d.b.h.

Total aboveground wood biomass did not differ significantly between treatments at age 10 (p = 0.33); the highest value was 53.0 (± 14.3) Mg ha^{-1} in the WT+NS treatment, followed by the WT+NS+CA and WT treatments with 51.0 (± 15.5) and 47.5 (± 15.3) Mg ha^{-1}, respectively. Total aboveground wood biomass in each plot by block and treatment are displayed in Figure 1. The WT, WT+NS, and WT+NS+CA treatments had an average d.b.h. of 4.44 (± 1.75) cm, 4.62 (± 1.98) cm, and 4.65 (± 1.98) cm, respectively.

Individual Tree Species

Pin cherry (Fig. 2) was the most abundant species in these 10-year-old stands regardless of treatment, followed by black cherry and sweet birch, yellow-poplar, red maple, Fraser magnolia, and cucumbertree.

Yellow-poplar and cucumbertree exhibited significantly higher total aboveground wood biomass in the WT+NS+CA treatment (p = 0.09 and 0.10, respectively). Aboveground wood biomass of yellow-poplar in the WT+NS+CA treatment was 90 percent higher than in the WT+NS treatment and 79 percent higher than in the WT treatment. Cucumbertree followed a very similar trend in the WT+NS+CA treatment with an 84 percent and 88 percent higher aboveground wood biomass than in the WT+NS and WT treatments, respectively. Yellow-poplar did not have the highest relative density, but its average d.b.h. was significantly higher in the WT+NS+CA treatment compared to the WT and WT+NS treatments (p = 0.03). The average d.b.h. for yellow-poplar in the WT+NS+CA treatment was 5.74 (± 1.19) cm compared

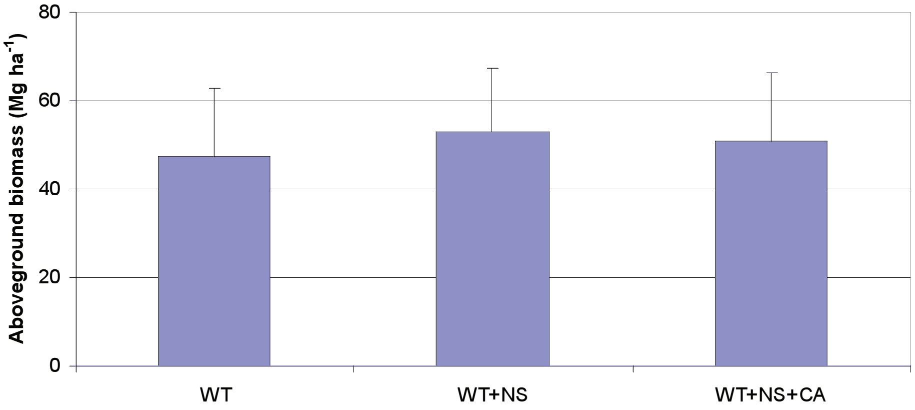

Figure 1.—Total aboveground wood biomass values by treatment for the 10-year-old Long-Term Soil Productivity site. Treatments are unfertilized whole tree harvest (WT), whole tree harvest plus annual nitrogen and sulfur additions (WT+NS), and whole tree harvest plus nitrogen, sulfur, and dolomitic lime (WT+NS+CA).

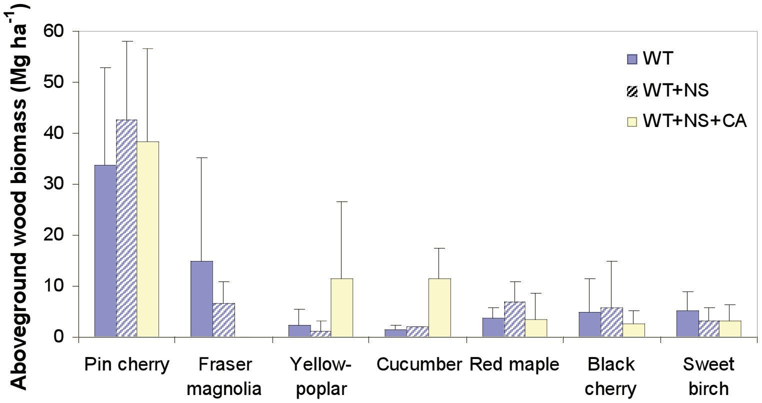

Figure 2.—Comparison of the dominant species' wood biomass component on the Fernow Long-Term Soil Productivity site between treatments. Treatments are unfertilized whole tree harvest (WT), whole tree harvest plus annual nitrogen and sulfur additions (WT+NS), and whole tree harvest plus nitrogen, sulfur, and dolomitic lime (WT+NS+CA).

to 3.38 (± 0.21) cm and 3.40 (± 0.26) cm in the WT+NS and WT treatments, respectively. Fraser magnolia was the only species that was not present within all treatments; it was absent in the WT+NS+CA treatment plots even though it had a large wood biomass component (14.9 Mg ha^{-1}) in the WT treatment. Aboveground wood biomass for red maple was not statistically different between treatments even though average d.b.h. was significantly greater (4.55 ± 0.20 cm) in the WT+NS treatment than in the WT+NS+CA treatment (3.02 ± 0.55 cm; $p < 0.05$). No other abundant species (pin cherry, black cherry, and sweet birch) showed large variations in diameter or aboveground wood biomass among treatments (Table 2).

Projected Stands

Although the 10-year-old treated and control stands did not differ in the total aboveground biomass, growth projections (Fig. 3) suggest that around age 30, growth in the WT+NS+CA treatment may exceed the growth in the WT and WT+NS treatments by 16 and 12 percent, respectively. SILVAH's final projection at 80 years yielded a 34 percent higher aboveground wood biomass at 349.7 Mg ha^{-1} than both the WT and WT+NS treatments (230.3 and 229.9 Mg ha^{-1}, respectively). Greater biomass in the WT+NS+CA treatment can be attributed to differences in quadratic mean diameter between the treatments at 80 years of age. The WT+NS+CA treatment had a 7 percent projected higher quadratic mean diameter (28.7 cm) than the 26.5 cm and 26.7 cm values for the WT and WT+NS treatments, respectively.

DISCUSSION

Total Aboveground Wood Biomass Production of 10-Year-Old Stands

After 10 years of regeneration following whole-tree harvest and elemental additions, which delivered a total of 350 kg N ha^{-1} and 400 kg S ha^{-1}, total aboveground wood biomass in our study was not significantly affected by either increased N and S inputs or liming. In contrast, 23-year-old trees in a

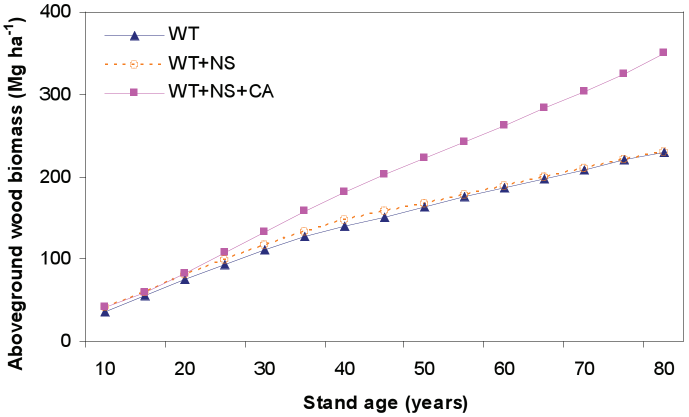

Figure 3.—Projected growth in aboveground wood biomass over 80 years by treatment. Treatments are unfertilized whole tree harvest (WT), whole tree harvest plus annual nitrogen and sulfur additions (WT+NS), and whole tree harvest plus nitrogen, sulfur, and dolomitic lime (WT+NS+CA).

watershed-level N and S addition study also conducted at the FEF exhibited significantly higher annual net growth than control trees 4 years after treatment had begun (DeWalle et al. 2006). Other acidification studies have also shown an increase in wood biomass production due to increased N availability for biomass growth with N and S additions (Nelleman and Thomsen 2001, Magill et al. 2004, Wallace et al. 2007).

The lack of differences in biomass between treatments in our study may be attributed to factors associated with the young age of these stands. Full site occupancy (observed as canopy closure) has been reached only recently in these stands, and light and nutrient limitations may not have affected overall stand productivity. Therefore, trees did not yet respond to nutrient additions. Trees that receive N, S (WT+NS), and liming (WT+NS+CA) amendments do not yet show a response compared to the WT trees because there appear to be sufficient nutrient resources to support this level of biomass, allowing all sites to be productive. This conclusion is supported by soil N chemistry assessments (Wallenstein et al. 2006) at the LTSP site 5 years into treatment, which demonstrated no difference in soil percent-N, net N mineralization, and nitrification among all treatments. However, soil pH was significantly greater in the WT+NS+CA treatment compared to the WT and WT+NS treatments, which may further increase site productivity in this treatment. Already at stand age 10, dolomitic lime additions seem to be able to reverse some effects of N and S additions. For example, Piatek et al. (2009) found that 10 years of N and S additions (WT+NS) lowered the capacity of foliar litter for N immobilization and that dolomitic lime reversed the effect.

Treatment Effects at Species Level

Even though our study shows no stand-level differences in aboveground wood biomass between treatments, yellow-poplar and cucumbertree have demonstrated significantly more wood biomass accumulation in the WT+NS+CA treatment at 10 years. Yellow-poplar has also shown a positive response in basal area growth to N and N+P fertilization as higher foliar N concentrations boost photosynthesis rates (Auchmoody and Smith 1977). Similar species results were observed in the FEF watershed study. Growth plots dominated by yellow-poplar and black cherry on the amended watershed yielded higher relative radial growth rates and basal area increment for 7 years since the start of N and S additions; plots with mainly sweet birch and red maple also demonstrated greater cubic volume growth for this time period (DeWalle et al. 2006). The greater wood biomass that we observed in some species in the WT+NS+CA treatment compared to the WT and WT+NS treatments is suggestive of differential species responses to soil pH caused by dolomitic lime additions. These differences may also be evidence of beginning competition for nutrient resources in these stands.

Pin cherry had the highest basal area, relative density, and aboveground wood biomass in all treatments (WT, WT+NS, and WT+NS+CA) in our study. The prevalence of pin cherry results from its vigorous early successional behavior after a clearcut and from high N soil conditions (Nyland et al. 2007) in the LTSP sites. For example, pin cherry has demonstrated greater germination rates with the addition of N fertilizer (Auchmoody 1979) and with more N available in soil solution (Bjorkbom and Walters 1986, Nyland et al. 2007). As an early successional species, however, pin cherry is expected to be lost from these stands approximately 35 years after stand regeneration due to natural mortality (Marquis 1967, Marks 1974, Heitzman and Nyland 1994, Nyland et al. 2007). Therefore, individual species' responses to the expected change in species composition in addition to excess N deposition are inevitable yet unclear at this point.

Potential Future Stand Productivity

Growth projections with SILVAH suggest that the WT+NS+CA treatment will be most productive by 80 years of age, producing 34 percent more aboveground wood biomass than the WT and WT+NS treatments. SILVAH is not sensitive to treatment in that it does not use treatment-specific equations for biomass growth. Therefore, differences in projected growth among treatments are likely driven by increased diameters of yellow-poplar and cucumbertree at age 10. There are no replicates of the liming amendments at the watershed scale at the FEF to compare with these results, but estimates from SILVAH provide insight as to how the WT+NS+CA treatment may result in greater tree productivity of a hardwood stand over a complete rotation. Alternatively, these results may indicate the potential of a lower soil pH, as seen in the WT and WT+NS treatments (Wallenstein et al. 2006), to reduce forest productivity compared to the WT+NS+CA treated plots. The reportedly lower soil pH may have altered cation availability, most notably Ca, which can explain the observed species' responses to a decade of dolomitic lime additions. The way in which acidification ultimately impacts species composition and stand productivity at the LTSP site has important implications for C-sequestration and financial returns for landowners.

CONCLUSIONS

The results from this study suggest that stand-level total aboveground wood biomass, therefore apparent productivity, has not been affected by increased acidic deposition or liming additions after 10 years. SILVAH results and comparisons of individual species' diameters between treatments indicate the WT+N+CA sites may have higher productivity over the next several decades. The increase in diameter growth in yellow-poplar and cucumbertree alongside the changes that have resulted in higher soil pH in the WT+NS+CA treatment suggest that liming may be effective at ameliorating acidified soil conditions. These results also imply that forested sites that receive high rates of ambient N deposition may experience reduced productivity compared to sites that receive dolomitic lime amendments. Therefore, applying lime to forests that experience elevated levels of N deposition, have acidic soils, and have a stand composition similar to the LTSP sites could increase aboveground wood biomass, likely resulting in a greater financial return for the landowner.

ACKNOWLEDGMENTS

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APPENDIX

List of common and scientific names of the tree species present on the Fernow Long-Term Soil Productivity site.

Common Species Name	Scientific Species Name
Pin cherry	*Prunus pensylvanica* L.f.
Fraser magnolia	*Magnolia fraseri* Walt.
Yellow-poplar	*Liriodendron tulipifera* L.
Cucumbertree	*Magnolia acuminata* L.
Red maple	*Acer rubrum* L.
Black cherry	*Prunus serotina* Ehrh.
Sweet birch	*Betula lenta* L.
Striped maple	*Acer pensylvanicum* L.
E. hophornbeam	*Ostrya virginiana* (Mill.) K. Koch
Yellow birch	*Betula alleghaniensis* Britton
Sassafras	*Sassafras albidum* (Nutt.) Nees
White ash	*Fraxinus americana* L.
Sugar maple	*Acer saccharum* Marsh.
Black locust	*Robinia pseudoacacia* L.
Northern red oak	*Quercus rubra* L.
Sourwood	*Oxydendron arboreum* (L.) DC.

FACTORS INFLUENCING AVIAN COMMUNITIES IN HIGH-ELEVATION SOUTHERN ALLEGHENY MOUNTAIN FORESTS

Harry A. Kahler and James T. Anderson[1]

Abstract.—Myriad factors may influence bird community characteristics among subalpine, central, and northern hardwood forest cover types of the southern Allegheny Mountains. Differences in forest cover types may result from natural characteristics, such as tree species composition, topography, or elevation, as well as from past influences, such as poor logging practices. Our objectives were to: 1) compare breeding bird diversity, richness, and density among 90+ year-old central hardwood (white oak-black oak-Northern red oak) (*Quercus alba-Q. velutina-Q. rubra*), northern hardwood (black cherry-maple) (*Prunus serotina-Acer* spp.), and subalpine (red spruce-yellow birch) (*Picea rubens-Betula alleghaniensis*) stands; and 2) analyze avian community compositions among the three forest categories (n = 30 plots per cover type). We conducted our study on the Monongahela National Forest in Pendleton, Pocahontas, and Randolph Counties, WV. Overall, 57 species of birds were tallied. The most numerous species were red-eyed vireos (*Vireo olivaceus*) and black-throated green warblers (*Dendroica virens*). We found no differences in avian species' diversity, richness, or overall density among a central hardwood, northern hardwood, and subalpine forest type ($P > 0.05$). However, avian community composition varied among the three forest types. Of 27 species analyzed, only 6 had similar densities among cover types. Increased basal area of yellow birch and sugar maple (*Acer saccharum*) together increased the likelihood of occurrence of the Blackburnian warbler (*Dendroica fusca*), black-throated blue warbler (*Dendroica caerulescens*), and winter wren (*Troglodytes troglodytes*). Basal area was a consistent covariate among analyses of diversity richness, and density. The ability to support avian communities is relatively equal among mature forest stands (i.e., >90 yrs) of the three main forest classes within southern Allegheny Mountain forests, yet the likelihood of occurrence of individual species varies with individual stand characteristics. Our results will be useful in formulating management strategies for avian conservation in high-elevation forests.

INTRODUCTION

Habitat fragmentation is a major factor in the loss of forest biodiversity (Hagan et al. 1996, Villard et al. 1999). Wildlife population declines have been attributed not only to direct losses of suitable habitat, but also to isolation effects (i.e., habitat configuration). Increased amounts of habitat edges also have negatively affected wildlife population levels (Hagan et al. 1996, Villard et al. 1999). Poor timber-harvesting practices of the past, such as those throughout the late 1800s in the southern Allegheny Mountains of West Virginia (Clarkson 1993), are often cited as causes of forest fragmentation. Incipient harvesting and fragmentation affect wildlife population levels quite differently from residual and historical causes (Hagan et al. 1996).

A topic less discussed by conservationists is that forest fragmentation can coalesce from natural processes and anthropomorphic disturbances and natural processes. The Allegheny Mountains are within the central hardwoods region, yet northern hardwood and boreal forest types also can be found within the immediate area (Eyre 1980, Hicks 1998). The physiographic Allegheny Mountain section of the Appalachian Plateau runs southwesterly from central Pennsylvania to the highest peaks of West Virginia

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(Fenneman 1938). At the highest elevations of the Allegheny Mountains in West Virginia, generally above 1,000 m, relict patches of boreal forests remain from cooler, periglacial times (Lesser 1993). Moving down in elevation, forests become a mosaic between higher, north-facing northern hardwood types and lower, south-facing central hardwood stands (Hicks 1998).

Furthermore, since the 1960s, evidence shows that boreal forests of North America are shrinking in area, mainly due to increasing mortality rates of red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* L.) at higher elevations (Stephenson and Adams 1993). Coupled with these natural processes, Allegheny Mountain forests in West Virginia were cleared to establish farmsteads, red spruce tracts at higher elevations were girdled and burned to produce cattle pastures, and subsequent timber logging altered forest composition (Clarkson 1993, Stephenson and Adams 1993). Removal of the timber has left mostly a mosaic of second- and third-growth forests (Stephenson 1993). Preferential harvesting and introduced diseases and pests also have changed stand composition over time (Carvell 1986, Acciavatti et al. 1993). In view of these processes, our objectives were to compare avian community composition, diversity, and density among central hardwood, northern hardwood, and boreal forest cover types of the southern Allegheny Mountains region and relate bird occurrence to plot characteristics.

STUDY AREA

The study was conducted on the Potomac and Greenbrier Ranger Districts of the Monongahela National Forest in Pendleton, Pocahontas, and Randolph Counties, WV during 2000 and 2001. In reaction to past over-harvesting and subsequent fire damage, the Monongahela National Forest was formed in 1920 to protect the forest resources in the southern Allegheny Mountains (Clarkson 1993).

All study plots were within 27 km of a geographic center near Lost Run in Highland County, VA, which is about 11.8 km east of the Greenbrier District Ranger Station in Bartow, WV. Elevation ranges from 540 m to 1,481 m, with some slopes near 70 percent grade. In general, elevations above 1,000 m contain boreal forests that are relicts from periglacial periods (Hall 1983). Below the boreal cover, forests are typically a mosaic of higher, north-facing northern hardwood types and lower, south-facing central hardwood stands (Hicks 1998). Site indices typically range from 35 to 80, indicating the expected height of trees after 50 years growth (Pyle et al. 1982, Estepp 1992, Flegel 1999). Stands averaged 103 years old and had an average basal area of 26-27 m^2/ha.

METHODS

Plot Establishment

Ninety 50-m radius study plots were divided evenly among white oak (*Quercus alba* L.)-black oak (*Q. velutina* Lam.)-northern red oak (*Q. rubra* L.) (WO-BO-NRO), which includes the sub-type scarlet oak (*Q. coccinea* Munchh.)-chestnut oak (*Q. Montana* Willd.); black cherry (*Prunus serotina* Ehrh.)-maple (*Acer* spp.) (BC-M); and red spruce-yellow birch (*Betula alleghaniensis* Britton) (RS-YB) cover types (Eyre 1980). These types represent central hardwood, northern hardwood, and boreal forests, respectively.

We randomly selected appropriate forest stands from a Monongahela National Forest database of stands >90 years to establish study plots (Kahler and Anderson 2006). We avoided areas with recent or intense management activity. Each plot was within one mapped stand, and plots were at least 250 m apart for independent sampling (Ralph et al. 1995).

Plot Inventory

In summer months we estimated percentage overstory cover (codominant and dominant canopy), understory cover (2 m tall to overtopped canopy), and shrub cover (<2 m tall) at center points and estimates at three random equidistant points about 25 m from the plot center, for average plot values (Kahler and Anderson 2006). Center locations were marked with a geographic positioning system unit, and point slope and prevailing aspect also were recorded (Marcot 1983, Marzluff and Lyon 1983). Plot elevations were determined from digital elevation grids (with cell sizes of 90 m) using ArcView GIS software (ESRI, Redlands, CA).

We sampled center points with a basal-area factor-10 prism to determine basal area and tallied all trees >10 cm diameter at breast height (d.b.h.) within plots (DeGraaf and Shigo 1985, Kahler and Anderson 2006). For each tallied tree the species, d.b.h., and height (determined with a clinometer) were recorded. Plot composition, basal area, and number of standing trees were estimated from prism-tally information (Avery and Burkhart 1997).

Breeding Bird Counts

We estimated relative bird abundance using a 50-m fixed radius point count method on all plots (Ralph et al. 1995). Thirty original plots (10 per forest type) were established and visited twice between 27 May and 2 July 2000. All 90 plots were surveyed twice between 26 May and 4 July 2001. Counts were 10 minutes in duration, and all sky and wind conditions were acceptable as per Ralph et al. (1995). Plot information was pooled between visits but separated by year. For comparisons among forest types, all maximum yearly plot tallies were used in statistical analyses.

Statistical Analyses

Maximum species abundance values between the two yearly point counts were used to determine yearly richness and density (number of birds counted divided by area of the plot) for each plot (Nur et al. 1999) and we used Shannon's Index to quantify yearly plot diversities (Nur et al. 1999). Because of unequal plot sample sizes between years, data were analyzed by two principle methods to include information from all points in both years. We tested the equality of occurrence for species among the three forest types in 3x2 χ^2 contingency tests using maximum count data by point from 2000-2001 (Dowdy and Wearden 1991, Zar 1999). Only species with expected frequencies (i.e., total number of observed frequencies/3 for each forest type) of >5 individuals/forest type were tested (Dowdy and Wearden 1991, Zar 1999). We used logistic regression models to determine whether individual species' presence on plots was related to the following plot characteristics: basal area, stem density, overstory cover, understory cover, shrub cover, elevation, and basal areas and stem densities of the eight most common tree species (Nur et al. 1999). Hosmer and Lemeshow goodness-of-fit tests were used to measure model significance (Cody and Smith 1997). Between-year data were tested using a nested analysis of variance (ANOVA) design; forest types were treatment groups, with 10 plots per treatment, and two replications per plot (Dowdy and Wearden 1991). Diversity, richness, and total species abundance were tested using the nested design.

RESULTS

Fifty-seven bird species were tallied among the three forest cover types. Thirty-eight species were found in RS-YB plots, 42 were counted in BC-M, and 39 were in WO-BO-NRO plots. The 2001 maximum tally of all species on all plots totaled 1,020 birds; 412 were counted in RS-YB stands, 313 individuals in BC-M stands, and 295 individuals in WO-BO-NRO stands. Using the maximum species abundance values between years for each plot (birds/ha/year), the maximum densities were 10.6 in RS-YB plots, 8.9 in BC-M stands, and 7.7 in WO-BO-NRO plots.

We recorded 27 species at least 15 times using maximum tallies at each plot for each species (Table 1). Only 6 of the 27 species showed equal occurrences among all forest cover types. The most numerous species among all plots per breeding season were red-eyed vireos (See Table 1 for scientific names of most bird species) and black-throated green warblers, each recorded 60 times in 2001. Only dark-eyed juncos were found on all RS-YB plots. Red-eyed vireos were most widespread among BC-M and WO-BO-NRO plots, occupying 28 and 24 of 30 plots, respectively. In contrast, red-eyed vireos occupied only 10 RS-YB plots.

Logistic regression models explained the likelihood of occurrence of 13 bird species (Table 2).The presence of three species varied positively with both elevation and shrub cover (percent). The presence of two species varied negatively with those variables. Among tree species, increased basal area per plot of yellow birch and sugar maple (*Acer saccharum* Marsh.) together increased the likelihood of occurrence of Blackburnian warblers, black-throated blue warblers, and winter wrens. Separately, the likelihood of four species increased with greater yellow birch stem densities while the presence of three species increased with higher sugar maple stem densities.

Species diversity between years was similar among RS-YB ($\bar{X}$ = 0.94, SE = 0.024), BC-M ($\bar{X}$ = 0.85, SE = 0.040), and WO – BO – NRO ($\bar{X}$ = 0.84, SE = 0.039) forest types ($F_{2,27}$ = 1.95, P = 0.162). Likewise, overall species richness was similar among RS-YB ($\bar{X}$ = 9.4, SE = 0.48), BC-M ($\bar{X}$ = 8.1, SE = 0.71), and WO-BO-NRO ($\bar{X}$ = 7.95, SE = 0.64) cover types when considering both years' data ($F_{2,27}$ = 1.70, P = 0.202). Furthermore, total species densities among RS-YB ($\bar{X}$ = 15.5, SE = 0.93), BC-M ($\bar{X}$ = 12.7, SE = 1.15), and WO-BO-NRO (= 12.8, SE = 0.98) were not significantly different ($F_{2,27}$ = 2.53, P = 0.099).

DISCUSSION

Forests of the southern Allegheny Mountains are a mosaic of hardwood, northern hardwood, and boreal forest cover types (Hicks 1998). Because of the differences in silvicultural composition, we hypothesized that wildlife species diversity, richness, and densities would differ among these forest classes as well. Using RS-YB, BC-M, and WO-BO-NRO forest cover types to represent the three forest classes, we found no evidence to support the hypotheses that bird species diversity, richness, and density differ among the forest cover types. Thus, it appears that the ability to support avian communities is relatively equal among mature forest stands (i.e., >90 yrs) of the three main forest classes within southern Allegheny Mountain forests, yet the likelihood of occurrence of individual species varies with individual stand characteristics.

Of habitat structure, the basal area of standing wood was the only consistent covariate in wildlife guild diversity, richness, and density models. In central Allegheny Mountain hardwood forests bird species richness and abundance sharply increased in stands with basal areas below 18 m^2/ha (but not for interior forest species), and decreased sharply in stands with basal areas exceeding 26 m^2/ha (due to diminishing edge species) (Ross et al. 2001). The mean basal area of our study plots was 26-27 m^2/ha (Kahler 2002). Higher basal areas are generally associated with lower shrub and understory density. In turn, greater vertical diversity (i.e., higher shrub and understory densities) may accommodate greater avian diversity and abundances (Rodewald and Smith 1998, Hobson and Bayne 2000). Thus, management strategies involving timber harvesting at 90- to 100-yr rotations should mimic small gap disturbances within forest patches to optimize bird diversity and richness among forest edge and interior species.

Forest Cover Types

Point count surveys did not detect differences in bird species diversity or richness among forest cover types, yet avian community structure within southern Allegheny Mountain forests varies along an elevational gradient. Some species were recorded only in RS-YB stands, such as Swainson's thrush and the red crossbill. Other species, such as winter wren and hermit thrush, were counted only within the northern forest types. Three species were found only in BC-M stands, yet only alder flycatchers (*Empidonax alnorum* Brewster) were recorded more than once. At lower elevations, white-breasted nuthatch, tufted titmouse, and wood thrush appeared only in hardwood stands, while eastern wood-pewee and black-and-white warbler (*Mniotilta varia* L.) were observed only in WO-BO-NRO plots.

Differences in forest structure, such as basal area, understory cover, and shrub cover, among stands of the same forest type may shape differences in breeding bird community structure. Chances of black-throated green warbler presence seemed to increase with increased stand basal area and decreased stem densities and the Blackburnian warbler also was associated with larger-diameter trees. Likewise, Hobson and Bayne (2000) found these species more abundant on contiguous forest tracts than on fragmented areas. Openings in understory and shrub cover negatively impact black-throated blue warbler forest movements (Belisle et al. 2001, Harris and Reed 2001). Thus we found black-throated blue warbler presence associated with denser shrub layers. Moreover, we found Canada warbler only in RS-YB and BC-M plots with shrub cover >75 percent, with rhododendron (*Rhododendron maximum*) the major shrub component. Hobson and Schiek (1999) found significantly more Canada warblers in 28-year-old post-harvest stands than on uncut stands, possibly due to the denser shrub layer on post-harvest stands.

Table 1.—Most common bird species recorded in 50-meter point count plots in Monongahela National Forest, 2000-2001. Numbers reflect maximum tally for each plot (n = 30 for each forest type).

	Forest Type[a]				
Species	S	N	C	χ^2	P
Acadian flycatcher (*Empidonax virescens*)	1ad	2ad	13bd	16.625	<0.001
American robin (*Turdus migratorius*)	10a	8a	6a	1.000	0.607
Blackburnian warbler (*Dendroica fusca*)	38a	17b	15b	13.914	0.001
Black-capped chickadee[b] (*Poecile atricapilla*)	36a	14b	9b	20.983	<0.001
Black-throated blue warbler (*Dendroica caerulescens*)	33a	8b	8b	25.510	<0.001
Black-throated green warbler (*Dendroica virens*)	25a	30a	20a	2.000	0.368
Blue jay (*Cyanocitta cristata*)	8a	9a	8a	0.080	0.961
Blue-headed vireo (*Vireo solitarius*)	12a	17a	13a	1.000	0.607
Brown creeper (*Certhia americana*)	15a	7a	0b	15.364	<0.001
Cedar waxwing (*Bombycilla cedrorum*)	7a	10a	1b	7.000	0.030
Dark-eyed junco (*Junco hyemalis*)	48a	24b	4c	38.316	<0.001
Downy woodpecker[b] (*Picoides pubescens*)	2a	9b	12b	6.870	0.032
Golden-crowned kinglet *(Regulus satrapa*)	33a	6b	0c	47.538	<0.001
Eastern wood-pewee (*Contopus virens*)	0a	0a	15b	30.000	<0.001
Hermit thrush (*Catharus guttatus*)	12a	17a	0b	15.793	<0.001
Magnolia warbler (*Dendroica magnolia*)	39a	20b	3c	31.387	<0.001
Ovenbird (*Seirus aurocapillus*)	0a	11b	12b	11.565	0.003
Red-breasted nuthatch[b] (*Sitta canadensis*)	25a	3b	1b	36.690	<0.001
Red-eyed vireo (*Vireo olivaceus*)	10a	37b	36b	16.940	<0.001
Acadian flycatcher (*Empidonax virescens*)	1ad	2ad	13bd	16.625	<0.001
Scarlet tanager (*Piranga olivacea*)	6a	11a	14a	3.161	0.206
Swainson's thrush (*Catharus ustulatus*)	20a	0b	0b	40.000	<0.001
Tufted titmouse[b] (*Baeolophus bicolor*)	0a	5a	14a	15.895	<0.001
Veery (*Catharus fuscescens*)	16a	22a	18a	1.000	0.607
White-breasted nuthatch[b] (*Sitta carolinensis*)	0a	15b	27b	26.143	<0.001
Wood thrush (*Hylocichla mustelina*)	0a	9b	12b	11.143	0.004
Yellow-bellied sapsucker[b] (*Sphyrapicus varius*)	1a	2a	14b	18.471	<0.001

[a] Forest types are as follows: S-subalpine (red spruce-yellow birch) forest cover type; N-northern hardwood (black cherry-maple) forest cover type; and C -central hardwood (white oak-black oak-Northern red oak) forest cover type.

[b] Species demonstrates at least facultative use of tree cavities.

[c] 3x2 χ^2 test ($\chi^2_{0.05,2} = 5.991$).

[d] Same letters indicate no likelihood separation, 2x2 χ^2 test ($\chi^2_{0.05,1} = 3.841$).

Blue-headed vireo presence was associated with understory cover, in concurrence with results from a Canadian boreal forest (Drolet et al. 1999). In contrast, Drolet and others (1999) found American robin in association with poorly forested landscapes. Similarly, American robin was associated with increased stems counts of black cherry, an early successional species (Marquis 1990), and red maple (*Acer rubrum* L.), which is common on poor growing sites (Walters and Yawney 1990).

Furthermore, wood thrush, Swainson's thrush, hermit thrush, and veery are all considered ground-foraging species, yet foraging heights of the thrush species were stratified among species present from 0-8 m above ground level (Holmes and Robinson 1988). Wood thrushes spend >98 percent of foraging time <2 m from the ground (Holmes and Robinson 1988). Similarly, we found the likelihood of wood thrush presence increased significantly with increased overstory cover, which suggests less understory and shrub cover presence. Furthermore, Swainson's thrushes will use a

Table 2.—Logistic regression models based on presence of bird species on 90 plots, Monongahela National Forest, 2000-2001.

Species	Parameter[a]	Estimate	χ^2	*P*
Acadian flycatcher	overstory cover (%)	7.432	4.172	0.041
Empidonax virescens	elevation (m)	-0.021	15.664	<0.001
(*n* = 15)	n. red oak basal area (m^2/ha)	1.360	5.000	0.025
	Hosmer-Lemeshow goodness-of-fit[b]		4.714	0.788
American robin	overstory cover (%)	7.432	4.172	0.041
Turdus migratorius	elevation (m)	-0.009	7.158	0.008
(*n* = 21)	black cherry density (stems/ha)	0.961	8.281	0.004
	red maple density (stems/ha)	0.585	4.000	0.046
	red spruce density (stems/ha)	0.666	4.584	0.032
	yellow birch density (stems/ha)	0.685	5.867	0.015
	Hosmer-Lemeshow goodness-of-fit[b]		4.890	0.769
Blackburnian warbler	sugar maple basal area (m^2/ha)	0.787	8.643	0.003
Dendroica fusca	yellow birch basal area (m^2/ha)	0.749	15.531	<0.001
(*n* = 50)	white oak density (stems/ha)	0.747	5.892	0.015
	Hosmer-Lemeshow goodness-of-fit[b]		3.900	0.866
Black-throated blue warbler	shrub cover (<2 m) (%)	3.589	10.524	0.001
	elevation (m)	0.011	10.313	0.001
Dendroica caerulescens	sugar maple basal area (m^2/ha)	0.744	7.348	0.007
(*n* = 40)	yellow birch basal area (m^2/ha)	0.470	6.058	0.014
	Hosmer-Lemeshow goodness-of-fit[b]		7.897	0.444
Black-throated green warbler	basal area (m^2/ha)	4.944	3.568	0.059
	inventory density (stems/ha)	-4.732	6.929	0.009
Dendroica virens	elevation (m)	0.011	14.291	<0.001
(*n* = 62)	red spruce density (stems/ha)	-1.038	5.199	0.023
	Hosmer-Lemeshow goodness-of-fit[b]		9.010	0.341
Blue-headed vireo	understory cover (>2m) (%)	1.834	2.952	0.086
Vireo solitarius	Hosmer-Lemeshow goodness-of-fit[b]		9.010	0.341
(*n* = 39)				
Canada warbler	understory cover (>2m) (%)	-4.056	3.338	0.068
Wilsonia canadensis	shrub cover (<2 m) (%)	5.309	9.112	0.003
(*n* = 10)	Hosmer-Lemeshow goodness-of-fit[b]		4.486	0.811
Scarlet tanager	basal area (m^2/ha)	4.919	4.359	0.037
Piranga olivacea	sugar maple density (stems/ha)	1.444	9.941	0.002
(*n* = 31)	white oak density (stems/ha)	1.077	12.613	<0.001
	Hosmer-Lemeshow goodness-of-fit[b]		7.910	0.442
Swainson's thrush	shrub cover (<2m) (%)	3.517	7.827	0.005
Catharus ustulatus	yellow birch density (stems/ha)	0.525	6.484	0.011
(*n* = 17)	Hosmer-Lemeshow goodness-of-fit[b]		4.456	0.726
Veery	inventory stems	-2.252	4.379	0.036
Catharus fuscescens	understory cover (> 2m)	2.854	5.519	0.019
(*n* = 43)	elevation	0.004	3.706	0.054
	sugar maple stems	0.457	2.915	0.088
	Hosmer-Lemeshow goodness-of-fit[b]		6.920	0.545

continued

Table 2.— Continued.

Species	Parameter[a]	Estimate	χ^2	*P*
White-breasted nuthatch	basal area	4.180	3.209	0.073
Sitta carolinensis	shrub cover (< 2m)	-1.861	3.565	0.059
(*n* = 30)	yellow birch stems	-0.915	11.054	0.001
	Hosmer-Lemeshow goodness-of-fit[b]		5.568	0.696
Wood thrush	overstory cover	4.284	3.730	0.054
Hylocichla mustelina	shrub cover (< 2m)	-3.027	6.530	0.011
(*n* = 20)	yellow birch stems	-0.527	3.423	0.064
	Hosmer-Lemeshow goodness-of-fit[b]		4.442	0.815
Winter wren	understory cover (> 2m)	-3.949	4.025	0.045
Troglodytes troglodytes	sugar maple basal area	2.911	4.822	0.028
(*n* = 12)	yellow birch basal area	0.857	7.326	0.007
	sugar maple stems	-2.788	2.926	0.087
	Hosmer-Lemeshow goodness-of-fit[b]		4.442	0.815

[a] All independent variables with P<0.10 are left in the model.

[b] All P>0.05 show significant model fit.

slightly higher foraging substrate (Holmes and Robinson 1988). Likewise, the likelihood of Swainson's thrush presence increased significantly with increased shrub cover. Thus, the presence or absence of a particular bird species may not wholly depend on forest cover type; the amount and quality of sub-canopy vegetation also may influence avian community structure.

The occurrences of 9 of 13 species were directly related to amounts of sugar maple and yellow birch present in stands. These tree species occur together in greatest proportion in an elevational gradient between the pure red spruce stands and northern hardwood forest types such as BC-M, maple-beech (*Fagus grandifolia* Ehrh.)-birch, and beech-sugar maple (Eyre 1980). Thus, edge effects (i.e., increased species occurrences) may happen between forest cover types of similar ages.

As with foraging substrate resources, we found evidence that cavity tree resources may influence dependent, secondary cavity-nesting bird densities. Conifers usually will not hold durable and usable cavities for secondary species (Van Balen et al. 1982). Indeed, we observed the tufted titmouse and white-breasted nuthatch only among hardwood stands. Moreover, cavity tree abundances were highest within the WO-BO-NRO forest cover type, along with 75 percent and 66 percent of all tufted titmouse and white-breasted nuthatch observations, respectively. Tree hardness influences nest-site choices of excavating birds (Schepps et al. 1999). We observed weak-excavating species (i.e., red-breasted nuthatch, black-capped chickadee) mostly in the RS-YB forest cover type (85 percent and 63 percent of all observations, respectively), where the softer, decayed wood of red spruce and yellow birch may provide a substrate easier to excavate than other hardwood species. Furthermore, territoriality has been shown to influence differential habitat use among sympatric chickadees (Hill and Lein 1989). The larger tufted titmouse and white-breasted nuthatch may out-compete the smaller red-breasted nuthatch and black-capped chickadee for territories, relegating weak-excavators to that part of their niche where there is no sympatric overlap.

All three cover types are important for maintaining overall avian diversity in the Southern Allegheny Mountains. Species composition varied among cover types and hence species-specific management may be best suited to a particular cover type. Based on trends in cover type abundance, we recommend a focus on restoration of subalpine cover types to ensure long-term maintenance of avian diversity.

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FOREST CHANGE IN HIGH-ELEVATION FORESTS OF MT. MITCHELL, NORTH CAROLINA: RE-CENSUS AND ANALYSIS OF DATA COLLECTED OVER 40 YEARS

Laura Lusk, Matt Mutel, Elaine S. Walker, and Foster Levy[1]

Abstract.—The Black Mountain range of western North Carolina supports some of the most extensive but threatened high-elevation forests in the southern Appalachians. Of particular note, the insect pathogen, balsam woolly adelgid (*Adelges piceae* Ratzeburg), has been present on Mt. Mitchell for more than 50 years. In anticipation of potential changes in forest composition, vegetation surveys were first conducted in 1966 on nine 1-acre plots near the summit of Mt. Mitchell. These plots were resurveyed in 1978, 1985, and 2002. The purpose of this study was to survey those plots again and use those data to analyze long-term trends in forest composition for fir, spruce-fir, and spruce-fir-hardwood forest types. Since the 1960s and 1970s, all three forest types have experienced a transition away from an understory with a preponderance of Fraser fir (*Abies fraseri* [Pursh] Poir.) seedlings and saplings, to forests with higher densities of canopy and sub-canopy fir. Canopy red spruce *(Picea rubens* Sarg.) has similarly increased in density in the fir and spruce-fir types but declined in the spruce-fir-hardwood forest type. In all types, hardwood seedlings/saplings have declined sharply since a hardwood seedling explosion in 1978. The current analyses indicate that fir and spruce-fir forests have regenerated since the most severe die-offs and that each forest type will experience future impacts from balsam woolly adelgid but in a non-synchronous pattern.

INTRODUCTION

The spruce-fir forest of the southern Appalachians is considered a critically endangered ecosystem because of past impacts such as land development, logging, and soil degradation, as well as more recent threats that include air pollution, climate change, and the balsam woolly adelgid (*Adelges piceae* Ratzeburg) (BWA) (Hain and Arthur 1985, Noss et al.1995). The two characteristic conifer species of this ecosystem are red spruce (*Picea rubens* Sarg.), which in the southern Appalachians is disjunct from its main range in the northeastern United States, and Fraser fir (*Abies fraseri* [Pursh] Poir.), a regionally endemic species with a limited range and patchy distribution (Burns and Honkala 1990).

The most extensive spruce-fir forests in the southern Appalachian region are found at Mt. Rogers and environs in southwest Virginia, at Roan Mountain in east Tennessee and western North Carolina, in the Black Mountains in western North Carolina, and in Great Smoky Mountains National Park (Tennessee and North Carolina). Of these, the Black Mountains have been subjected to the longest period of infestation by BWA. The first report of BWA in the southern mountains, in 1957, was on Mt. Mitchell in the Black Mountains (Speers 1958). Fir mortality on Mt. Mitchell reached 95-98 percent in spruce-fir and spruce-fir-hardwood stands, but only 83 percent in fir stands (Witter and Ragenovich 1986). This severe and long-standing infestation exceeds the generation time of Fraser fir, which may be as short as 15 years but longer under shaded and less optimal conditions (Burns and Honkala 1990). Because the Mt. Mitchell infestation has persisted through at least one and possibly three generations of fir, this site provides an opportunity to examine long-term effects of BWA (and other factors) on forest composition. Moreover, Mt. Mitchell has a long vegetation research history that

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includes data from permanent plots that have been surveyed periodically since 1966–that is, beginning just 9 years after the first report of BWA on the mountain.

The purpose of this study was to resurvey permanent plots that had been established on Mt. Mitchell and to examine trends in forest composition that have occurred over 42 years. We compared data from the current study with those from the initial survey in 1966 (Witter and Ragenovich 1986) and subsequent surveys in 1978 and 1985 (Witter and Ragenovich 1986, Witter 1989) and 2002 (Sanders 2002). For forests in which fir trees were dominant or co-dominant, we hypothesized the progressive decline in juvenile firs noted in earlier studies would continue as small trees mature and the canopy closes. Similarly, we expected to find a continuing increase in nonjuvenile fir as the juveniles move into larger size classes. These hypotheses were contingent upon maintenance of non-epidemic infestations of BWA. If a new wave of widespread fir die-off was initiated during the past decade, however, we expected to observe a dramatic increase in the numbers of dead nonjuvenile fir.

STUDY AREAS

The study was conducted in the Black Mountains of North Carolina. Census plots were located within Mt. Mitchell State Park or on adjoining property of the Blue Ridge Parkway.

METHODS

Field Methods

Less than 10 years after the balsam woolly adelgid was first noted on Mt. Mitchell, a study was initiated to examine long-term changes in the spruce-fir forests. In 1966, nine 1-acre plots were established; each was subdivided into 10 square subplots, 66 ft on a side, or one-tenth of an acre (Fig. 1). The nine plots were apportioned with three plots in each high-elevation forest community that included a significant component of fir trees; from higher to lower elevations these communities were fir, spruce-fir, and spruce-fir-hardwood forest types. Plots were located in stands that had been impacted by BWA (Witter and Ragenovich 1986).

To resurvey these historic plots, we located the corner of each plot from permanent markers that had been placed by

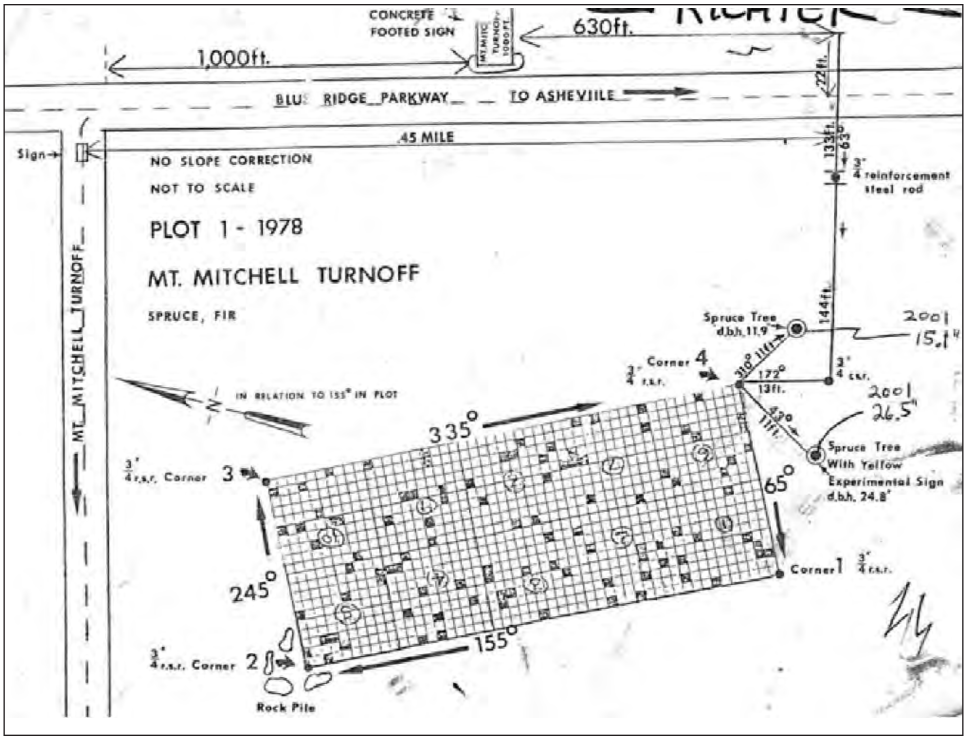

Figure 1.—Schematic of Plot 1 with subplots labeled 1-10 (handwritten numbers in circles). Each subplot contains 100 milacres. From Sanders (2002).

Sanders (2002). Sample plots within each subplot were randomly selected using a random number generator to calculate distances corresponding to “x” and “y” coordinates that were used to delineate sample plot center points. From these points, censuses of all woody plants were conducted in circular sample areas with a 10.7 ft radius.

We collected data consistent with methods used by Witter and Ragenovich (1986) and subsequent studies (Witter 1989, Sanders 2002). For each sample plot within the 90 subplots, each woody plant was identified by species and the following measurements were recorded: height estimated to the nearest foot; diameter at breast height (d.b.h.); canopy position (canopy, sub-canopy, understory [>1 ft], or ground layer [≤1 ft]). Seedlings were defined as ≤6 inches in height. To make comparisons with previous studies, juveniles were defined as ≤8 ft and adults and nonjuveniles were >8 ft. Height and d.b.h. of dead fir trees were also tallied.

Mountain ash (*Sorbus americana* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) constituted 80-100 percent of the hardwoods in the canopy and 77-93 percent of all hardwoods in each forest type. Numbers of hardwoods were combined across species to conform to data analysis in prior studies and because, other than mountain ash and yellow birch, no hardwood species made up more than 10 percent of either the canopy hardwoods or the total number of hardwoods.

Statistical Methods

Data Analysis

For comparisons among species and forest types with maximum resolution in tree sizes, data from the 2008 survey were organized by canopy position. For each canopy position, numbers of trees per species were compared across forest types using the heterogeneity chi-square test of 3 x 3 contingency tables (three species, three forest types). To facilitate comparisons of tree size distributions among forest types, trees were categorized into eight height classes, measured in feet (0.1-8; 8-19; 20-29; 30-39; 40-49; 50-59; 60-69; 70-79). Correlation was used to examine the relationship between height and d.b.h., and between numbers of individuals of juvenile, nonjuvenile, and dead trees within and among species.

Temporal Trends

To compare data from 2008 to earlier surveys, it was necessary to use the juvenile/nonjuvenile data categorization of the earlier studies. To test for temporal trends over a 42-year period, data from the current study were combined with comparable data from the four prior studies. For the current study, the subplot sample area of 359.50 sq. ft. represented 1/121 acre. Data from the 10 subplots within each plot were summed and multiplied by 12.1 to convert to a per-acre scale. Numbers of individuals per acre were regressed over time in a general linear model with separate regressions for juvenile and adult fir, spruce, hardwoods, and dead fir trees.

Statistical analyses were conducted using SAS version 9.1 (SAS Institute, Cary, NC). Stand Visualization Software was used to graphically display forest plot composition across census years (McGaughey 2002).

RESULTS

Current Demographic Patterns

The numbers of trees of each species varied dramatically among the three forest types as shown by highly significant differences in species composition among types for each forest canopy position (for all four canopy positions: χ^2 = 63.6-611.6; df = 4; P <0.0001; n = 325-1643). Fir numerically dominated fir forest types in all forest strata of all fir forest plots (Fig. 2). In the canopy of the fir forest, the number of fir was significantly higher than that of spruce or hardwoods. In spruce-fir and spruce-fir-hardwood plots, the canopy and sub-canopy strata were a more even mix of fir, spruce, and hardwoods (primarily mountain ash and yellow birch). In these forests, however, hardwoods were less common in lower strata (Fig. 2), and the relative dominance of fir and spruce varied by plot. Significant plot-to-plot differences in composition occurred for each forest type. For example, in the spruce-fir forest type, spruce was more prevalent in one plot and fir in two plots, while in the

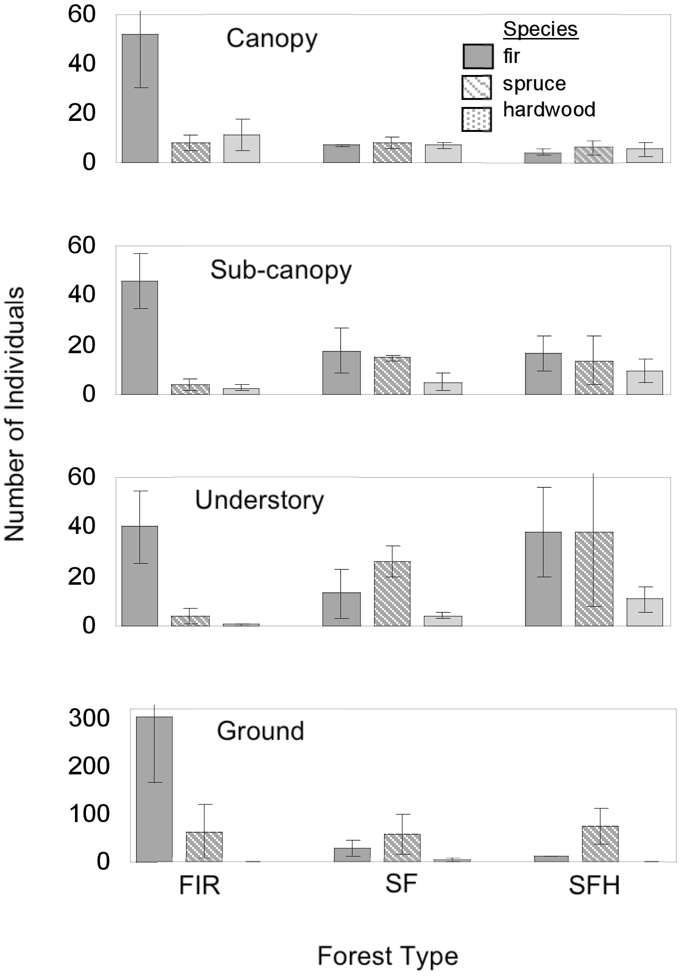

Figure 2.—Number of trees in each forest stratum by species and forest type. From 2008 census. Error bars represent standard error of the mean of three plots within each forest type. Area of three plots represents 1/40 acre. Forest Types: FIR; SF=Spruce-Fir; SFH=spruce-fir-hardwood.

spruce-fir-hardwood type, the distribution of fir, spruce and hardwoods was more even on average but also more variable by plot (Table 1). In the understory, juvenile fir again dominated in the fir forest type, but both spruce and fir were common in the spruce-fir and spruce-fir-hardwood types (Fig. 2). For all forest strata, hardwoods were at most, an equal or sub-equal component of the spruce-fir and spruce-fir-hardwood forests, but as in the fir forests, hardwoods were a minor component of lower strata (Fig. 2).

In the spruce-fir type, nonjuvenile dead fir were the most abundant component of one of the three plots and common in the other two plots (Table 1). In contrast, nonjuvenile dead fir in the fir forest type were absent in two of three plots and a minor component of the third plot (Table 1); in that plot, all dead fir trees were relatively small in size (≤19 ft) (Table 3). Juvenile dead fir followed a pattern of occurrence similar to nonjuvenile dead fir in that plots with more nonjuvenile dead fir tended also to have more juvenile dead fir (Table 2). In one plot of the spruce-fir type, the number of nonjuvenile dead fir greatly exceeded the number of live trees of any species (Table 1). Thus, live fir were most prevalent in the fir forest type, dead fir were most prevalent in the spruce-fir forest type, and there was a more even distribution of each species in the spruce-fir-hardwood forest type.

Significant negative correlations occurred between the numbers of fir and spruce in the canopies of fir and spruce-fir forests (r = -0.39, P = 0.04; r = -0.30, P = 0.03; respectively) and in the understory of the spruce-fir-hardwood forest (r = -0.30, P = 0.05). Other associations were not significant for any other canopy stratum.

The size distribution of species also differed among species and forest types. Large (≥50 ft in height) fir trees were more common than large spruce in the spruce-fir forest. Large trees of all species, however, were most numerous in the spruce-fir-hardwood forest, in large part because this was the only type that supported large hardwoods. There they outnumbered large spruce and fir (Table 3). Large trees were rare (an order of magnitude less common) in the fir forest. In the spruce-fir type, small (<20 ft) and large spruce were most common but at intermediate heights, there were more fir trees (Table 3). Fir seedlings were most numerous in the fir forest and relatively rare in the spruce-fir-hardwood forest compared to spruce seedlings, which were common in all forest types. Hardwood seedlings were rare in all forest types.

Temporal Trends in Forest Composition

Forest composition changed dramatically and in a forest type-specific manner over more than 40 years. For all of the significant trends we report, regressions of number of trees on time explained a high proportion of the variation in numbers of individuals (adj. r^2 = 0.77-0.98). The numbers of juvenile fir declined significantly in spruce-fir and spruce-fir-hardwood forests and showed a marginally significant decline in the fir type (Table 4; Fig. 3). In the fir type, the number of dead

Table 1.—Number of nonjuvenile (height >8 ft) fir, dead fir, spruce, and hardwood trees per acre by forest type and plot in 2008.

Forest type			Fir	Dead fir	Spruce	Hardwood
Fir		Plot				
		5	532	109	230	61
		8	2,432	0	12	121
		9	1,210	0	157	339
	Mean		1,392	36	133	169
Spruce-fir						
		1	508	1,742	363	157
		4	387	254	278	266
		6	169	61	641	145
	Mean		351	690	424	194
Spruce-fir-hardwood						
		569	97	157	339	569
		36	24	774	157	36
		508	97	24	375	508
	Mean	375	73	315	290	375

Table 2.—Number of juvenile (height ≤8 ft) fir, dead fir, spruce, and hardwood trees per acre by forest type and plot in 2008.

Forest type			Fir	Dead fir	Spruce	Hardwood
Fir		Plot				
		5	1,803	339	2,239	0
		8	2,795	0	0	24
		9	7,608	0	182	0
	Mean		3,969	109	811	12
Spruce-fir						
		1	24	266	218	218
		4	944	85	593	24
		6	593	73	2,977	12
	Mean		520	145	1,258	85
Spruce-fir-hardwood						
		2	545	36	315	182
		3	145	0	2,626	12
		7	714	157	835	73
	Mean		472	61	1,258	85

nonjuvenile fir decreased exponentially as demonstrated by a significant fit of a linear regression on the logarithm of number of trees but a non-significant fit to untransformed data. Nonjuvenile spruce experienced a significant increase in the spruce-fir type while in the spruce-fir-hardwood type, nonjuvenile fir increased but hardwoods decreased in numbers. Nonjuvenile fir peaked and then declined in fir and spruce-fir types (Table 4; Fig. 3).

DISCUSSION

Current Forest Composition

After the massive fir die-off at Mt. Mitchell in the 1960s and 1970s, fir has returned to dominance in the canopy of the fir forest type and to co-dominance in the spruce-fir and spruce-fir-hardwood types (Fig. 3). In each type, juveniles and seedlings are present in abundance but their densities

Table 3.—Number of fir, spruce, and hardwood species per acre by height class and forest type in 2008.

Forest type	Species	Height class (ft)							
		0.1-8	8-19	20-29	30-39	40-49	50-59	60-69	70-79
Fir									
	Fir	11,906	1,089	1,186	1,162	629	109	0	0
	Spruce	2,420	97	85	73	73	61	12	0
	Hardwood	24	36	109	266	97	12	0	0
	Dead fir	290	109	0	0	0	0	0	0
Spruce-fir									
	Fir	1,561	182	436	230	85	48	73	12
	Spruce	3,787	532	363	121	157	73	36	0
	Hardwood	254	109	121	230	109	0	0	0
	Dead fir	169	121	36	48	12	0	0	12
Spruce-fir-hardwood									
	Fir	1,404	750	206	36	24	48	12	36
	Spruce	3,775	472	194	145	48	73	12	0
	Hardwood	266	182	182	157	194	48	48	48
	Dead fir	436	871	593	520	133	36	0	12

Table 4.—Stem densities per acre of juvenile (height ≤8 ft) and nonjuvenile (height >8 ft) fir, dead fir, spruce, and hardwood species by forest type from 1966-2008. For significant temporal trends detected by regression analysis, P values associated with regressions are shown below columns, where *P <0.05; **P <0.01; ***P <0.001; (*)P = 0.05-0.10

		Fir		Dead fir		Spruce		Hardwood	
Forest type	Year	≤8ft	>8ft	≤8ft	>8ft	≤8ft	>8ft	≤8ft	>8ft
Fir	1966	13,407	323	237	1,523	230	83	43	247
	1978	7,409	320	650	450	294	203	1,666	294
	1985	2,990	1,690	720	230	130	220	610	160
	2002	433	2,347			77	120	13	317
	2008	3,969	1,392	109	36	811	133	12	169
		(*)			**				
Spruce-Fir	1966	15,540	6	420	273	1,754	247	40	73
	1978	7,973	423	1,403	118	6,723	207	2,033	193
	1985	5,000	2,030	950	60	6,970	320	1,510	410
	2002	330	887			1,070	433	150	217
	2008	550	351	145	690	1,258	424	85	194
		**					*		
Spruce-Fir-Hardwood	1966	3,047	17	67	347	333	233	744	717
	1978	2,007	20	3	97	867	213	1,730	793
	1985	1,680	120	10	20	2,280	190	2,410	530
	2002	600	340			1,463	363	287	297
	2008	472	375	61	73	1,258	315	85	290
		***	**						*

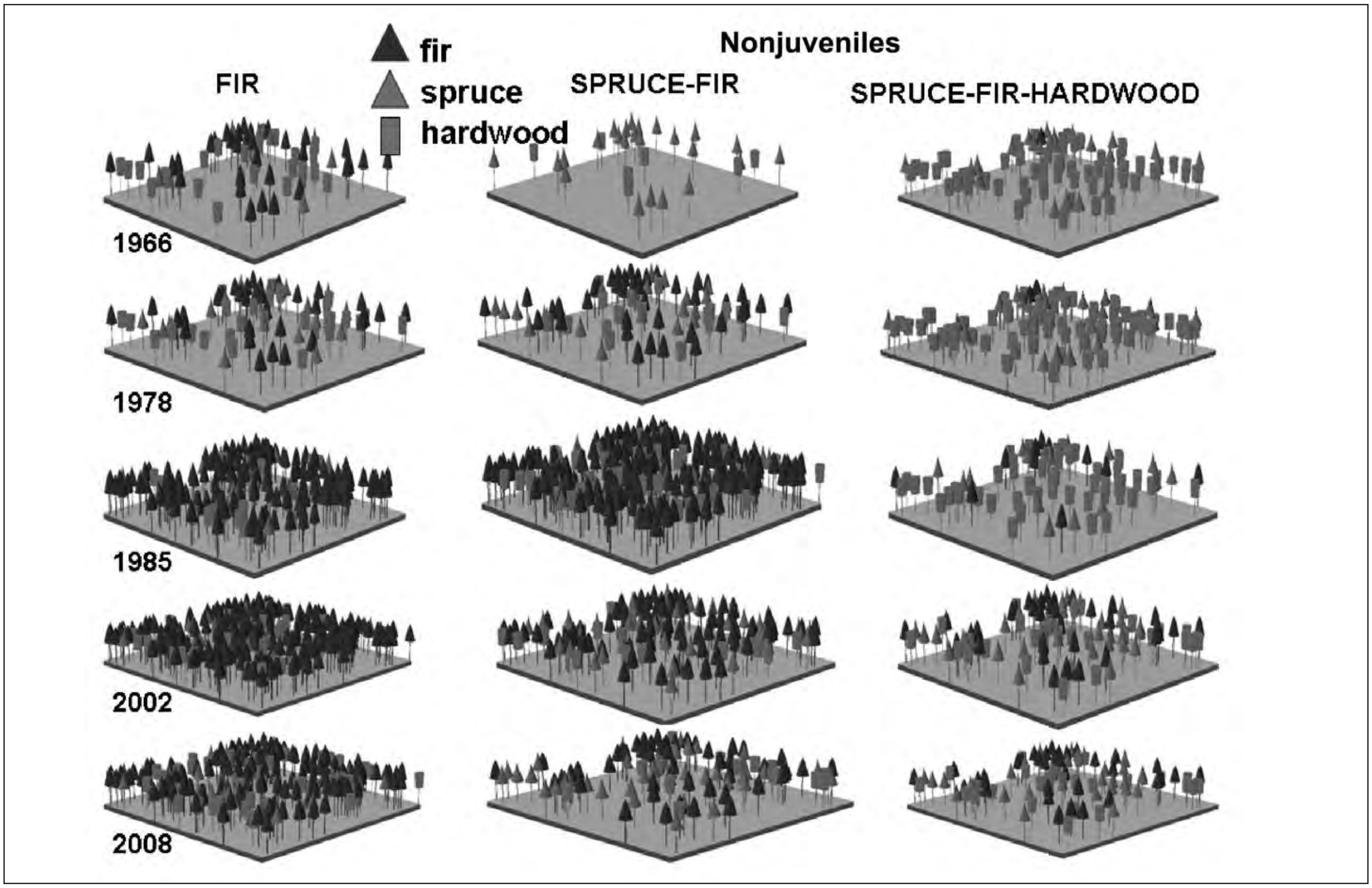

Figure 3.—Graphical views of nonjuvenile trees for each census period from 1966 to 2008 in each forest type. To facilitate resolution of trees and tree species, trees are shown at 10 percent of actual density.

decline with canopy closure. The fir forest type is most densely populated with fir trees in all forest strata but with fewer large trees compared to other forest types. Fir does not typically attain its maximum size in the highest-elevation pure fir stands, such as those near the summits of the Black Mountains (Burns and Honkala 1990). In the fir and spruce-fir forest types, the numbers of canopy fir and spruce were negatively correlated as they were in the understory of the spruce-fir-hardwood type. The negative correlations between fir and spruce may reflect differences in niches or competitive interactions. BWA maintains a presence in each forest type as noted by direct observation, as well as by numerous mature dead fir in each forest type.

Fir populations were recently surveyed on five mountains in Great Smoky Mountains National Park, the only more southern expanse of Fraser fir relative to the Black Mountains (Moore et al. 2008). Comparisons between the Great Smokys and the Black Mountains may be instructive because they both have long histories of BWA infestation. Both the Smoky Mountains and Mt. Mitchell showed plot-to-plot differences in composition. The mountains surveyed in the Smokies were chosen to encompass a time series, from 1970-1990, of major BWA infestation dates that corresponded to elevation and directional infestation trends (Smith and Nicholas 2000, Allen and Kupfer 2001). The fir forest type of Mt. Mitchell was most similar to Mt. LeConte in showing high densities (>400 stems per acre) of saplings (2- to 6-inch d.b.h.), but otherwise the Mt. Mitchell fir forest supported more fir saplings than any of the mountains in the Smoky Mountains. In larger size classes, the number of fir trees in the Mt. Mitchell fir forests was more similar to mountains in the Smoky Mountains. In the spruce-fir and spruce-fir-hardwood types of Mt. Mitchell, however, larger fir trees tended to be less common than in the mountains of the Smokies.

Temporal Trends

Although data collection in the Mt. Mitchell permanent plots began in 1966, even by 1985 it was acknowledged that insufficient time had passed for an accurate assessment of long-term consequences of BWA impacts because regenerating fir trees had not reached reproductive maturity (Witter and Ragenovich 1986). Such an assessment is now feasible, however; in the ensuing 30-40 years, fir seedlings that established under open canopies have attained mature sizes and realized their reproductive potential.

It was not possible to thoroughly examine patterns of temporal change within forest strata at Mt. Mitchell because prior surveys did not report canopy positions for individual trees. Nonetheless, the prior studies delineated size as greater or less than 8 ft, which permitted temporal analyses based on differences between juvenile and nonjuvenile trees. Declines in juvenile fir, from thousands of individuals per acre to less than 500 by the 2002 survey, were noted in all forest types. Although fir seedlings were abundant in most Mt. Mitchell plots in 1966, by 1978 a pattern of decreasing seedling numbers, particularly in spruce-fir and spruce-fir-hardwood forests was first noted (Witter and Ragnovich1986). With the current data, it is now evident that in each forest type, these declines were accompanied by increases in nonjuvenile fir, although in the spruce-fir type, nonjuvenile numbers peaked in 1985 and then declined. The relationship between numbers of juvenile and nonjuvenile fir was highlighted by very strong negative correlations between numbers of juvenile and nonjuvenile fir in the fir ($r = -0.90$; $P = 0.04$) and spruce-fir-hardwood ($r = -0.93$; $P = 0.02$) forest types. The numbers of juvenile and dead nonjuvenile fir showed a positive correlation in the fir forest ($r = 0.96$; $P = 0.04$). In the spruce-fir-hardwood type, juvenile fir tended to thrive under hardwoods, as shown by a strong positive correlation between the numbers of juvenile fir and nonjuvenile hardwood ($r = 0.89$; $P = 0.04$).

The correlations between juvenile and nonjuvenile or dead fir trees suggest that juvenile fir are most successful after the loss of fir in the canopy. Further, the declines in juvenile and increases in nonjuvenile fir in the aftermath of widespread die-offs of mature fir probably reflect natural succession to forests in which fir will again be a major component of the sub-canopy and canopy. Reductions in juvenile fir, including seedlings, may reflect natural thinning in densely stocked stands caused by competitive interactions and a transition to less favorable conditions, characterized by poor sunlight penetration and a deepening litter layer.

In 1986, Witter and Ragenovich acknowledged that a full determination of the impact of BWA was premature, but based on the magnitude of fir regeneration and growth between 1966 and 1986, they suspected that the initial wave of fir regeneration was sufficient to maintain fir as a major constituent of the Mt. Mitchell high-elevation forests. While BWA continues to infest these forests, our observations show regenerated fir are producing cones and seedlings in numbers that vary in a plot- and forest type-specific manner. Whereas Witter and Ragenovich reported no trees with d.b.h. greater than 4 in., our 2008 survey found fir trees larger than that size in all nine plots. All but one plot harbored fir trees between 6 and 9 in. d.b.h. Moreover, greater than 16 percent of all fir trees were between 40 and 70 ft in height and trees this size were found in all plots. These data indicate that regenerated fir continues to mature on Mt. Mitchell.

A deterministic model of BWA-fir dynamics showed that after loss of mature fir trees, a likely outcome is cyclic oscillations in BWA and fir populations with plot-specific dynamics that are dependent upon dispersal of each species and the effects of temperature on BWA survival (Dale et al. 1991). Cycles, rather than extinction, are predicted because BWA tends not to feed on young fir. Significant increases in fir were also noted between 1993 and 2003 in the spruce-fir forests of the Noland Divide Watershed of Great Smoky Mountains National Park (Moore et al. 2008). Fir biomass increased nearly fourfold across an elevation gradient while spruce and birch biomass showed either no differences or more modest increases. Fir, however, also experienced an increase in mortality. On Mt. Mitchell, current forest composition and long-term trends pointed to the re-emergence of forest stands with fir as a canopy dominant. Our observations are consistent with predictions of forest composition following BWA infestation based on models and derived from empirical observations: all indicate that the re-emergence of fir in the forest canopy is not unexpected.

CONCLUSIONS

1. Fir dominated all strata of high-elevation pure fir stands and is a co-dominant with spruce and hardwoods (mountain ash, yellow birch) in spruce-fir and spruce-fir-hardwood forests.

2. Numbers of canopy spruce and fir showed an inverse relationship.

3. Significant temporal decreases in juvenile fir were accompanied by increases of nonjuvenile fir in all three forest types.

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ABUNDANCE OF RED SPRUCE REGENERATION ACROSS SPRUCE-HARDWOOD ECOTONES AT GAUDINEER KNOB, WEST VIRGINIA

Albert E. Mayfield III and Ray R. Hicks, Jr.[1]

Abstract.—The abundance of red spruce (*Picea rubens* Sarg.) in the Central Appalachian Mountains has been drastically reduced over the past 100 to 150 years. The purpose of this study was to examine the potential for increases in the relative abundance of overstory red spruce in a Central Appalachian, high-elevation forest by measuring the abundance of red spruce regeneration on transects which crossed transitional spruce hardwood ecotones. Six transects were located in the Gaudineer Knob area of the Monongahela National Forest, WV, in 1996. Ninety-four transect plots were classified into three cover types (red spruce, ecotone, or northern hardwood) using a joining cluster analysis, which grouped plots according to relative basal area of red spruce and northern hardwoods. Forest canopy composition and ecotone abruptness were examined using basal area and stem density data collected at each transect plot. Mean numbers of seedlings (height ≥7.5 cm to <90 cm) and saplings (height ≥90 cm but diameter at breast height <7.5 cm) per hectare for all tree species were computed for each forest cover type.

In this study, red spruce occurred across the entire elevation range sampled (1,090 to 1,350 m). Spruce-hardwood ecotones varied in abruptness and their location was not consistently associated with elevation or aspect. Comparisons using rank-transformed values of mean seedling and sapling densities revealed that red spruce was the most abundant species of regeneration in both the red spruce and ecotone cover types, and was a substantial component of the sapling population in the northern hardwood cover type. The abundance of red spruce regeneration in the ecotone and adjacent hardwood cover types may represent an opportunity, through silvicultural treatments, to increase the relative abundance of overstory red spruce and spruce-dominated stands in the Gaudineer Knob area.

INTRODUCTION

The distribution of red spruce (*Picea rubens*) in eastern North America extends from the mountains of western North Carolina and eastern Tennessee northeastward into central Quebec and New Brunswick (White and Cogbill 1992). Although red spruce can occur at low elevations in the northeastern United States, Canada, and a few disjunct New Jersey populations (Webb et al. 1993), it is restricted to upper elevations in the Central and Southern Appalachian Mountains. Spruce forests were apparently widespread even at low elevations throughout the Appalachian region following the Wisconsin glaciation, but the period of maximum post glacial warmth 8,000 to 4,000 years ago corresponded with a displacement of red spruce to the higher Appalachian peaks and ridges (White and Cogbill 1992). This climate correlated shift in distribution reflects the fact that red spruce is well adapted for growth in a cool climate (Blum 1990) and several studies suggest a physiological basis for the relationship between red spruce growth and temperature (Cook and Zedaker 1992, Vann et al. 1994, Alexander et al. 1995).

In the Central Appalachians of West Virginia, red spruce forests are unique natural areas occurring primarily above an

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elevation of 915 m on the highest ridges, high valleys, and plateaus of the Allegheny Mountain Section (Clarkson 1960). These cool, moist, high-elevation sites likely serve as "climatic islands" suitable for red spruce growth and development. The vegetative composition and structure of both old growth and second growth red spruce and spruce hardwood forests in West Virginia have been documented by several authors (Core 1929, Stephenson and Clovis 1983, Adams and Stephenson 1989, Pauley 1989). In these forests, pure stands of red spruce on the highest knobs and ridges often grade into mixtures, or transitional "ecotones" (Risser 1995), with northern hardwood species at lower elevations. Cogbill and White (1991) analyzed the latitude elevation relationship for Appalachian montane spruce fir forests and described the gradient of vegetation change across these ecotones. In their generalized model, low-elevation deciduous trees and temperate conifers decline in importance as elevation increases and give way to northern hardwood species, dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton). Yellow birch reaches peak importance at higher elevations than do maple and beech, becoming conspicuous in the ecotone as red spruce enters the forest in a mixture of hardwoods. Red spruce then increases in importance as elevation increases (Cogbill and White 1991). Elevations in the Central Appalachians are insufficient to allow for the development of fir-dominated stands above the spruce-dominated zone, as is observed in other parts of the Appalachian spruce-fir range (Cogbill and White 1991).

Spruce-hardwood ecotones in the Central Appalachians may have been sharpened and shifted as a result of anthropogenic disturbances that drastically reduced the abundance of red spruce in the last 100 to 150 years. Conversion of spruce wilderness to agricultural land in the 1800s (Clarkson 1960), followed by widespread logging and associated fires in the late 19th and early 20th centuries, favored the rapid replacement of red spruce with deciduous northern hardwood species and other early successional vegetation (Korstian 1937, Minkler 1945, Clarkson 1964). Thus, while early estimates of the extent of red spruce in the 1700s ranged from approximately 200,000 to 600,000 ha (Hopkins 1891, 1899), more recent estimates indicated that only 17,500 to 44,500 ha of West Virginia forests contain a red spruce component (Mielke et al. 1986, DiGiovanni 1990, Stephenson 1993).

Given the dynamic history of red spruce abundance and distribution in the Central Appalachians, the question of whether the red spruce distribution will increase, decrease, or remain stable over the next several decades is one that is both interesting and timely. Red spruce decline in Adirondack and northeastern Appalachian red spruce forests, characterized by mortality, branch dieback, and distinct diameter growth reductions, has been of special concern over the past 20 years, and several biotic, abiotic, and anthropogenic contributing factors have been proposed (Johnson and Siccama 1983, Eagar and Adams 1992, Johnson 1992, Reams and Van Deusen 1993). Although decline in the Central Appalachians has not received as much research attention as the Northeast, Mielke et al. (1986) classified 33 percent of the cubic foot volume in West Virginia as dead or declining, and Adams et al. (1985) provided evidence that Central Appalachian red spruce had experienced radial growth reductions similar to those reported for several northern Appalachian sites. Furthermore, significant shifts in plant species ranges in response to climate change have been proposed, and concern exists that certain high elevation species (perhaps including Central-Appalachian red spruce) may be pushed upslope until local extirpation occurs (Pastor and Post 1988, Peters 1990).

Despite the potential threats to red spruce, other factors could favor an increase in its abundance in the Central Appalachians. The destructive fires and intense logging that characterized the early 1900s have been rare or absent in the last 80-90 years on most upland sites that were converted from red spruce to northern hardwood species. Pielke (1981) suggested that during this period, upland northern hardwoods in the Central Appalachians have matured, improving the soil through nutrient recycling and creating a more favorable microclimate beneath their canopies for successful spruce germination and growth. Hornbeck and Kochenderfer (1998) reported that annual growth rates in three natural red spruce stands and three plantations in West Virginia had stabilized and even shown slight increases following marked declines in the 1960s and 1970s. Their data suggest that there are healthy, productive red spruce forests in West Virginia and that their aerial extent could be enhanced through silviculture, especially in areas where red spruce already exists in the understory. More recent studies simulating future growth in mixed spruce-hardwood forests in West Virginia suggest that silvicultural manipulations could accelerate succession toward stands with a greater red spruce overstory component (Schuler et al. 2002, Rentch et al. 2007). Given that red spruce forests are habitat for rare and endangered plant and animal species, are popular recreation areas, and provide a high-quality wood resource, expansion of red spruce forests in the state could be particularly desirable.

The purpose of this study was to examine the potential for increases in the relative abundance of overstory red spruce in a Central Appalachian, high-elevation forest by measuring the abundance of red spruce regeneration on transects which crossed transitional spruce hardwood ecotones.

DESCRIPTION AND HISTORY OF THE STUDY AREA

Gaudineer Knob (summit elevation 1,355 m) and the surrounding area on Shavers Mountain, Monongahela National Forest, West Virginia (Fig. 1) was chosen for study because it contains a typical mountain top population of red spruce and northern hardwood cover types, as well as transitional ecotones. Average January temperature in this portion of Randolph County is less than -1.1 °C and the area receives more than 132 cm of precipitation annually (Hicks and Mudrick 1994). The geologic substrata in the area surrounding Gaudineer Knob are part of the Hinton formation, consisting of red, green, and medium-gray shales and sandstones. Well drained Inceptisols and Ultisols of the Dekalb Buchanan Association are present, in addition to very sandy Spodosols of the Leetonia series, which typically have a large percentage of coarse fragments (USDA Soil Conservation Service 1978). Adams and Stephenson (1989) found soils at Gaudineer Knob to be predominantly sandy, characterized by high acidity, high levels of organic matter, and low levels of major nutrients.

Between 1824 and 1847 the Parkersburg and Staunton Turnpike (now U.S. Route 250) was constructed from Virginia to the Ohio River, crossing Shavers Fork River at Cheat Bridge (Fig. 1). A small settlement grew here, but as late as 1880 the rest of "Cheat Mountain," as this area is called locally, was essentially wilderness (Deike 1978). In 1884, extensive timber operations commenced along the Shavers Fork River (Hopkins 1899). By 1890, James Dewing and Company began to clear obstructions from the banks of the river north of Cheat Bridge, built a dam, and constructed a railroad 7 km into the woods to extract timber. Timbering in the area progressed for several years until the company folded and sold large tracts of land to the West Virginia Pulp and Paper Company, which logged the

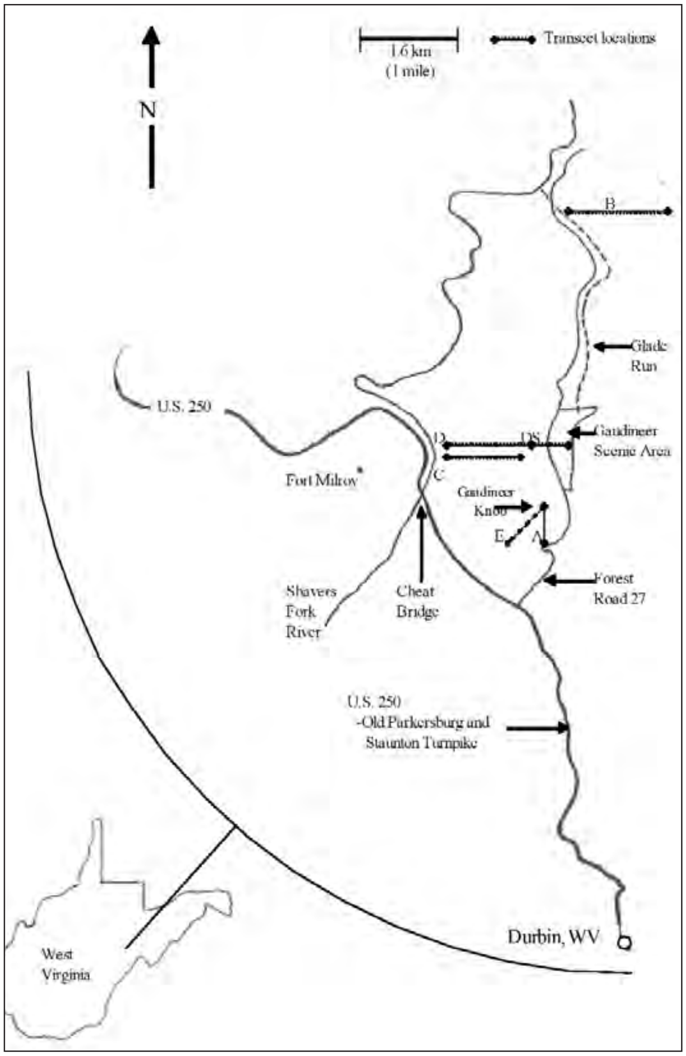

Figure 1.—Map of Gaudineer Knob, WV, and surrounding area. Location of study transects are shown and labeled with capital letters.

area between Cheat Bridge and Glade Run (Fig. 1), continuing as late as the 1930s (Deike 1978). Many areas of the spruce forest also burned over after logging, the fires being fueled by logging slash and deep litter layers. Although most of Cheat Mountain was steadily logged throughout the late 1800s and early 1900s, one 57 ha tract, just 0.4 km east of the Gaudineer Knob summit, was completely spared of any cutting, due to a surveyor's error during pre Civil War times (Brooks 1965).

The late 1800s marked a time of severe mortality and stress in the spruce forests near Gaudineer Knob. Hopkins (1891, 1899) specifically mentions the Cheat Bridge area as having high rates of red spruce mortality. Upon reaching "the battle field of Cheat Mountain" (perhaps the site of Fort Milroy, Fig. 1), where "an extended view was had of the Cheat Mountains extending on all sides," Hopkins (1891) stated that "thousands upon thousands of acres of what must have been a magnificent black green forest of living spruce, was now viewed as an immense waste of dead and decaying trees, presenting a desolate and dreary landscape." Hopkins (1899) implicated bark beetle activity (notably *Polygraphus rufipennis* Kirby and *Dendroctonus frontalis* Zimmerman) in conjunction with severe droughts (notably the drought of 1882) as mortality factors, but the actual contributing factors cannot be stated with certainty.

The summit of Gaudineer Knob had been harvested by 1915 (Mohlenbrock 1990), except for the area mentioned previously. Soils on Gaudineer's summit were spared from fire, permitting successful re-establishment of spruce from seed blown in from the adjacent old-growth stand (Clarkson 1960). Evidence of fire and conversion from spruce forest to hardwood thicket just 0.9 km north of the summit has been documented (Stewart and Aldrich 1949). Since the U.S. Forest Service acquired the land in 1936, partial harvests have been performed in certain parts of the Gaudineer area at various times, which have added to the multi cohort nature of some stands. The tract of old-growth spruce spared from harvest by the survey error has remained uncut and is managed by the U.S. Forest Service as the Gaudineer Scenic Area.

METHODS

Transect and Plot Establishment

Six transects were established in the Gaudineer Knob area of Shavers Mountain (Fig. 1) between June and August 1996. Black and white aerial photographs were used to identify areas in which a gradient of cover types (progressing upslope from hardwoods through mixed spruce-hardwood ecotones and into spruce-dominated stands) appeared to exist, and the six transects were established with a general perpendicular relationship to the contour in these gradient areas, cutting across the ecotone. Transects D and DS both begin at a point near the peak of the Gaudineer Knob ridgeline and run in opposite directions (Fig. 1). A series of 0.04 ha circular plots was established along each transect. To ensure adequate sampling of the ecotone on each transect, the 0.04 ha plots were spaced more closely on transects where an abrupt ecotone was indicated on the aerial photographs than on transects where the transition was expected to be gradual. The elevation in meters of each plot was estimated from U.S. Geological Survey 7.5 minute quadrangle topographic maps. Table 1 provides summary information for each transect, including the number of plots, plot spacings, transect length, aspect, and elevation range of the transects. Ninety-four plots were established.

Measurement of Forest Overstory, Regeneration, and Ground Cover

Within each 0.04 ha plot, the d.b.h. (diameter at 1.37 m above ground) of all live trees 7.5 cm in diameter or greater was measured and recorded in 2.5 cm diameter classes. Regeneration density was measured on five 10.5-m^2 circular subplots established within each 0.04-ha plot. One subplot was established in the center of the 0.04-ha plot, with the other four subplots located in the four cardinal directions at distances of 9.5 m from the center. Numbers of seedlings and saplings for all tree species were counted and recorded within each 10.5-m^2 subplot. A seedling was defined as a live stem at least 7.5 cm tall but less than 90 cm tall. A sapling was defined as a live stem 90 cm tall or greater, but less than 7.5 cm d.b.h. Deciduous hardwood seedlings or saplings were not tallied if they possessed fewer than two mature leaves. Distinction was not made between stems of

Table 1.—Summary information for six transects crossing spruce-hardwood ecotones at Gaudineer Knob, WV.

Transect	No. of 0.04 ha plots on transect	Spacing between plots (m)	Transect length (m)	Aspect	Elevation range (m)
A	13	60, 40[a]	604	S	1,213-1,329
B	15	100	1,408	W	1,116-1,256
C	12	180	1,811	W	1,091-1,299
D	26	60	1,509	W-NW	1,091-1,296
DS	8	60	423	NE	1,220-1,296
E	20	60	1,147	SW-W	1,189-1,290

[a] The ecotone on transect A was more abrupt than anticipated from aerial photos; plot spacing was therefore shortened from 60 m to 40 m during the sampling procedure for seven plots in the middle of the transect in order to adequately sample the ecotone. Otherwise, plot spacings were determined prior to sampling.

seed origin and those of vegetative origin; thus, the term "seedling" in this study was only an indicator of size.

Classification of Plots into Forest Cover Types

A joining q-mode cluster analysis (StatSoft, Inc., Tulsa, OK) was used to group the 0.04-ha plots (n = 94) into three cover type categories: northern hardwood, ecotone, and red spruce. This hierarchical classification technique joined 0.04-ha plots into successively larger clusters, based on the similarity of values for specified variables (Swan and Sandilands 1995). The variables used in this analysis were the relative basal area (BA) of red spruce on a plot (i.e., red spruce BA expressed as a percent of total plot BA) and the relative BA of northern hardwood species on a plot. Euclidean (straight-line) distance was chosen as the measure of similarity between plots, and plots were linked according to the nearest neighbor linkage algorithm (Swan and Sandilands 1995). A dendrogram with three distinctly dissimilar clusters of plots was produced. The cluster of 21 plots with the lowest (<10 percent) relative red spruce BA was classified as the "northern hardwood" cover type, the cluster of 41 plots with intermediate (10-80 percent) relative red spruce BA was classified as the "ecotone" cover type, and the cluster of 32 plots with the greatest (>80 percent) relative red spruce BA was classified as the "red spruce" cover type. The relative BA of red spruce on each 0.04-ha plot was plotted against estimated elevation for each of the six transects, providing a graphical representation of the changes in red spruce abundance with elevation.

Comparison of Mean Regeneration Densities

Mean number of stems per hectare and mean basal area per hectare by species were computed from the 0.04-ha plot data for each of the three forest cover types defined in the cluster analysis (northern hardwood, ecotone, and red spruce). For seedling and sapling densities (stems/ha) and ground-cover variables, the five 10.5-m^2 subplot values were averaged for each 0.04-ha plot, and the larger plot values were used to compute means for each cover type. One way analysis of variance (ANOVA) (Dowdy and Wearden 1991) was used to test the null hypothesis that mean densities for the following four regeneration categories did not differ within cover type: red spruce seedlings, red spruce saplings, northern hardwood seedlings, and northern hardwood saplings. Levene's test for homogeneity of variance revealed heterogeneous class variances that were correlated with means, situations that violate the assumptions of ANOVA. The raw data were therefore transformed using a rank transformation (Conover and Iman 1981) in which all values were replaced with their ranks (assigning the smallest value a rank of 1, the second smallest value a rank of 2, and so on). Average ranks were assigned in the case of ties. ANOVA was then performed on the rank-transformed values (Conover and Iman 1981). Mean ranks were compared using Scheffe's method (Dowdy and Wearden 1991).

RESULTS

Forest Overstory Composition

The total mean BA per hectare and total mean density of stems ≥7.5 cm diameter at breast height (d.b.h.) for each of the three forest cover types is presented by major species in Table 2. Red spruce was a very small component of the plots

Table 2.—Mean (SE) basal area and density of major treea species by forest cover type, on transects crossing spruce-hardwood ecotones at Gaudineer Knob, WV.

	Basal area (m^2/ha)			Density (stems/ha)		
Species	Northern hardwood	Ecotone	Red spruce	Northern hardwood	Ecotone	Red spruce
Acer pensylvanicum	0.2 (0.1)	0.2 (0.1)	0.0 (0)	30 (12.2)	17 (5.6)	0 (0)
Acer rubrum	5.1 (1.4)	5.6 (1.0)	0.2 (0.1)	88 (28.1)	104 (15.4)	12 (4.4)
Acer saccharum	1.7 (0.9)	0.0 (0.02)	0.0 (0)	24 (9.2)	2 (1.8)	0 (0)
Amelanchier arborea	0.3 (0.1)	0.1 (0.1)	0.0 (0)	10 (4.4)	6 (3.2)	0 (0)
Betula alleghaniensis	2.9 (1.1)	5.4 (0.6)	0.7 (0.2)	76 (21.2)	201 (22.1)	76 (16.5)
Fagus grandifolia	4.7 (0.8)	1.4 (0.4)	0.0 (0)	144 (22.3)	48 (12.8)	0 (0)
Fraxinus americana	0.7 (0.6)	0.0 (0.03)	0.0 (0)	6 (3.4)	2 (2.4)	0 (0)
Ilex montana	0.0 (0)	0.0 (0.01)	0.0 (0.01)	0 (0)	5 (2.8)	2 (1.1)
Magnolia acuminata	1.4 (0.6)	0.2 (0.1)	0.0 (0)	16 (6.6)	12 (4.1)	0 (0)
Picea rubens	0.1 (0.03)	8.5 (0.7)	23.2 (1.2)	18 (6.0)	158 (11.1)	609 (68.8)
Prunus serotina	4.2 (1.6)	0.7 (0.3)	0.0 (0)	36 (13.0)	11 (3.3)	0 (0)
Other species[b]	0.0 (0.04)	0.0 (0.04)	0.0 (0)	1 (0.9)	1 (1.1)	0 (0)
ALL SPECIES	21.3 (1.9)	22.3 (1.0)	24.0 (1.2)	450 (36.0)	571 (20.0)	698 (64.0)

[a] Includes stems ≥7.5 cm d.b.h.

[b] "Other species" were *Acer spicatum, Magnolia fraseri, Ostrya virginiana, Prunus pensylvanica,* and *Sorbus americana.* Species nomenclature follows Gleason and Cronquist (1991).

classified as northern hardwood cover type, occupying on average less than 1 percent (0.1 m^2/ha) of the total BA and only 4 percent (17.9 stems/ha) of the total stem density. Red maple (*Acer rubrum* L.) and American beech were the most abundant trees in terms of BA and stem density. Yellow birch and black cherry (*Prunus serotina* Ehrh.) were also substantial components of the northern hardwood cover type (Table 2). In the plots classed as ecotone cover type, red spruce on average occupied 38 percent (8.5 m^2/ha) of the total BA and 43 percent (157.9 stems/ha) of the total stem density. Compared with the northern hardwood cover type, yellow birch and red maple were more abundant in the ecotone, while American beech and black cherry were less abundant (Table 2). In the red spruce cover type, an average of 96 percent (23.1 m^2/ha) of the total BA and 87 percent (608.6 stems/ha) of the stem density was red spruce. Only yellow birch and red maple shared canopy space with red spruce in the red spruce cover type, while mountain holly [*Ilex montana* (T. & G.) A. Gray] was present as an understory shrub (Table 2).

Ecotone Elevation and Abruptness

Red spruce relative BA versus elevation for each of the six transects is presented in Figure 2. Four transects (A, B, DS, and E) displayed a transition from northern hardwood canopy to red spruce canopy as elevation increased, each passing through a spruce hardwood ecotone phase (Fig. 2a). The elevation at which spruce entered as a canopy component varied among these four transects (from 1,175 m on Transect B to 1,310 m on Transect A), as did abruptness of the ecotone transition zone (e.g., sharp on Transect A, more gradual on Transect B). In contrast, the primarily west facing transects C and D did not display a smooth elevational gradient from hardwood to ecotone to spruce (Fig. 2b). Notably, both pure hardwood stands and pure red spruce stands could be found at the same elevations (between 1,235 and 1,300 m) in the study area.

Regeneration Density

In the red spruce cover type, mean red spruce regeneration densities (19,433 seedlings/ha, 10,189 saplings/ha) were significantly greater than the mean hardwood regeneration densities (Fig. 3, Table 3). Only mountain holly and yellow birch were notable contributors to hardwood regeneration in the red spruce cover type. In the ecotone cover type, mean red spruce regeneration densities (6,350 seedlings/ha, 5,608 saplings/ha) were significantly greater than the mean densities of all northern hardwood species combined (3,663 seedlings/ha, 2,187 saplings/ha), with beech, yellow birch, maple, mountain holly, and black cherry accounting for the greatest hardwood regeneration densities. In the northern hardwood cover type, although the mean densities of all hardwood species combined (13,188 seedlings/ha, 2,936 saplings/ha) were significantly greater than red spruce densities (666 seedlings/ha, 1,196 saplings/ha), red spruce accounted for the second-highest sapling density of all species. Much of the hardwood regeneration in this cover type consisted of black cherry seedlings and vegetative sprouts of American beech (Fig. 3, Table 3).

DISCUSSION

In observing transitional ecotones along several transects on elevation gradients at our study area, we found forest overstory composition to be similar to the hardwood spruce transition described by Cogbill and White (1991). Using a linear regression model based on latitude and elevation, Cogbill and White (1991) predicted the spruce hardwood ecotone on Cheat Mountain, WV (region that includes Gaudineer Knob) to occur at 1,259 m elevation, but documented a possible range from 910 to 1,340 m. At our site, the ecotone transitions varied from very sharp to more diffuse. The effect of elevation on cover type position was

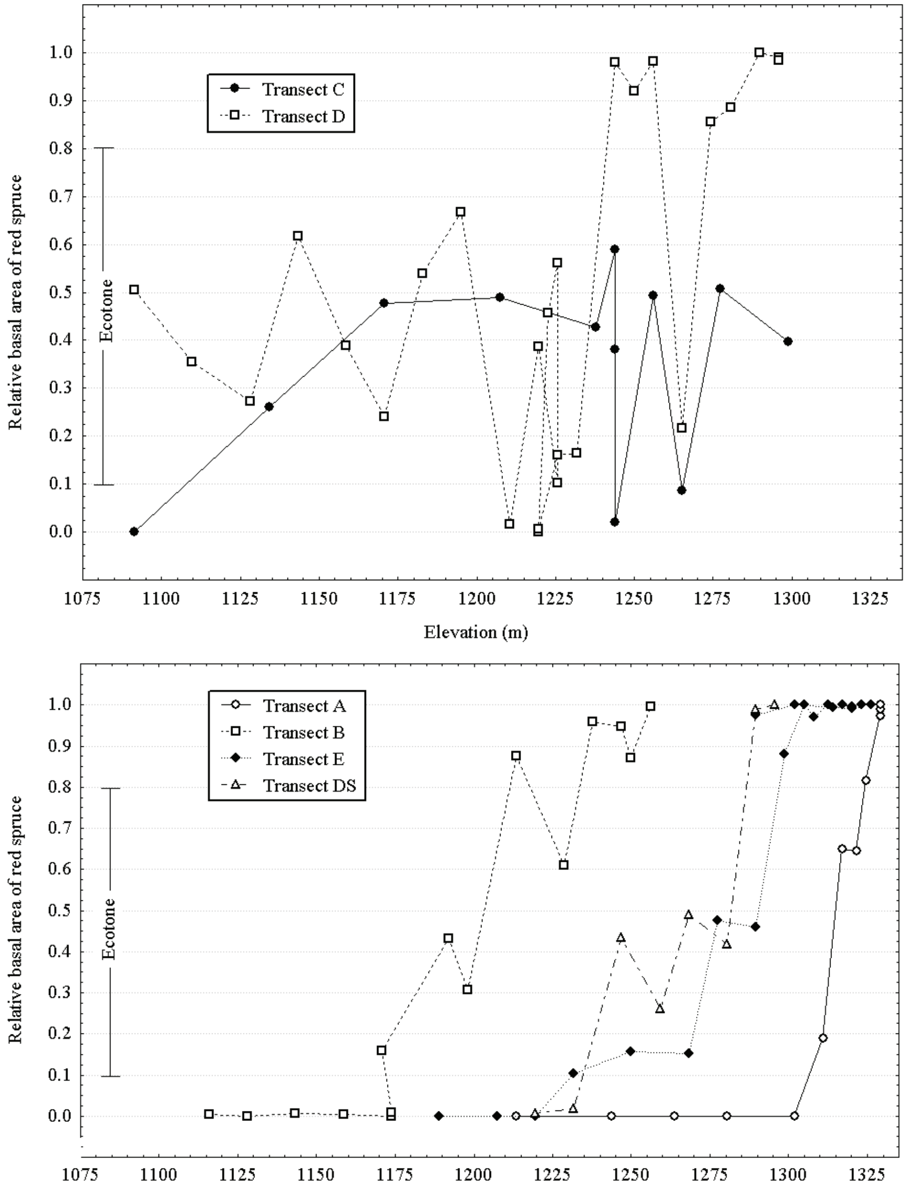

Figure 2.—Relative basal area of red spruce versus elevation for six transects crossing spruce-hardwood ecotones at Gaudineer Knob, WV. A) Transects A, B, E, and DS. B) Transects C and D.

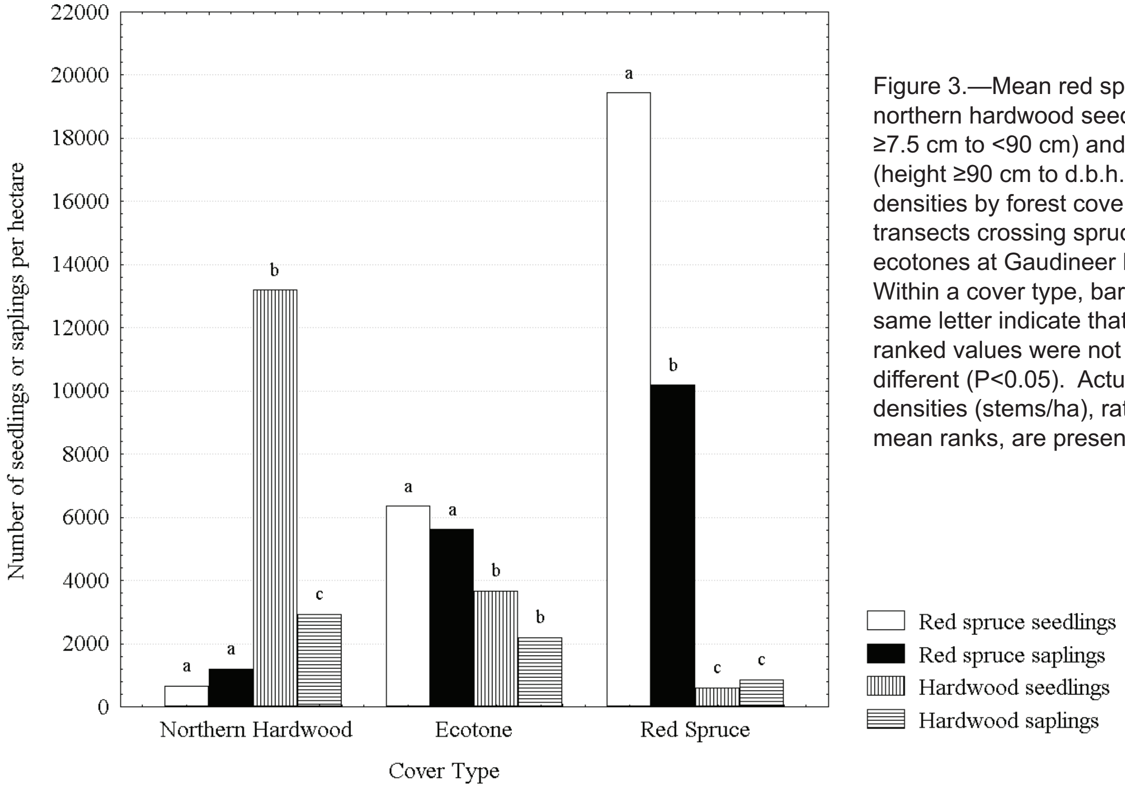

Figure 3.—Mean red spruce and northern hardwood seedling (height ≥7.5 cm to <90 cm) and sapling (height ≥90 cm to d.b.h.<7.5 cm) densities by forest cover type, on transects crossing spruce-hardwood ecotones at Gaudineer Knob, WV. Within a cover type, bars with the same letter indicate that the means of ranked values were not significantly different (P<0.05). Actual mean densities (stems/ha), rather than the mean ranks, are presented.

Table 3.—Mean (SE) seedling and sapling[a] densities of major tree species by forest cover type, on transects crossing spruce-hardwood ecotones at Gaudineer Knob, WV.

	Seedling Density (stems/ha)			Sapling Density (stems/ha)		
Species	Northern hardwood	Ecotone	Red spruce	Northern hardwood	Ecotone	Red spruce
Picea rubens	666 (176)	6,350 (876)	19,433 (2,478)	1,196 (434)	5,608 (677)	10,189 (2,365)
Total N. Hardwoods	13,188 (2,770)	3,663 (593)	601 (140)	2,936 (522)	2,187 (273)	862 (216)
Acer pensylvanicum	1,015 (324)	353 (110)	0 (0)	625 (186)	121 (36)	0 (0)
Acer rubrum	634 (147)	399 (118)	24 (19)	154 (93)	204 (57)	18 (13)
Acer saccharum	181 (73)	0 (0)	0 (0)	299 (201)	19 (11)	0 (0)
Amelanchier arborea	54 (54)	46 (26)	0 (0)	18 (18)	14 (10)	0 (0)
Betula alleghaniensis	372 (139)	664 (199)	184 (58)	172 (78)	362 (54)	256 (72)
Fagus grandifolia	5,212 (1,212)	840 (243)	0 (0)	1,604 (375)	297 (78)	0 (0)
Ilex montana	227 (124)	650 (142)	375 (129)	18 (18)	1,096 (291)	588 (207)
Magnolia acuminata	100 (52)	65 (34)	0 (0)	0 (0)	14 (8)	0 (0)
Prunus serotina	5,384 (2,280)	622 (221)	0 (0)	45 (45)	23 (12)	0 (0)
Other hardwoods[b]	9 (9)	23 (10)	18 (18)	0 (0)	37 (23)	0 (0)

[a] Seedlings were stems ≥7.5 cm tall, but <90 cm tall. Saplings were stems ≥90 cm tall, but <7.5 cm d.b.h.

[b] Other hardwoods were *Acer spicatum, Magnolia fraseri, Ostrya virginiana, Prunus pensylvanica,* and *Sorbus americana.* Species nomenclature follows Gleason and Cronquist (1991).

not consistent, with almost pure stands of red spruce being scattered over a 200 m range. However, the great majority of plots with over 70 percent relative spruce basal area occurred above 1,225 m elevation. Additionally, no consistent association between aspect and relative red spruce basal area was detected on the six transects we examined. Some transects on west facing aspects had a significant red spruce component at elevations as low as or lower than those on north and east aspects. The latter are generally regarded as "cooler" slopes due to the sun angle, so one might expect lower ecotones on these slopes. However, high precipitation and cloud cover at high elevations can depress the contrasts in temperature and insolation often seen at lower elevations due to slope aspect (White and Cogbill 1992). Furthermore, differences in soils and previous disturbance/land-use history can influence vegetative composition across a landscape, and although our methodology did not address these variables, they are possible factors affecting red spruce distribution at the study site.

After segregating our plots into red spruce, northern hardwood and ecotone cover types (based on relative BA of spruce and hardwoods in the overstory), we found that red spruce was successfully regenerating in all three cover types. Under both red spruce and ecotone cover types, red spruce existed at higher average densities than all hardwood species combined and red spruce was the second most-abundant species in the sapling size class in the northern hardwood cover type. The presence and abundance of sapling sized red spruce indicates that it was not merely a rotating seedling crop, but that plants had become well established and were capable of growing into the overstory.

Projecting the possible composition of these stands requires making some assumptions about the disturbances that could occur and applying some knowledge of the silvical characteristics of the various species involved. First, these stands exist in areas of the Monongahela National Forest that are of recreational value and recognized as habitat for threatened and/or endangered species, such as the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus* Shaw) and the Cheat Mountain salamander (*Plethodon nettingi* Green). Therefore, large clearcuts or prescribed fires in these areas are not likely to be recommended. Red spruce is known to undergo "cohort mortality" as whole even age cohorts simultaneously reach senescence, but red spruce is relatively long lived. Such an occurrence is probably centuries away, especially on the Gaudineer peak, where stands appeared to be 80-90 years old, based on our own increment cores and the harvest time frame reported by Molhenbrock (1990). Anthropogenic impacts of air pollution and acidic deposition, if coupled with climate stresses and/or insects and diseases, could hasten the onset of cohort mortality in red spruce. If these types of impacts are not severe, however, the most common disturbances will probably be individual tree fall gaps that produce relatively small openings. Occasional wind, snow, or glaze storms will create larger gaps.

Under pure or nearly pure stands of red spruce at Gaudineer Knob, healthy red spruce seedlings had been recruited in the low light environment of a closed canopy and released to sapling height where partial disturbances created overstory gaps. Mean seedling density (19,432 stems/ha) and sapling density (10,190 stems/ha) values in the red spruce cover type suggested that dominance by *Picea rubens* would continue on these sites in the years to come. Red spruce seedlings are very tolerant of shade (Hart 1959, Blum 1990) and can persist and develop slowly in the understory (Seymour 1992, Fajvan and Seymour 1993). Partial disturbances can establish a cohort of seedlings, creating enough light in the understory to allow increased sapling growth rates and enabling them to eventually reach canopy status (White et al. 1985, Fajvan and Seymour 1993). Even severely suppressed red spruce saplings that are many decades old can be important contributors to future canopy composition because of their ability to respond with increased growth rates upon release and their initial height advantage over other seedlings (Davis 1991).

In the spruce-hardwood ecotone cover type transected by our plots, red spruce dominated the seedling and sapling populations. Mean red spruce regeneration density was more than double the total mean hardwood density in this cover type (Table 3). This regeneration may represent the potential for increasing the overstory abundance of red spruce, and thus the area occupied by spruce-dominated stands on this mountain. Although diameter distributions in the cover type indicated that hardwoods would be a dominant feature of the main canopy in coming years, the shade-tolerant spruce persisting in the understory could eventually become the canopy dominants following natural or intentional creation of gaps in the overstory. Beech bark disease, which results from attack by the scale insect Cryptococcus fagisuga followed by one of two Nectria fungi (Hicks and Mudrick 1994), appeared to be a significant cause of American beech mortality in the Gaudineer area that could positively influence red spruce recruitment to canopy positions.

The ecotone data in this study may be compared with regeneration densities reported by Nicholas et al. (1992) for spruce-fir stands in the Great Smoky Mountains. Our sapling category (height 90 cm to <7.5 cm d.b.h.) is a size class similar to the combination of their large-seedling and understory categories (height 100 cm to <5.0 cm d.b.h.). For this size class, they reported red spruce densities of 627 stems/ha and 1,053 stems/ha in stands with 42 percent and 58 percent red spruce by density in the overstory (>5.0 cm d.b.h.), respectively. In our ecotone plots, which averaged 43 percent red spruce by density in the overstory (stems ≥7.5 cm d.b.h.), we found higher sapling densities (5,608 stems/ha), which represent a larger proportion of the total understory population. The stands studied by Nicholas et al. (1992) differ from ours in that they are 300-500 m higher in elevation, are slightly more dense in the overstory (610-632 stems/ha versus 570 stems/ha in our stands), and contain a substantial proportion of Fraser fir [*Abies fraseri* (Pursh) Poir.], a species our plots lacked completely.

In the northern hardwood cover type at the Gaudineer Knob area, red spruce seedling and sapling occurrence was scattered, and densities of *Picea rubens* were not as high as total hardwood regeneration densities. However, recruitment of red spruce appeared to be favorable where beech was dying, and spruce saplings were more abundant than any other individual hardwood species except American beech. Although red maple and yellow birch will probably continue to be the dominant species in these stands in the near future, the long lived, shade tolerant spruce could persist in the understory and be released to canopy positions over time, producing mixed spruce hardwood stands. It remains to be seen how red spruce will compete with the more-abundant hardwood regeneration in this cover type. There is a significant component of black cherry mixed with American beech, yellow birch, and maples. Cherry is the shortest lived of these species and will most likely create some small canopy gaps over the next 100 or so years as trees mature and die. Because of the fairly small crowns of mature cherry trees, however, these gaps will be relatively small and quickly sealed by expansion of neighboring tree crowns. In the short term, the most likely scenario to cause a major impact in the understory is the infection of many American beech with beech bark disease and the associated canopy gaps that may result.

The observations from this single-year study alone are insufficient to conclude that the geographic range of red spruce in the Gaudineer Knob area is naturally expanding. Detection of true range expansion or reduction would require monitoring changes in forest composition over time, or possibly by applying the advancing-front theory of forest migration presented by Solomon and Leak (1994), which predicts that species range expansion should be represented by a decrease in maximum tree age over distance from an outpost seed source. However, the abundance of red spruce regeneration in the spruce hardwood ecotone and its presence in adjacent hardwood stands may represent an opportunity, through silvicultural manipulation, to increase the relative overstory abundance of red spruce and restore the presence of more spruce-dominated stands in the Gaudineer area.

If restoration management were to be initiated, as suggested by Hornbeck and Kochenderfer (1998) and Rentch et al. (2007), the possibilities are promising for success in the Gaudineer Knob area. Red spruce enhancement through silvicultural treatments could be achieved in hardwood and ecotone stands where red spruce saplings are already established in the understory. Treatments that remove dominant hardwood species in single tree selection cuts or small patch cuts could be applied. Resulting gaps should be large enough to provide light to release understory red spruce saplings (which often have a height advantage over other less shade-tolerant hardwoods), but small enough to prevent fast growing, early-successional species from dominating gap vegetation. Overstory thinning could be coupled with understory application of a hardwood specific herbicide, which would help prevent vigorous stump sprouting of competitive hardwood species. Treatments of this type in areas with adequate red spruce regeneration have been conducted experimentally at other sites (Rentch et al. 2007) and could accelerate red spruce growth rates and result in stands with a well stocked red spruce overstory.

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SPECIES COMPOSITION AND STAND STRUCTURE OF A LARGE RED SPRUCE PLANTING 67 YEARS AFTER ITS ESTABLISHMENT IN WESTERN NORTH CAROLINA

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Abstract.—Red spruce (*Picea rubens* Michx.) is a large and long-lived species that dominated high-elevation forests of the southern Appalachians before most stands were heavily logged in the early 1900s. Restoration of spruce forests by artificial methods has been studied since the 1920s, but little information is available on characteristics of older planted stands. Woody vegetation was inventoried in part of a 50 ha stand of red spruce planted in the Pigeon River watershed of the Pisgah National Forest from 1941 to 1943. The purpose of this study was to determine vegetative composition and structure of the stand, and effects of site variables on growth of red spruce. The spruce component of the stand averaged 1,310 stems ha^{-1} ranging in diameter at breast height from 0.1 cm to 37.5 cm; basal area averaged 29.7 m^2 ha^{-1}. Red spruce basal area was correlated strongly ($r = -0.75$, $p<0.0001$) with an index of site landform and somewhat with aspect ($r = -0.52$, $p<0.01$). This large, even-aged planting of red spruce provides an opportunity for immediate and long-term study of stand dynamics and site relationships associated with restoration of this forest type to a larger part of its former range in the southern Appalachians, as well as investigation of questions related to climate change and growth decline.

INTRODUCTION

Red spruce (*Picea rubens* Sarg.) is a long-lived, shade-tolerant, coniferous tree species that is common in the New England states and Canada; in the southern Appalachian Mountains it occupies an elevation zone between 1,675 m to 1,900 m (Whittaker 1956). Fraser fir (*Abies fraseri* [Pursh] Poir.), a smaller and shorter-lived conifer, is usually associated with red spruce (Korstian 1937) and increases dominance on sites above 1,800 m (Whittaker 1956). Red spruce forests were harvested extensively during the early 1900s and wildfires in logging debris reduced both site quality of the highly organic soils and seed sources for natural regeneration in many areas of the species' former occurrence (Korstian 1937). Forests dominated by red spruce and Fraser fir are estimated to occupy 7,500 ha in the Southern Appalachian Mountains of North Carolina (Dull et al. 1988). Red spruce is a component of high-elevation stands that provide foraging habitat for the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*) (Loeb et al. 2000). Some stands of red spruce show evidence of decline in vigor and increased mortality resulting possibly from changes in air quality and climate (LeBlanc et al. 1992, Busing and Pauley 1994).

Reforestation of cutover and burned high-elevation forests has been investigated since the 1920s (Korstian 1937). Forest managers concluded that artificial means was the most favorable method because of the lack of natural regeneration following burning of heavy logging slash and limited distance of dispersal of spruce and fir seeds (Minckler 1945). Early survival and growth in plantings made for evaluation of non-native species at Mount Mitchell, NC, were studied for 14 years, with the conclusion that the native species of red spruce and Fraser fir were best for reforestation (Minckler 1945). Information is lacking on development of older red spruce stands in the Southern Appalachians.

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One of us (JHH) recently became aware of a stand totaling 50 ha that had been established by planting on a previous spruce site from 1941-1943, in the Pisgah National Forest in western North Carolina (Mead 1942). This planting had been established by the United Daughters of the Confederacy in cooperation with the Pisgah National Forest to memorialize Civil War veterans of North Carolina and is explained more fully elsewhere (Hyatt 2001). Although the planting was mapped by the U.S. Department of Agriculture, Forest Service and records of its establishment had been preserved by one of us (TMO), value of the stand for study of red spruce restoration purposes was realized only recently.

The primary objective of this study was to document the location of the memorial forest and to describe current characteristics of the tree and shrub vegetation. A secondary objective was to investigate environmental factors associated with basal area of the spruce component of the stand. Results reported here are preliminary because only a small part of the stand was sampled.

STUDY AREA

The red spruce stand was established in the Pisgah District of the Pisgah National Forest, (35.30087°N, 82.90408°W) at an elevation of 1,700 m in the Pigeon River watershed of the Balsam Mountains, in Haywood County, NC. Precipitation likely exceeds approximately 150 cm annually and is uniformly distributed. Temperature averages around -2.8 °C in January and 17.2 °C in July. Bedrock formations consist of metamorphosed gneisses and schists derived largely from granites. Soils are in the Wayah clay loam series, which are classed as Inceptisols. Soils are generally shallow, <100 cm deep, and well drained, but moisture availability is likely high during the growing season as a result of frequent precipitation and high organic content. Natural vegetative communities in the high-elevation ecosystems, below the Fraser fir forests, are dominated by red spruce on exposed ridges and slopes, and hardwoods in valleys and protected slopes (Schafale and Weakley 1990). Much of the original red spruce forests in this area was harvested in the early 1900s. Following harvesting, uncontrolled fires in the heavy logging slash resulted in consumption of the highly organic soil, mortality of natural regeneration, and loss of a seed source for regeneration. In July 1922, 4 years after logging and 2 years after burning, a typical upper slope in the Pigeon River watershed "... had grown up to blackberries, fire cherry, and yellow birch" (Fig. 1). Red spruce and Fraser fir forests of the Balsam Mountains account for about 10 percent of the high-elevation type in North Carolina (Dull et al. 1988).

Administrative records indicate that red spruce seeds from the Monongahela National Forest (lot 14 34) were used to produce seedlings at a Forest Service nursery near Parsons, WV. Four-year-old seedlings (grown 2 yrs from seed, then transplanted and grown another 2 yrs) were field planted using a short-handled mattock at a density averaging about

Figure 1.—Four years after cutting an almost pure stand of red spruce for sawtimber and pulpwood, and 2 years following fire in the dense logging slash, a dense cover of blackberry, pin cherry, and yellow birch dominates the area of a former stand of red spruce in the upper portion of the Pigeon River watershed. (July 1922 photo by C. Korstian, USDA Forest Service).

2,470 seedlings ha^{-1}. Field establishment maps indicated the memorial forest consisted of several tracts. About one-third of the total area was planted during the winter of each year, from 1941 to 1943. In December 1954, administrative records show seedling survival averaged 78 percent and height averaged 0.6 m; most red spruce seedlings were overtopped by a dominant canopy of pin cherry (*Prunus pensylvanica* L. f.). The 1954 field notes state: "Blank spots [with no surviving seedlings] seem to be in open spaces. Spruce seems to do better in the shade of birch, blackberries and laurel bushes."

METHODS

The area used for our study was on a west-facing slope extending down from a ridge crest that bordered the Blue Ridge Parkway, at the Mt. Hardy overlook. Shrub and tree vegetation were inventoried on temporary circular sample plots located at approximately 50-m intervals along five randomly oriented transects that generally paralleled the contours. Plot radii ranged from 5 to 20 m depending on uniformity of site topography and density of vegetation; smaller plots were used where shrub vegetation was dense. Live and dead standing stems ≥0.1-cm diameter at breast height (d.b.h.) were recorded by species and 5-cm diameter class (e.g., 0.1-4.9, 5.0-9.9). Total height and d.b.h. were measured on one dominant or co-dominant red spruce on each odd-numbered plot for estimation of stand site index. Those data were supplemented with total height of a healthy red spruce in the intermediate or suppressed crown classes measured on even-numbered plots to develop a regression model predicting height as a function of d.b.h. Site index (total height at 50 years) was estimated using relationships developed from second-growth red spruce stands in New England (Meyer 1929).

Topographic variables measured at each sample plot consisted of aspect (azimuth from north in degrees), gradient (slope steepness at right angles to contours measured in percent), and terrain shape index (t.s.i.), a quantitative expression of meso-scale landform of the site, as delineated by the plot boundary, that generally ranges between -100 percent (highly convex), through 0 (planar), to +100 percent (highly concave). Briefly, t.s.i. represents the average inclination in percent of the sample plot land surface measured from the center to the boundary in eight equally spaced directions (McNab 1989).

Simple relationships between red spruce basal area and topographic variables were determined through correlation analysis. Regression was used to investigate the individual and combined effects of the three topographic variables on basal area of red spruce at each sample plot. All tests of significance were made at the 0.05 level of probability.

RESULTS AND DISCUSSION

Study Area

Twenty-one sample plots, ranging in area from 0.0058 ha to 0.0546 ha, were established in the stand in October 2008, resulting in a total area sampled of 0.197 ha. Aspect of the study area averaged 327° (range 270° to 007°) and slope gradient averaged 29.2 percent (range 16 to 50 percent). The t.s.i. averaged -2.25 (range -19.2 to +7.0), which indicates that landform of the sample plots was generally slightly convex, but ranged from highly convex to slightly concave. Arborescent vegetation was present on all plots; shrubs were absent on one plot. Although the red spruce seedlings had been planted, appearance of the stand did not resemble a typical plantation of uniformly spaced trees, because rows were not discernable.

Species Composition and Structure

Woody vegetation consisted of nine arborescent and three shrub species that averaged 4,785 stems ha^{-1} and 49.7 m^{2} ha^{-1} of basal area (Table 1). Trees made up 41 percent of stem density and 94 percent of the basal area. Red spruce was the dominant tree species, accounting for more than 60 percent of stem density and basal area, followed by yellow birch (*Betula alleghaniensis* Britton), which made up an additional 25 percent of stand density and basal area. Red spruce and yellow birch trees were present on all plots sampled. Except for mountain ash (*Sorbus americana* Marsh.), species of other trees were sparse, particularly eastern hemlock (*Tsuga canadensis* [L.] Carr.), sugar maple (*Acer saccharum* Marsh.), and black cherry (*Prunus serotina* Ehrh.), which were

Table 1.—Density, stocking, and basal area of species present on 21 plots sampled in a stand of red spruce planted in the Pisgah National Forest in 1941-1943.

Species (Scientific name)	Density (S.D.)[a]		Frequency	Basal area (S.D.)[a]	
	N/ha		*N plots*	*m²/ha*	
Red spruce (*Picea rubens* Sarg.)	1,310.0	(754.8)	21	29.7	(15.5)
Yellow birch (*Betula alleghaniensis* Britton)	520.7	(341.5)	21	11.4	(11.0)
Mountain ash (*Sorbus americana* Marsh.)	48.1	(66.2)	6	1.3	(3.4)
Mountain maple (*Acer spicatum* Lam.)	31.7	(81.8)	4	0.1	(0.2)
Pin cherry (*Prunus pensylvanica* L. f.)	13.6	(38.4)	3	0.3	(0.9)
Northern red oak (*Quercus rubra* L.)	9.8	(34.7)	2	3.3	(13.7)
Eastern hemlock (*Tsuga canadensis* [L.] Carr.)	8.2	(37.4)	1	0.1	(1.0)
Sugar maple (*Acer saccharum* Marsh.)	7.2	(33.2)	1	0.2	(0.8)
Black cherry (*Prunus serotina* Ehrh.)	7.2	(33.2)	1	0.4	(2.0)
All trees	1,954.9	(900.8)	21	46.8	(16.7)
Catawba rhododendron (*R. catawbiense* Michx.)	2,672.4	(3,341.0)	19	2.5	(2.3)
Mountain holly (*Ilex montana* Torr. & Gray)	150.8	(425.0)	4	0.3	(1.1)
Viburnum (*Viburnum lantanoides* Michx.)	6.7	(21.7)	2	0.1	(1.1)
All shrubs	2,829.9	(3,315.0)	20	2.9	(2.4)
All live trees and shrubs	4,784.6	(5,615.4)	21	49.7	(16.9)
All dead standing trees	441.7	(303.8)	20	5.2	(4.0)

[a]Calculated with zero for sample plots where the subject species was absent.

represented by single stems. The shrub layer of most plots was dominated by catawba rhododendron (*Rhododendron catawbiense* Michx.), which accounted for 94 percent of stem density and 86 percent of the shrub basal area. Composition of the major species of this planted stand was similar to that recorded on areas in the same watershed following harvest (Korstian 1937).

Red spruce and yellow birch trees were mostly present in diameter size classes up to 39 cm (Table 2). The largest tree present on the sample plots was a northern red oak (*Quercus rubra* L.) measuring 72 cm d.b.h. Almost all shrubs were less than 9 cm d.b.h. Pooling of both trees and shrubs produces a diameter distribution that resembles the reverse J-curve characteristic of uneven-aged, natural stands of mixed species.

The size class distribution of red spruce alone suggests an almost normal distribution of diameters with a modal class of 12.5 cm d.b.h. (Fig. 2). Diameter distributions are available for comparison with natural stands of mixed red spruce and Fraser fir (Korstian 1937, Oosting and Billings 1951), but data are lacking for pure stands of red spruce, a species composition that is somewhat unusual for high-elevation forests (Korstian 1937). Fraser fir trees are present in the vicinity of the memorial forest, but did not occur in the area sampled.

The diameter distribution of standing dead trees differed from that of the live trees, with the modal size occurring in the 0 to 9 cm d.b.h. class, followed closely by the 10 to 19 cm class (Table 2). Basal area of the standing dead trees averaged 5.2 m^2 ha^{-1}. The 442 dead trees/ha consisted primarily of yellow birch (44 percent) and red spruce (25 percent). The ratio of dead trees to live trees ranged from 1:2.9 for the smallest d.b.h. class to 1:16.5 for the largest class. Only one tree was windthrown – a red spruce measuring 28 cm d.b.h., which had grown in a layer of organic matter 30 cm thick that had accumulated on solid rock. Past stand dominance by pin cherry was indicated on the forest floor by abundant remnants of stem bark, which was characterized by large, prominent horizontal lenticels. McGill and others (2003) reported that pin cherry can

Table 2.—Diameter distribution for a stand of planted red spruce and mixed tree and shrub species on the Pisgah National Forest at 67 years of age.[a]

		Diameter class (cm)					
Species	Basal area	0-9	10-19	20-29	30-39	40-49	50+
	m^2/ha	*Number of stems/ha*					
Red spruce	29.7	370.5	585.8	300.4	53.7	-	-
Yellow birch	11.4	195.7	180.9	122.9	18.6	2.6	-
Northern red oak	3.3	-	-	-	2.6	-	7.2[b]
Mountain ash	1.3	7.2	16.3	22.6	-	-	-
Black cherry	0.4	-	-	7.2	-	-	-
Pin cherry	0.3	-	9.5	4.1	-	-	-
Sugar maple	0.2	-	7.2	-	-	-	-
Mountain maple	0.1	31.7	-	-	-	-	-
Eastern hemlock	0.1	8.2	-	-	-	-	-
Total trees	46.8	613.3	799.7	457.2	74.9	2.6	7.2
Catawba rhododendron	2.5	2,662.5	9.9	-	-	-	-
Mountain holly	0.3	142.6	8.2	-	-	-	-
Viburnum	0.1	6.7	-	-	-	-	-
Total shrubs	2.9	2,811.8	18.1	-	-	-	-
Total live	49.7	3,425.1	817.8	457.2	74.9	2.6	7.2
Dead standing	5.2	209.0	205.1	27.6	-	-	-

[a] Mean site index for red spruce at 50 years = 11.3 m.

[b] d.b.h. = 72.5 cm.

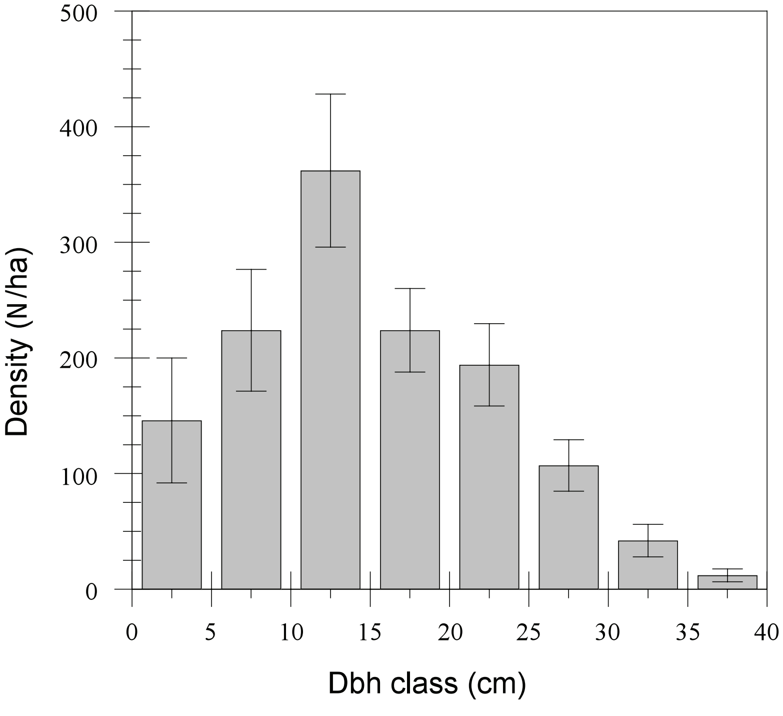

Figure 2.—Density (± SE mean) of the red spruce component of a stand established by planting in the Pisgah National Forest from 1941-1943.

quickly dominate sites severely disturbed by timber harvest or fire, resulting in seedling densities that can exceed 40,000 ha^{-1}. Evidence of fire was not observed in the area sampled.

Although data were not adequate for analysis, observations suggest the presence of two vegetation associations: 1) a dense red spruce overstory with sparse shrub understory; and 2) sparse red spruce overstory with increased yellow birch and other tree species and a dense shrub understory. The former association tended to occur on convex landforms; the latter on planar and concave landforms.

The largest trees observed in the area studied (outside of the sample plots) were two red spruces in a somewhat inaccessible location: between two shallow drains in a dense patch of catawba rhododendron. Both trees exceeded 75 cm d.b.h. and are believed to be remnants of the original stand. The presence of these trees suggests the possibility for restoration of desirable stand characteristics through management activities, such as thinning (Rentch et al. 2007).

Spruce Component of the Stand

Total height of the dominant and co-dominant red spruce component of the stand averaged 14.6 m and ranged from 11.5 to 17.7 m (Table 3). Site index of the 67-year-old red spruce stand averaged 11.3 m, and ranged from 9.1 to 13.7 m. A regression model was developed for estimation of total height from d.b.h. based on 21 sample trees, one from each plot, which included all crown classes:

$$t.h._{m} = -4.94 + 5.99 * \log (d.b.h.) \qquad (1)$$

where $t.h._{m}$ is total height (m) of red spruce and log (d.b.h.) is the natural logarithm of tree d.b.h. (cm). Equation (1) has a standard error of 1.9 m and explains 66 percent of the variation of total height (Fig. 3).

Basal area of the red spruce component on each of the 21 sample plots ranged from 4.2 m^2 ha^{-1} to 58.0 m^2 ha^{-1} (Table 3). Scatter plotting suggested a strong negative correlation between basal area of the red spruce stand component and land surface shape quantified by t.s.i. ($r = -0.75$, $p<0.0001$) and a weaker negative relationship of basal area with aspect ($r = -0.52$, $p = 0.01$). Regression analysis indicated that variation in red spruce basal area was significantly associated with only one of the topographic site variables:

$$b.a._{rs} = 25.901 - 1.692 * (t.s.i.) \qquad (2)$$

where $b.a._{rs}$ is basal area (m^2 ha^{-1}) of red spruce and t.s.i. is the terrain shape index. Equation (2) has a standard error of estimate of 10.4 m^2 ha^{-1} and r^2 of 0.56. The coefficient of the independent variable in equation (2) indicates that red spruce basal area on a planar site in the stand (i.e., t.s.i. = 0)

Table 3.—Range in size of 11 dominant and co-dominant red spruce trees measured for site index and stand characteristics on 21 sample plots in a 67-year-old planting in the Pisgah National Forest.

Stand characteristic	N	Mean	Range
Total height (m) [a]	11	14.6	11.5-17.7
d.b.h. (cm) [a]	11	26.8	22-38
Site index (m) [a]	11	11.3	9.1-13.7
Density (N/ha) [b]	21	1,310.0	304-2,740
Basal area (m^2/ha) [b]	21	29.7	4.2-58.0

[a] One dominant or co-dominant tree on 11 plots.

[b] All trees on each of 21 sample plots.

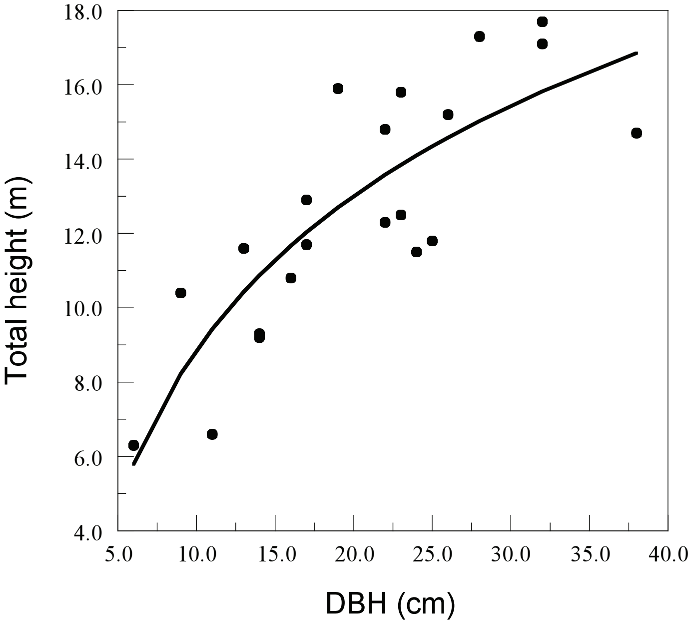

Figure 3.—Relationship of total height to d.b.h. for red spruce ranging in crown class from suppressed to dominant for 21 trees planted in the Pisgah National Forest from 1941-1943.

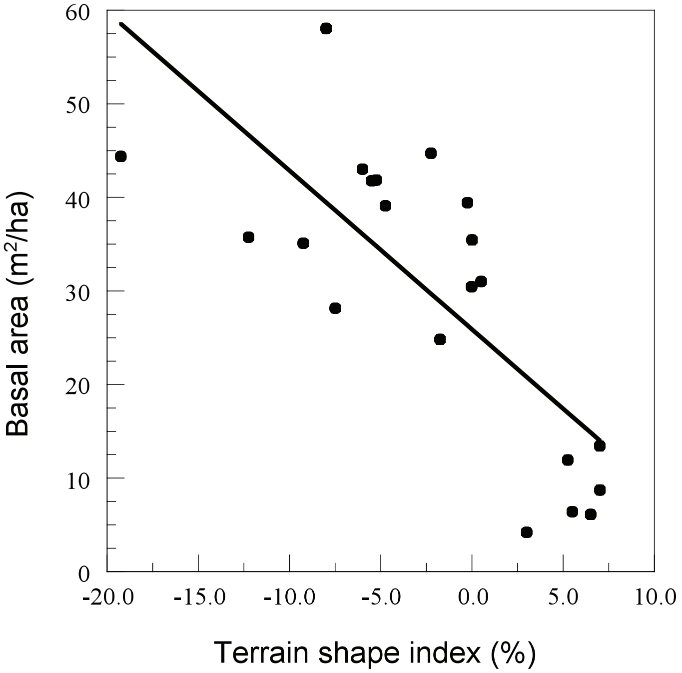

Figure 4.—Relationship of basal area of red spruce to terrain shape index for a planting established in the Pisgah National Forest from 1941-1943.

is estimated as 25.9 m^2 ha^{-1}. Basal area of the red spruce component of sample plots decreased on concave sites and increased on convex sites, as shown in Figure 4. Equation 2 is presented only to suggest a possible relationship of basal area with an environmental variable; the prediction equation should not be used for management decisions until the relationship has been tested elsewhere. Although red spruce basal area was significantly correlated with aspect, that predictor variable was also strongly correlated with terrain shape index ($r = 0.67$, $p = 0.0008$). Multicollinearity between the two predictor variables was likely an artifact of the data set that was collected in a small part of the stand.

Site quality relationships of red spruce have not been reported elsewhere in the Southern Appalachian Mountains, although results from one study suggested that aspect might be important (Minckler 1940). He found that survival of red spruce was slightly higher on south compared to north slopes in test plantings on Mt. Mitchell after 14 years. The effect of aspect on stand basal area of red spruce could not be properly evaluated in this study because data were limited to a single quadrant: northwest. Landform of the sample plot, quantified by t.s.i., had a significant effect on basal area of red spruce, but additional study is needed to confirm that relationship.

In summary, this easily accessible, 50-ha planted stand of red spruce, established from 1941 to 1943, provides a good opportunity for additional study of stand dynamics, particularly for questions associated with restoration of the species on suitable sites in the Southern Appalachian Mountains. The influence of environmental variables on one measure of spruce response to site quality (i.e., stand basal area), should be more fully studied over a broader area of the stand. A series of standard permanent plots, such as those established elsewhere in natural stands (Busing 2004), is recommended for long-term ecological study of the composition, structure, and growth of an uncommon forest type that could be affected by a changing climate.

ACKNOWLEDGMENTS

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A COMPARISON OF THE STATUS OF SPRUCE IN HIGH-ELEVATION FORESTS ON PUBLIC AND PRIVATE LAND IN THE SOUTHERN AND CENTRAL APPALACHIAN MOUNTAINS

Randall S. Morin and Richard H. Widmann[1]

Abstract.—Red spruce (*Picea rubens* Sarg.) is the most important component of the high-elevation forest ecosystems of the southern and central Appalachian Mountains. These communities are characterized by mixed hardwood/coniferous forests often with overstory dominance by red spruce. Due to their restricted geographic and elevation ranges, all community types in this ecological group are rare. Red spruce forests provide the only viable habitats for the northern flying squirrel (*Glaucomys sabrinus fuscus*), a federally and state-listed endangered species, as well as for other animals of global and regional significance. Due to a variety of stressors, including exotic pests and pathogens, airborne pollution, wind shear, and climate change, these high-elevation spruce forests face an uncertain future. We use U. S. Department of Agriculture, Forest Service, Forest Inventory and Analysis (FIA) plot data from Tennessee, North Carolina, Virginia, West Virginia, and Pennsylvania to analyze the distribution of the red spruce trees, saplings, and seedlings across forest types, elevation classes, and ownerships. Most of the area classified as the red spruce forest type is public land (~90 percent), but only 72 percent of red spruce trees are on public land so there are significant numbers of red spruce trees in other forest types as well. Spruce regeneration is abundant relative to other species within the spruce/fir forest-type group, indicating that spruce is likely to maintain its dominance in those stands, but spruce regeneration is also an important component of seedling and saplings species composition in the maple/beech/birch forest-type group. One-third of stands in the maple/beech/birch forest-type group have a large red spruce component present as regeneration, indicating the potential for red spruce to increase its importance in future forests.

INTRODUCTION

Red spruce (*Picea rubens* Sarg.) is the most important component of the high-elevation forest ecosystems of the southern and central Appalachian Mountains. These communities are characterized by mixed deciduous/coniferous forests, often with overstory dominance by red spruce. All community types in this ecological group are rare because of their restricted geographic and elevation ranges. Most of these relict forest communities suffered severe compositional and structural degradation during the late 19th and early 20th centuries from heavy logging and burning and have never returned to previous conditions (Stephenson and Clovis 1983, Schuler et al. 2002). The geographic extent of red spruce communities has also been greatly reduced.

Restoration of red spruce-dominated forests has been explored in several studies (Schuler et al. 2002, Rentch et al. 2007), but a variety of biotic and abiotic stressors, including exotic pests and pathogens, airborne pollution, wind shear, land-use change, and climate change, currently threaten the health and sustainability of high-elevation spruce forests and potential restoration sites. Restoration of red spruce communities could increase the extent of this rare forest type and the amount of available habitat for characteristic species such as the endangered northern flying squirrel (*Glaucomys sabrinus fuscus*). Forests with a large red spruce component provide some of the best habitat for the northern flying squirrel (Odom et al. 2001, Ford et al. 2004) and other animals of global and regional significance.

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We use Forest Inventory and Analysis (FIA) plot data from Tennessee, North Carolina, Virginia, West Virginia, and Pennsylvania to analyze the distribution of red spruce trees, saplings, and seedlings across forest types, elevation classes, and ownerships. Some stands currently classified as another forest type but with a red spruce component in the overstory and/or understory, could convert to the red spruce type either through succession or silvicultural intervention.

The goal of this study is to summarize the distribution of red spruce on public and private lands in the central and southern Appalachian Mountains. Specific objectives are: 1) differentiating the distribution of red spruce forest-type from the distribution of red spruce trees; and 2) quantifying the proportion of red spruce trees, saplings, and seedlings in different forest-type groups to use as an indicator of future forest composition.

METHODS

The FIA program of the U.S. Department of Agriculture, Forest Service, the only congressionally mandated national inventory of U.S. forests, conducts a three-phase inventory of the forest attributes of the country (Bechtold and Patterson 2005). The FIA sampling design is based on a tessellation of the United States into hexagons of approximately 6,000 acres, with at least one permanent plot established in each hexagon. In Phase 1, the population of interest is stratified and plots are assigned to strata to increase the precision of estimates. The intent of Phase 1 is to classify the land into various remote-sensing classes for the purpose of developing meaningful strata. A stratum is a group of plots that have the same or similar remote-sensing classifications. Stratification is a statistical technique used by FIA to aggregate Phase 2 ground samples into groups to reduce variance when stratified estimation methods are used (Bechtold and Patterson 2005). In Phase 2, site attributes, such as forest type and stand size, and tree attributes, such as species and diameter, are measured for forested plots established in each hexagon. Phase 2 plots consist of four 24-foot fixed-radius subplots on which standing trees greater than 5 inches diameter at breast height (d.b.h.) are inventoried, and four 6.8-foot fixed-radius microplots on which saplings 1 inch to 4.9 inches d.b.h. and seedlings greater than 1 foot tall are inventoried.

In this study we utilized plot data from Tennessee, North Carolina, Virginia, West Virginia, and Pennsylvania. Plots were included in the analysis if at least one red spruce tree or seedling was sampled. Inventory data from 2002-2006 were used, and 86 inventory plots were included in the analysis. Annual net growth and mortality estimates, based on two sequential measurements, were computed using only plots from West Virginia. Annual net growth is computed as annual gross growth minus annual mortality (Bechtold and Patterson 2005). The FIA MapMaker 3.0 program was utilized to generate area, number of trees, volume, basal area, growth, and mortality estimates (Miles 2009). In the FIA forest-typing system, forest types are nested within forest-type groups. For example, the red spruce forest type (50 percent or more of the stocking in red spruce) is in the spruce/fir forest-type group. This terminology is used throughout the body of this paper. The proportion of the total number of red spruce trees, saplings, and seedlings on each FIA plot was computed from the raw FIA data to ascertain the importance of red spruce in the species composition of different tree size classes.

RESULTS

Distribution of the Red Spruce Forest Type

The majority of the area classified by FIA as the red spruce forest-type is in stands more than 60 years old (78 percent). Concentration in this age class resulted from widespread harvesting and burning of red spruce-dominated forests prior to the 1940s followed by decades of virtually no harvesting of red spruce (Steer 1948).

Nearly all of the 90,000 acres of the red spruce forest type is on public land (~90 percent). The majority of this land is administered by the Forest Service (35,000 acres), but the National Park Service (13,000 acres) and the states (26,000 acres) are major owners as well. Virginia and Pennsylvania have the largest amount of state-owned red spruce forest with 6,000 and 14,000 acres, respectively. Nearly 50 percent of the area of red spruce forest type is located in West Virginia; almost all is growing on federal land administered by the Forest Service.

About half of the red spruce forest-type acreage is classified by FIA as reserved status. This classification means the forest land is withdrawn by law, prohibiting management for wood products. Most of the reserved land is wilderness areas in the Monongahela National Forest in West Virginia and the Great Smokey Mountains in Tennessee. By contrast, the majority of nonreserved land is under private and state ownership in North Carolina, Pennsylvania, and Virginia.

It is well documented that red spruce grows at high elevations in the southern Appalachians (Burns and Honkala 1999a). FIA estimates that 83 percent (75,000 acres) of red spruce forest type occurs at elevations greater than 3,000 feet, but small areas are found at less than 3,000 feet in Virginia (1,500 acres) and Pennsylvania (14,000 acres).

Distribution, Growth, and Mortality of Red Spruce Trees

Although 90 percent of the area of the red spruce type is located on public ownerships, there are significant numbers of red spruce trees on privately owned land in other forest types; only 72 percent of red spruce trees are on public land. In fact, 52 percent of the red spruce volume (44 percent of red spruce basal area) is in the maple/beech/birch forest-type group. Only 34 percent of the red spruce volume (32 percent of red spruce basal area) is in the spruce/fir forest-type group.

Based on percentage of total live volume, the most important species growing with red spruce at elevations above 4,000 feet are yellow birch (*Betula alleghaniensis* Britton), 9 percent; sweet birch (*B. lenta* L.), 8 percent; American beech (*Fagus grandifolia* Ehrh.), 5 percent; northern red oak (*Quercus rubra* L.), 13 percent; red maple (*Acer rubrum* L.), 11 percent; black cherry (*Prunus serotina* Ehrh.), 5 percent; and eastern hemlock (*Tsuga canadensis* [L.] Carr.), 7 percent. The birches, particularly yellow birch, are the most common associates with red spruce above 5,000 feet in elevation. Annual growth estimates from West Virginia show that red spruce is growing faster than American beech and yellow birch (Fig. 1). Similarly, estimates from West Virginia show that red spruce has a lower annual mortality rate than American beech and yellow birch (Fig. 2).

Distribution of Red Spruce Trees, Saplings, and Seedlings

The proportion of the total number of red spruce trees, saplings, and seedlings on each FIA plot was computed and each mean is presented by FIA forest-type group (Fig. 3). The spruce/fir forest-type group has the highest proportion of red spruce trees, saplings, and seedlings, but the maple/beech/birch forest-type group has a surprisingly large component of red spruce saplings and seedlings. Although only 11 percent of trees tallied in the maple/beech/birch forest-type group are red spruce, 32 percent of tallied saplings and seedlings are red spruce. By contrast, red spruce is a much smaller component of stands in the oak/hickory forest-type group. One-third of stands in the maple/beech/birch forest-type group have a large red spruce component present as regeneration (greater than 40 percent of seedlings and saplings in red spruce). A more detailed look at the maple/beech/birch forest-type group reveals that red spruce regeneration is a larger component of the seedling and sapling tallies on federal land than on private land (Fig. 4).

DISCUSSION

Red spruce is the most important component of the high-elevation forests of the southern and central Appalachian Mountains and previously dominated forests over hundreds of thousands of acres. It currently makes up a large enough component of the species composition to qualify as the red spruce forest type on only approximately 90,000 acres. The majority of those forests (90 percent) are on public land, are mature (78 percent are in stands more than 60 years old), and at high elevation (83 percent at greater than 3,000 feet). Red spruce is also a significant component in other forest-type groups, particularly in the maple/beech/birch forest-type group, where approximately 52 percent of the red spruce trees are growing.

Concerns about the decline of red spruce were raised in the 1980s because of observed higher mortality rates, foliage loss, and a decrease in growth rates (Johnson 1983, McLaughlin et al. 1987). Potential causes of this decline include climatic change, insect pests, pathogens and diseases, stand dynamics, and atmospheric deposition. In contrast to studies reporting declining red spruce growth, current estimates from West

Virginia FIA data indicate that red spruce is growing faster and dying at a slower rate than its major competitors. Both sweet and yellow birch are susceptible to disease and decay at an early age (Burns and Honkala 1990b) and sweet birch is a short-lived species (Hicks, Jr. 1998). In addition, exotic pest activity has been linked to growth loss and mortality of two other species associated with red spruce in the central and southern Appalachian Mountains: American beech and eastern hemlock (Houston 1994, McClure et al. 2001, Morin et al. 2005).

Although crushing by hardwood litter is generally expected to cause seedling mortality in red spruce (Burns and Honkala 1990a), summaries by forest-type group indicate that 32 percent of the saplings and seedlings tallied in the

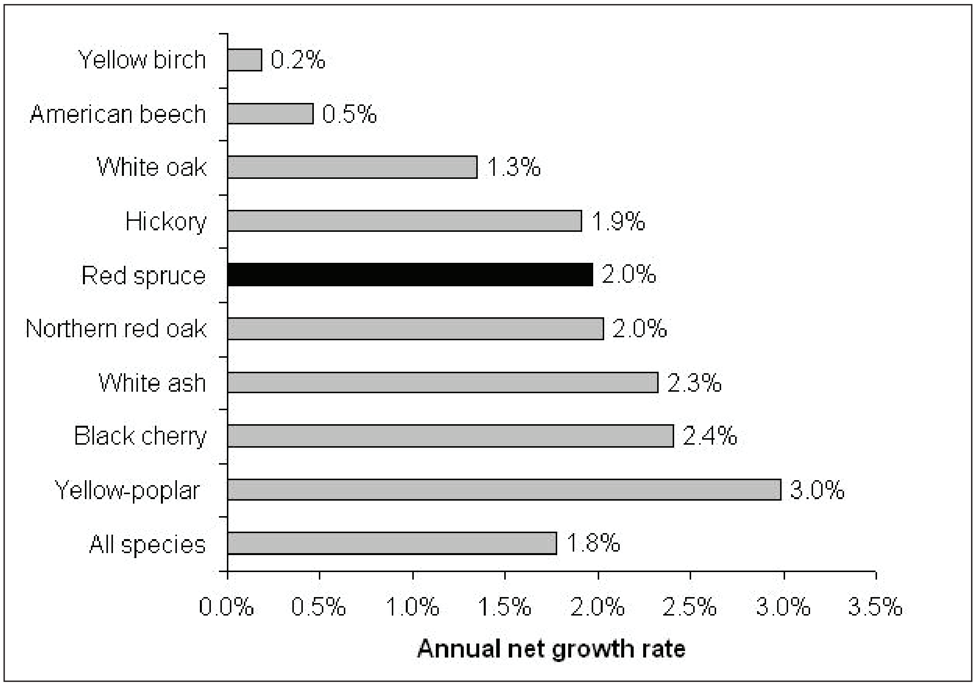

Figure 1.—Annual net growth rate of live volume for selected species on forest land, West Virginia, 2006.

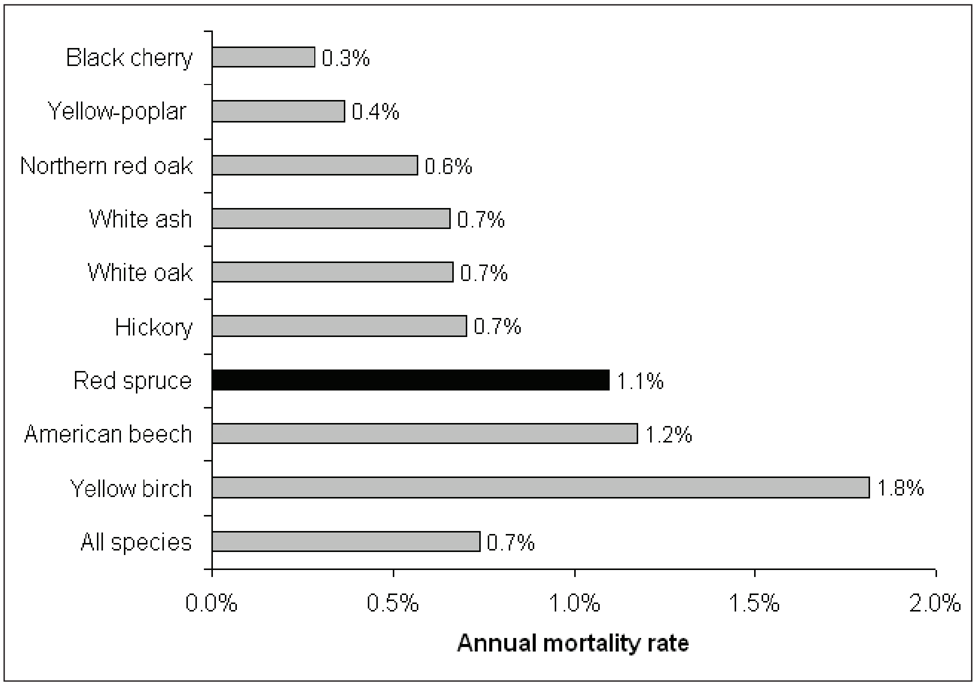

Figure 2.—Annual net mortality rate of live volume for selected species on forest land, West Virginia, 2006.

maple/beech/birch forest-type group were red spruce. In addition, one-third of stands in the maple/beech/birch forest-type group have a large red spruce component present as regeneration (greater than 40 percent of seedlings and saplings in red spruce). A more detailed look at the maple/beech/birch forest-type group reveals that red spruce regeneration is a larger component of the seedling and sapling tallies on federal land than on private land. Therefore, much of the restoration opportunity for red spruce occurs on federal lands where management options might be limited due to regulations.

Two factors indicate that red spruce may increase its distribution in the southern and central Appalachian Mountains in the coming years: the reproductive success of red spruce and the net growth and mortality estimates of red spruce and associated species. This is especially the case in the maple/beech/birch forest-type group, where the trend in levels of red spruce regeneration points toward the natural succession of more red spruce in future forests. Succession potentially could be accelerated through the use of silvicultural treatments, such as the release of understory spruce through the removal of overstory hardwoods (Rentch et al. 2007), but

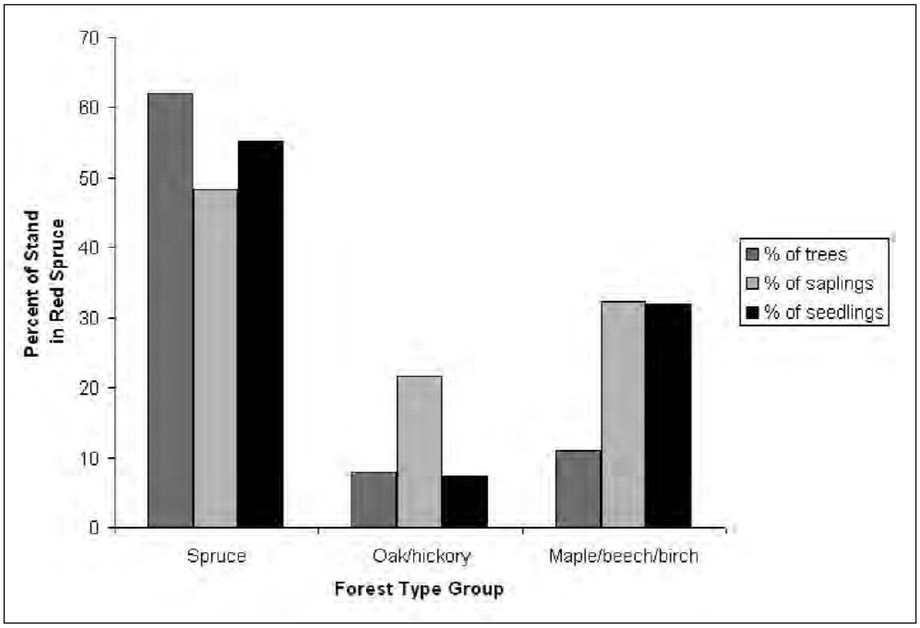

Figure 3.—Percent of tallied trees, saplings, and seedlings in red spruce by forest-type group, North Carolina, Pennsylvania, Tennessee, Virginia, West Virginia, 2006.

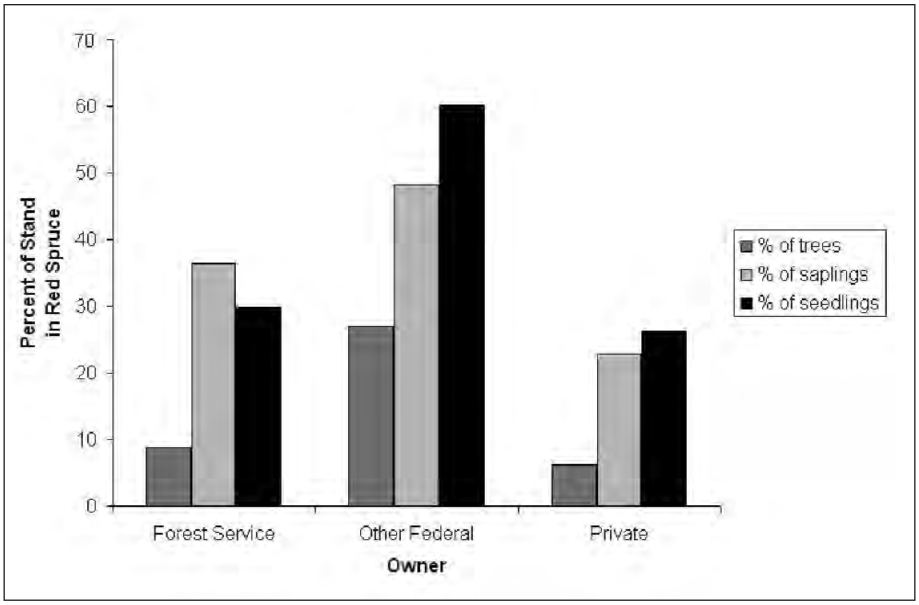

Figure 4.—Percent of tallied trees, saplings, and seedlings in red spruce in the maple/beech/birch forest-type group, North Carolina, Pennsylvania, Tennessee, Virginia, West Virginia, 2006.

management activities may be limited on much of the area where restoration might be appropriate.

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THE CURRENT STATUS OF RED SPRUCE IN THE EASTERN UNITED STATES: DISTRIBUTION, POPULATION TRENDS, AND ENVIRONMENTAL DRIVERS

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Abstract.—Red spruce (*Picea rubens* Sarg.) was affected by an array of direct (logging, fire, and grazing) and indirect human activities (acid deposition) over the past centuries. To adequately assess past impacts on red spruce, thus helping frame its restoration potential, requires a clear understanding of its current status. To achieve this, Forest and Inventory Analysis data from the U.S. Department of Agriculture, Forest Service, were analyzed from 2,458 plots having one or more red spruce trees (≥5 in. diameter at breast height). Red spruce was widespread across the Northeast, associating with many tree species. Southward, along the Appalachian Chain, red spruce became increasingly restricted to high elevations and had fewer associates. Red spruce stands in the Southern Appalachians were distinctly different from those in other regions, having higher red spruce density, basal area, and overall importance. No problems were detected with red spruce regeneration and recruitment under the current climate. In fact, populations were actually increasing in most cases, possibly reflecting natural recovery of red spruce after major contraction during the severe cutting and fire disturbances of the late 1800s and early 1900s. To help guide restoration efforts, temperature was found to be a useful predictor of red spruce in the Northeast, whereas elevation and snowfall were strong predictors in the Southern Appalachians. Future climate change might curtail the positive trends currently expressed by red spruce.

INTRODUCTION

Red spruce (*Picea rubens* Sarg.) is a cool temperate, shade-tolerant conifer of eastern North America. Although it is symbolically linked to the Southern Appalachians of Tennessee and North Carolina, the bulk of its distribution is actually in New England and southeastern Canada (Blum 1990). Red spruce is associated with a variety of tree species, including eastern hemlock *(Tsuga canadensis* [L.] Carr.), balsam fir (*Abies balsamea* [L.] Mill.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton). Fraser fir (*Abies fraseri* [Pursh] Poir.) is an oft-cited companion in the southern mountains.

The red spruce resource has been severely impacted by European settlers in accordance with the existing technology at the time of settlement. Low-elevation stands of coastal New England were first to be cut. Timbering proceeded slowly, however, as logging and milling technologies were rudimentary and timber demands were relatively low. European settlers' westward expansion in the mid-1700s was accompanied by widespread logging, which effectively bisected red spruce's distribution as people pushed across the colonies of New York and Pennsylvania. The remaining virgin red spruce stands, concentrated in remote, topographically inaccessible areas to the south (West Virginia, eastern Tennessee, and western North Carolina) and north (New England and Canada), were largely avoided until the coming of technologies for the railroad to transport the raw material and products and the steam-engine to power log skidders and saw mills. As such, it was not until the late 1800s that the red spruce resource begun to be cut in earnest (Clarkson 1964, Siccama et al. 1982, White and Cogbill 1992, Lewis 1998).

The appearance of modern technologies coupled with the existence of vast red spruce resources unleashed an unprecedented level of logging and environmental

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destruction along the Appalachian Chain (Brooks 1911, Korstian 1937, Clarkson 1964, Lewis 1998). Large-scale, clearcut logging was deemed necessary to recoup the huge initial investments in land purchase, railroad infrastructure, and highly mechanized logging equipment used in these remote and rugged parts (Hopkins 1899, Pyle and Schafale 1988, Lewis 1998). Wildfires often followed the axe, fueled by copious amounts of dead and down slash dried from exposure and ignited primarily through human activity. Multiple fires were particularly devastating to red spruce (Korstian 1937) because it is a non-sprouting species. These wildfires greatly reduced or eliminated red spruce on many landscapes, consuming its fire-susceptible seedlings, saplings, and remaining seed trees while rendering site conditions inadequate for regeneration (Brooks 1911, Korstian 1937, Minckler 1945, Allard and Leonard 1952, Pyle and Schafale 1988). Under these circumstances, hardwoods benefited vastly at red spruce's expense. This scenario is consistent with the near-universal reduction of conifers in other temperate forests caused by European disturbance, including the loss of hemlock and eastern white pine (*Pinus strobus* L.) in conifer-northern hardwoods (Elliott 1953; Kilburn 1960a; McIntosh 1972; Whitney 1987, 1990; Cole et al. 1998; Leahy and Pregitzer 2003; Schulte et al. 2007) and the loss of pine in former pine-oak systems (Kilburn 1960b, Nowacki and Abrams 1992, Abrams and Ruffner 1995, Cunningham 2007).

Following red spruce's widespread decline during the early 20th century, this recovering resource now faces new difficulties stemming from atmospheric pollutants, acid deposition and related calcium deficiency, ozone, and climate change (Siccama et al. 1982, McLaughlin et al. 1987, Johnson et al. 1988, Shortle and Smith 1988, Adams and Stephenson 1989, Iverson et al. 2008). However, controversy abounds regarding the extent of red spruce decline and its possible causes (Reams et al. 1994, Hornbeck and Kochenderfer 1998). To fully understand the magnitude of human impacts on this species and opportunities for future restoration, an assessment of its current status is needed. In this light, this paper strives to:

1. Depict current red spruce distribution and stand characteristics
2. Document regional differences among red spruce stands
3. Determine how red spruce is faring based on regeneration and population dynamics
4. Decipher the primary environmental drivers of red spruce occurrence

METHODS

Base data were derived from the U.S. Forest Service's Forest Inventory and Analysis (FIA) survey. FIA is a coarse-scale survey used to monitor the forest resources of the United States. Tree data are collected using a uniform method from a network of randomly distributed plots across the nation, averaging one plot per 6,000 acres (Bechtold and Patterson 2005). Only the most recent survey results from 2002-2006 were included to ensure focus on the current red spruce resource. A total of 2,460 plots having at least 1 red spruce tree (≥5 in. diameter breast height [d.b.h.]) were identified across the eastern United States. Two plots outside of red spruce's natural range in Ohio were excluded, leaving 2,458 plots for data analysis. Data were provided for three size classes representing trees (≥5 in. d.b.h.), saplings (≥1 in. to <5 in. d.b.h.), and seedlings (≥1 ft tall to <1 in. d.b.h.). Tree importance values by species were calculated for every plot using the following formula:

Importance Value = (relative density + relative basal area)/2

Plots were classified as to general forest type to evaluate whether red spruce grows primarily in conifer-dominated, mixed, or broadleaf-dominated forests. Plots were classified as conifer forests if total conifer importance was >75 percent. Plots were classified as mixed forests if conifers (or broadleaf trees) had a total importance ≥25 percent to ≤75 percent. Plots were classified as broadleaf forests if total broadleaf importance was >75 percent.

We used diameter, height, and regeneration data provided by FIA to examine the performance and population dynamics of red spruce relative to other species. Plot data were divided by region and six common associates selected for evaluation: red spruce, balsam fir, eastern hemlock, American beech, red maple, and sugar maple. These species were chosen because of their overall abundance and similar life-history strategies (e.g., shade tolerance, slow growth rates). Because of their conservative life histories (Loehle 1988), mortality rates were assumed to be equivalent among these species for analytical interpretation. Tree data for each plot were parsed into 5 non-overlapping diameter classes (seedlings, saplings, 5-9.9 in., 10-14.9 in., ≥15 in.) and height classes (≤29 ft, 30-39 ft, 40-49 ft, 50-59 ft, ≥60 ft), and relative densities calculated. Diameter and height class analyses were conducted separately. Only mature stands (plots with trees ≥15 in. in diameter; plots with trees ≥60 ft in height) were included as integrating young stands of small, short trees in this analysis would have obscured the determination of successional tendencies and population trends. Population pyramids, a simple and effective method to portray and evaluate human population trends (Ricklefs 1979), were constructed based on diameter- and height-class data. These forest profiles were, in turn, visually inspected to determine the population dynamics of the selected tree species. Forest profile shapes were used to categorize species as having increasing (pyramid), increasing then decreasing (barrel), stable (linear), decreasing then increasing (hourglass), or decreasing (inverse pyramid) population trends.

We used the FIA Phase 2 hexagon grid to identify the main environmental determinants of red spruce occurrence. The grid consists of a tiling of 6,000-acre adjoining hexagon cells, with each cell containing one randomly located FIA plot. We obtained the exact FIA plot coordinates (latitude, longitude) in order to intersect plots with the following environmental data layers in geographic information systems.

1. Precipitation (mm)
2. Snowfall (mm)
3. Relative Humidity (percent)
4. Mean Maximum Temperature (˚C)
5. Mean Annual Temperature (˚C)
6. Mean Minimum Temperature (˚C)
7. Elevation (m)
8. Slope (percent)
9. Aspect (Transformed)
10. Curvature

Climate data listed above were derived from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) spanning from 1961-1990. PRISM is an expert system that extrapolates station (point) data over a digital elevation model to generate spatially continuous grid estimates of climate parameters (Daly et al. 1994). Climate layers generated by PRISM are renowned for their realistic physical detail and comprehensive spatial extent.

Shuttle Radar Topography Mission elevation data, 1 arc-second (approximately 300 ft) data were processed using ArcGIS v 9.3 Spatial Analyst (ESRI, Redlands, CA), generating output rasters for slope, aspect, and curvature. For each raster cell, the Slope function calculated the maximum rate of change in value from that cell to its neighbors (3- x 3-cell neighborhood). Low slope values represent flat terrain whereas high slope values represent steep terrain. The Aspect function identified the down-slope direction of the maximum rate of change in value from each cell to its neighbors. Aspect can be thought of as the slope direction. The values of the output raster are the compass direction of the aspect. Aspect was transformed to an ecologically relevant continuum from warm and dry aspects (0) to cool and moist aspects (2) using the formula of Beers et al. (1966). The Curvature function generated the second derivative of the surface or the slope of the slope. The output raster is the curvature of the surface on a cell-by-cell basis, as fitted through that cell and its eight surrounding neighbors (3 -x 3-cell neighborhood). A positive curvature indicates the surface is upwardly convex at that cell. A negative curvature indicates the surface is upwardly concave at that cell. A value of zero indicates the surface is flat.

To evaluate whether environmental factors driving red spruce occurrence differed across the East, we divided the FIA grid into two logical groups using the low mountains in southern Pennsylvania (the “Pennsylvania Saddle”) as a natural break point. The “Northeast” sector contains the states of Maine, New Hampshire, Vermont, Massachusetts, New York, and Pennsylvania, whereas the “Southern” group consists of West Virginia, Virginia, North Carolina, and the eastern portion of Tennessee. All FIA grid cells within these two groups were filled with aforementioned environmental parameters and red spruce presence (1) or absence (0). Single-factor analysis of variance was used to statistically determine those parameters significantly linked to red spruce presence or absence. For predictive modeling of red spruce distribution, stepwise logistical regression in SAS (SAS Institute, Cary, NC) (P level for parameter entry = 0.0001) was applied to produce a "best fit" equation.

RESULTS

Red Spruce Distribution

We identified 2,458 FIA plots as having one or more red spruce trees (excluding 2 plots outside of the species' native range in Ohio). The distribution of these plots by red spruce importance is shown using the FIA hexagon grid (Figs. 1 and 2). Red spruce occurrence was widespread and its importance highest across the Northeast, specifically from the Adirondack Mountains northeastward. Immediately south of the Adirondacks, the distribution of red spruce becomes scattered and the species becomes lower in importance (in southern New York State and northern Pennsylvania), then dissipates entirely within the low mountains of southern Pennsylvania. Two distinct clusters of red spruce occur farther southward along the Appalachian Chain (Fig. 2), one centered in West Virginia and the other located in the high mountains of western Virginia, western North Carolina, and eastern Tennessee. Here, the importance of red spruce can be quite high.

Regional Differences in Stand Character

Plots were separated into five regions using natural breaks in red spruce's distribution to evaluate differences in stand characteristics. The regions were New England, Adirondacks, Northern Appalachians, Central Appalachians, and Southern Appalachians (Fig. 3). The vast majority of plots were located in New England and the Adirondacks (2,021 and 352 plots, respectively) relative to the more southern regions (Table 1). Red spruce's widespread distribution in New England probably explains the high number of tree associates encountered there (total number of tree species = 48). Plots possessing red spruce in the Southern Appalachians were in stark contrast to all other regions (Table 1). They had consistently higher total stand and red spruce density, total stand and red spruce basal area, and red spruce importance. The only consistent gradient across regions was total stand basal area, which sequentially decreased from the Southern Appalachians to New England (170 to 83 ft^2/acre).

Importance values of red spruce and common associates are arrayed in Table 2. Stands containing red spruce in New England and the Adirondacks shared many common associates, including balsam fir, red maple, sugar maple, American beech, yellow birch, and eastern hemlock. In addition, northern white cedar (*Thuja occidentalis* L.) and paper birch (*Betula papyrifera* Marsh.) are frequent in New England. Red maple, eastern hemlock, yellow birch, and American beech are common associates in the Northern and Central Appalachians. Black cherry (*Prunus serotina* Ehrh.) has an unusually high importance in the Central Appalachians, a unique feature among regions. Yellow and black birches (*Betula lenta* L.) were common in the Southern Appalachians and yellow birch was a common associate across all regions.

Averaging importance values for conifer and broadleaf categories revealed that conifers were most abundant in New England (57 percent), whereas broadleaf trees collectively dominated all other regions (55-69 percent; Table 3). When classified by general forest type (conifer, mixed, broadleaf), red spruce stands were largely mixed (43-52 percent), except in the Central Appalachians, where most stands were broadleaf dominated (50 percent). It may be quite noteworthy from a natural recovery perspective to observe the occurrence of spruce in broadleaf-dominated systems; i.e., areas where red spruce might have formerly dominated and where populations are currently rebounding.

Red spruce was successfully regenerating and recruiting across all regions based on seedling and sapling representation (Table 4), particularly in the Central Appalachians. More than 40 percent of saplings in that region were red spruce. Tree regeneration seemed rather imbalanced across the regions. Only a few species posted high tallies in the South and many species had high numbers in the North. American beech was a consistent competitor across all regions. Firs were strong understory competitors, with abundant Fraser fir regeneration in the Southern Appalachians and a vast amount of balsam fir in

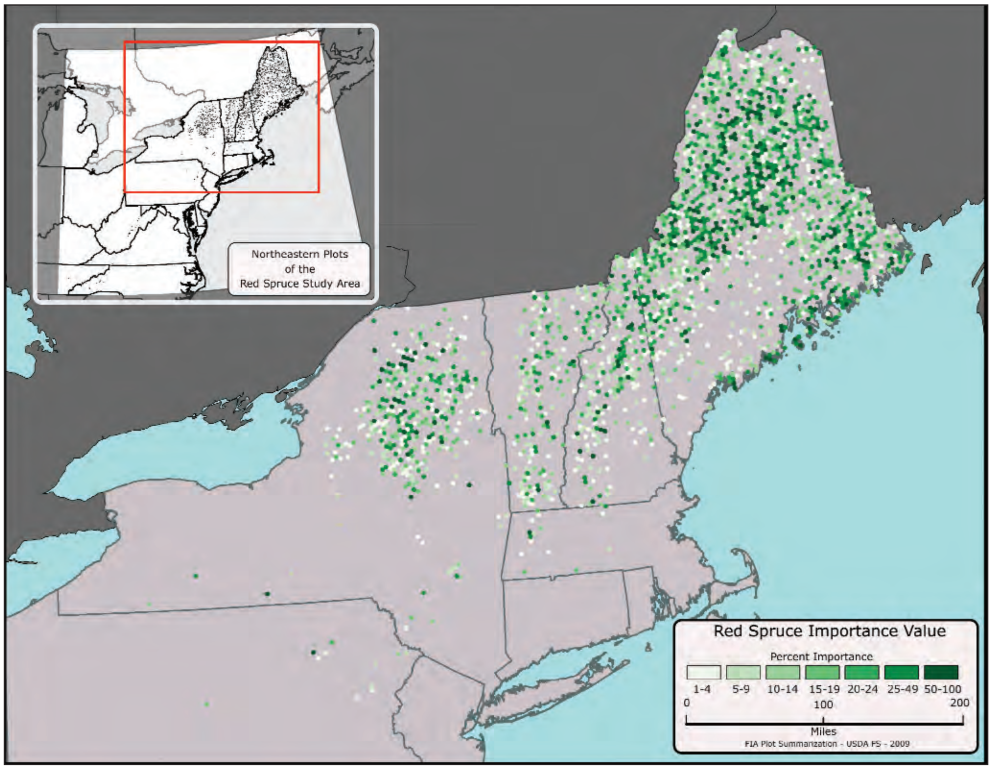

Figure 1.—Spatial projection of red spruce importance in the Northeast using the Forest Inventory and Analysis hexagon grid. Dots represent approximate plot locations.

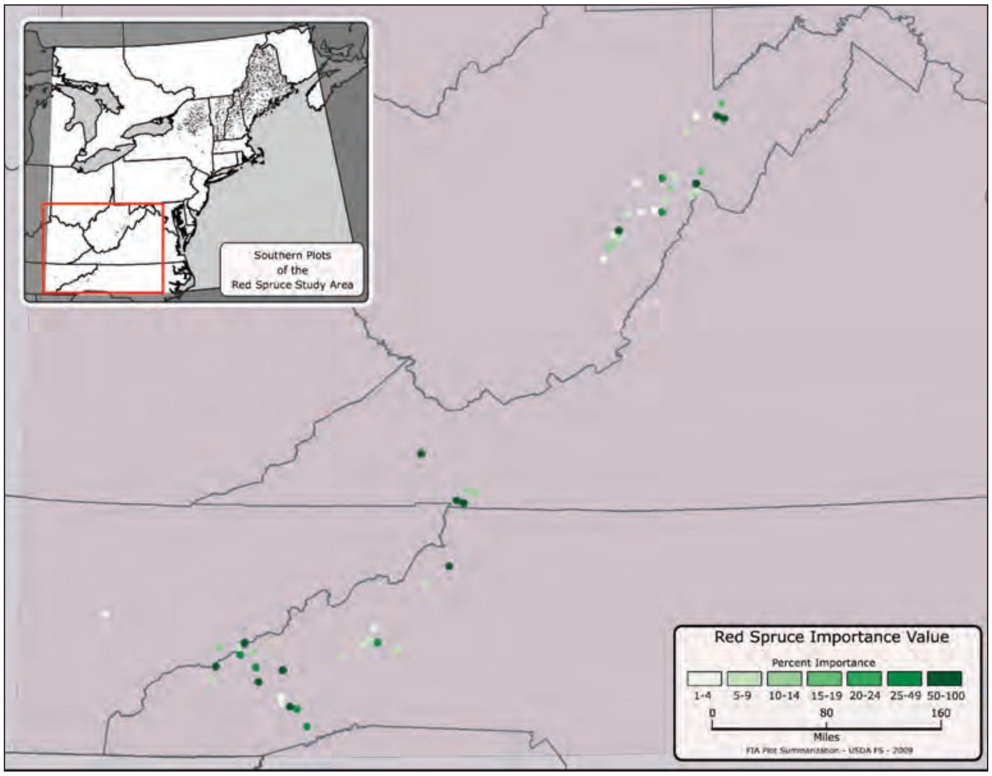

Figure 2.—Spatial projection of red spruce importance in the Central and Southern Appalachians using the Forest Inventory and Analysis hexagon grid. Dots represent approximate plot locations.

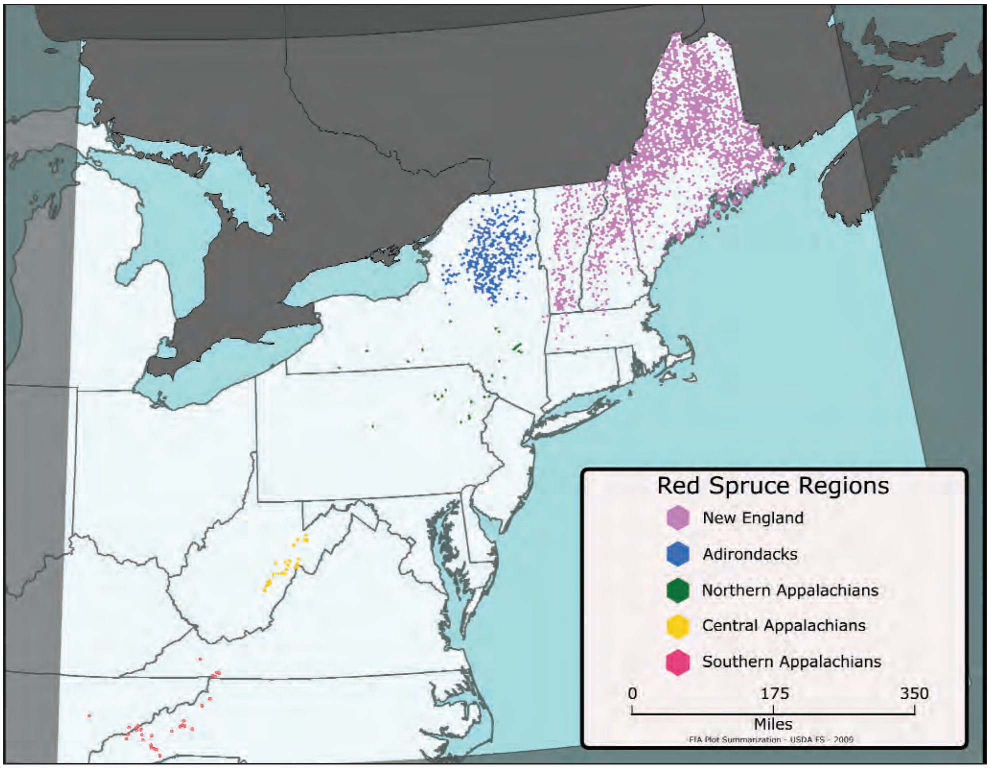

Figure 3.—Regional grouping of red spruce plots based on the Forest Inventory and Analysis hexagon grid.

Table 1.—Red spruce stand characteristics by region based on FIA plots with ≥1 red spruce tree (± standard error).

	Southern Apps	Central Apps	Northern Apps	Adirondacks	New England	All Regions
Total # of plots (n)	33	24	28	352	2,021	2,458
Total # of tree species	34	20	36	38	48	67
Total density (trees/acre)	245±28	192±11	200±21	185±4	190±2	190±2
Red spruce density and range	73±17 6-462	30±7 6-126	26±5 6-126	35±3 6-504	38±1 6-402	38±1 6-504
Red spruce relative density	29%	18%	19%	19%	21%	21%
Total basal area (sq. ft/acre)	170.0±17.6	123.6±9.1	105.5±10.9	96.8±2.1	83.3±1.0	87.1±0.9
Red spruce basal area and range	53.7±10.4 0.9-210.2	20.0±5.4 1.0-98.2	11.5±3.2 0.8-78.5	15.7±1.0 0.8-157.7	15.7±0.4 0.8-137.5	16.2±0.4 0.8-210.2
Red spruce relative basal area	33%	20%	17%	17%	20%	20%
Red spruce importance value	31%	19%	18%	18%	21%	20%
No. and percentage of plots with trees ≥15” dbh[a]	31 94%	21 88%	21 75%	268 76%	1,144 57%	1,485 60%
No. and percentage of plots with trees ≥60’ in height[b]	31 94%	22 92%	23 82%	323 92%	1,447 72%	1,846 75%

[a] Mature plots used for the diameter-class distribution analysis (see Appendix 1).

[b] Mature plots used for the height-class distribution analysis (see Appendix 2).

Table 2.—Importance values[a] for common tree species (species with at least one importance value ≥5) by regions (± standard error).

Species	Southern Apps	Central Apps	Northern Apps	Adirondacks	New England	All Regions
Picea rubens	31.1±4.9	19.2±4.6	18.1±4.8	18.1±1.0	20.7±0.4	20.4±0.4
Thuja occidentalis	0.0±0.0	0.0±0.0	0.0±0.0	1.1±0.0	7.6±0.4	6.4±0.3
Betula papyrifera	0.0±0.0	0.0±0.0	3.2±1.8	3.5±0.5	6.5±0.2	5.9±0.2
Abies balsamea	0.7±0.6	0.2±0.2	0.4±0.2	8.7±0.8	15.0±0.4	13.6±0.4
Acer saccharum	1.1±0.6	6.1±3.1	2.6±1.1	9.5±0.9	6.2±0.3	6.5±0.3
Fagus grandifolia	2.7±0.9	9.4±2.4	9.6±3.5	11.5±0.9	4.3±0.2	5.5±0.2
Acer rubrum	4.6±2.1	18.1±4.0	19.4±4.4	18.8±1.0	12.5±0.3	13.4±0.3
Tsuga canadensis	6.0±1.9	12.1±3.0	10.5±3.5	6.3±0.7	6.3±0.3	6.4±0.3
Prunus serotina	1.6±0.9	12.3±2.7	1.8±0.7	2.8±0.4	0.3±0.0	0.8±0.1
Betula alleghaniensis	21.8±4.1	13.9±2.8	6.8±2.5	11.1±0.7	7.1±0.3	8.0±0.2
Betula lenta	9.1±2.9	2.7±1.9	0.4±0.4	0.0±0.0	0.1±0.0	0.2±0.1

[a] Importance Value = (relative density + relative basal area)/2.

Table 3.—Average importance for total conifers and broadleaf trees, number of plots, and percentage of red spruce stands classified as conifer, mixed, and broadleaf forest types[a] by region.

	Importance Values		Total # of	% Forest Type		
	Conifer	Broadleaf	plots (n)	Conifer	Mixed	Broadleaf
New England	57	43	2,021	34.6	47.0	18.4
Adirondacks	39	61	352	15.1	44.0	40.9
N. Apps	45	55	28	25.0	42.9	32.1
Central Apps	31	69	24	8.3	41.7	50.0
S. Apps	40	60	33	15.2	51.5	33.3

[a] Stands were classified as conifer if total conifer importance was >75%. Stands were classified as mixed if conifers (or broadleaf trees) had a total importance ≥25% to ≤75%. Stands were classified as broadleaf if total broadleaf importance was >75%.

Table 4.—Saplings/seedlings per acre for red spruce and primary associates by region.

	Southern Apps	Central Apps	Northern Apps	Adirondacks	New England	All Regions
Picea rubens	152 / 647	228 / 3,526	123 / 600	138 / 4,090	129 / 7,109	132 / 6,481
Thuja occidentalis	0 / 0	0 / 0	0 / 0	2 / 133	23 / 7,051	19 / 5,816
Abies balsamea	0 / 0	3 / 19	3 / 54	153 / 15,737	446 / 26,058	388 / 23,680
Acer rubrum	2 / 150	13 / 3	54 / 295	55 / 2,873	103 / 5,583	94 / 5,007
Acer saccharum	5 / 14	13 / 109	0 / 26,249	24 / 1,529	26 / 9,631	25 / 8,439
Betula alleghaniensis	57 / 14	13 / 222	13 / 54	32 / 1,445	50 / 3,504	47 / 3,090
Tsuga canadensis	18 / 9	47 / 59	27 / 554	10 / 379	22 / 2,408	21 / 2,041
Fagus grandifolia	82 / 1,633	88 / 8,065	88 / 3,756	114 / 3,816	49 / 3,193	59 / 3,315
Abies fraseri	125 / 1,631	0 / 0	0 / 0	0 / 0	0 / 0	2 / 22
Total	670 /5,918	463 / 12,710	447 / 35,868	636 / 34,861	1,073 / 75,045	992 / 67,308

the Adirondacks and New England. Red maple, sugar maple, yellow birch, and eastern hemlock generally increased in numbers from the Southern Appalachians to New England. Overall, the absolute number of seedlings and saplings increased substantially northward, the exact opposite of overstory basal area.

Population Dynamics

At the broadest scale (summarizing all plots), red spruce was a model of stability, being fairly evenly distributed across diameter and height classes (Figs. 4 and 5). It represented a steady 20 percent of the trees across those diameter and height classes where the bulk of the population existed (5-15 in. diameter classes [Fig. 4a]; 25-75 ft height classes [Fig. 5a]). Red spruce representation generally declined over the highest diameter and height classes, perhaps due to disproportional removal of large red spruce by past logging, slower growth rates of red spruce compared to its competitors, or both. Subtle peaks of red spruce at larger diameter (e.g., 30 in. class) and height classes (115 ft class) may be vestiges of older individuals that escaped cutting (Figs. 4b and 5b).

The population dynamics of six common trees were derived from forest profiles of diameter and height classes (see Appendices A and B) and summarized in Table 5. Red spruce profiles often had hourglass shapes, indicating possible short-term declines followed by long-term increases. When considered across all regions, red spruce populations look quite stable, if not expanding. One exception might be in the Southern Appalachians, where red spruce appeared to be declining slightly. Populations of balsam fir, eastern hemlock, and American beech are foreseen to increase. Balsam fir, in particular, seems to be a strong competitor in the North, but its relatively short life span and lower survival rate in the understory may offset this trend somewhat (Loehle 1988, White and Cogbill 1992). Surprisingly, both sugar and red maple were in general decline across all regions. Maples were often chief benefactors of previous logging and fire disturbances; thus this projected retraction may merely reflect a return to pre-European disturbance levels.

Environmental Drivers of Red Spruce

Most of the environmental factors entered into the FIA grid were significantly related to red spruce occurrence (Tables 6 and 7). In the Northeast, a strong negative relationship existed between red spruce and temperature variables. Snowfall also was strongly associated with red spruce occurrence, though in a positive manner. Positive relationships were also found between red spruce and precipitation, relative humidity, and elevation. The congruence among these variables makes sense when the physical settings are considered. Red spruce occurrence increases as temperatures decrease; and snowfall, precipitation, and relative humidity increase along an elevational gradient.

Environmental relationships were not as strong in the Southern group as in the Northeast, probably due to the limited number of red spruce plots (57). Here, snowfall had the strongest relationship with red spruce occurrence, followed by elevation. Next, a series of climate variables had positive (relative humidity, precipitation) or negative (temperature) relationships with red spruce. Percent slope was positively linked with red spruce, probably reflecting red spruce's affiliation with higher, more rugged terrain.

Red spruce and environmental data were subjected to stepwise logistic regression for predictive modeling. Six environmental factors were ultimately selected to predict red spruce presence in the Northeast (Table 8). The relatively high, positive starting value of the intercept (+15) hints at red spruce's abundance and widespread distribution in the Northeast (i.e., that red spruce is present more often than not). Most variation was explained by the first entered variable, mean annual temperature; so much, in fact, that this factor alone can be used to effectively predict red spruce occurrence. Precipitation and elevation added some explanatory power to the equation, followed distantly by relative humidity, snowfall, and mean maximum annual temperature. Because the remaining unexplained variation changes at each step, note that coefficients (+/–) of latter factors may not coincide with that factor's direct association with red spruce presence (cf. Table 6).

Contrary to the Northeast, the rather low intercept (-10) reveals red spruce's relative scarcity in the Southern

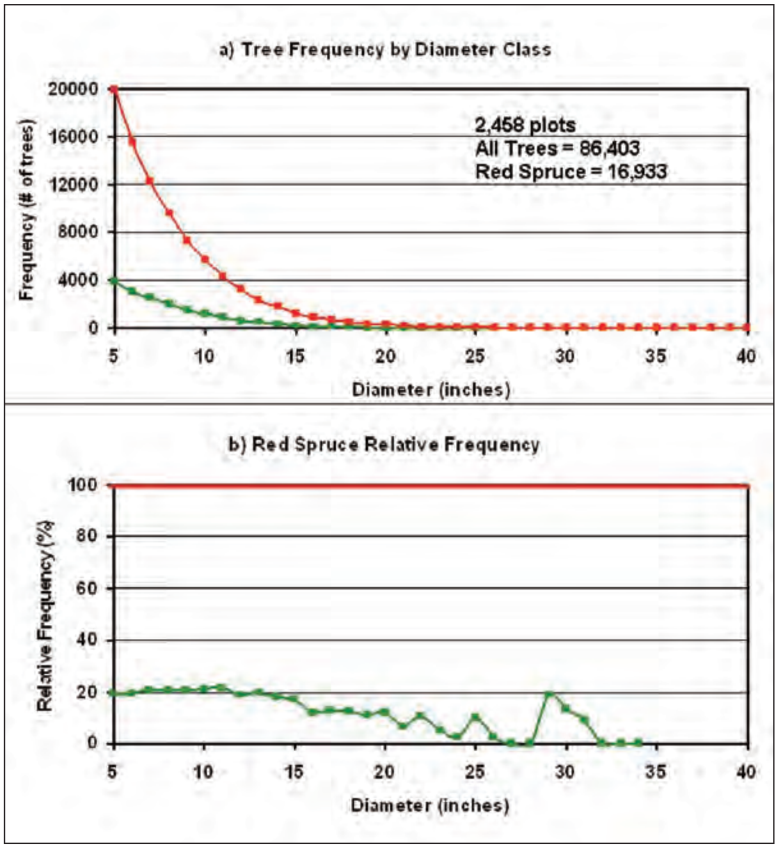

Figure 4.—Diameter-class frequency of all trees (red) and red spruce (green) (a) and relative diameter-class frequency of red spruce (b) based on 2,458 FIA plots.

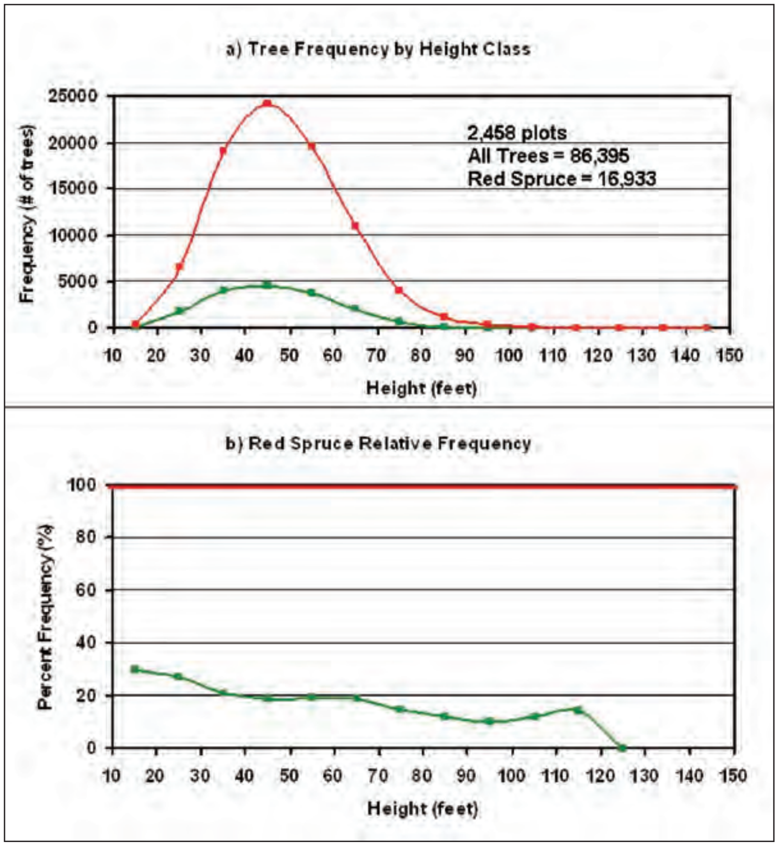

Figure 5.—Height-class frequency of all trees (red) and red spruce (green) (a) and relative height-class frequency of red spruce (b) based on 2,458 FIA plots.

Table 5. Population trends of six common tree species derived from diameter- and height-class forest profiles (Appendices 1 and 2) and summarized by region. Within regions (column), the first symbol represents the population trend by diameter class and the second symbol represents the population trend by height class.

	Southern Apps		Central Apps		Northern Apps		Adirondacks		New England		Overall
	Diam	Ht	Diam	Ht	Diam	Ht	Diam	Ht	Diam	Ht	
Picea rubens	▼	↓↑	↓↑	↓↑	↓↑	↓↑	▲	▲	↑↓	↔	↔
Abies balsamea			▲	▲	▲	▲	▲	▲		▲	
Tsuga canadensis	↔	▲	▲	▲	↔	▲	▼	▲	▼	▲	▲
Fagus grandifolia	▲	▼	▲	↑↓	▲	↔	▲	↑↓	▲	▲	▲
Acer rubrum	↑↓	↔	▼	▼	↑↓	↑↓	▼	▼	↑↓	▼	▼
Acer saccharum	↑↓	▼	▼	▼	↔	▼	▼	▼	↔	▼	▼

Symbols: ▲ = increasing; ↑↓ = increase then decline; ↔ = stable; ↓↑ = decline then increase; ▼ = declining.

Table 6.—Environmental factors significantly linked to red spruce occurrence based on single-factor analysis of variance for the Northeast group (P <0.01; 14,393 total grid cells; 2,401 grid cells with red spruce).

Factor	F-Value	Average Value with red spruce	Average Value w/o red spruce	Relationship with red spruce
Mean Annual Temperature	5,570	4.6 °C	7.8 °C	Negative
Mean Maximum Annual Temperature	5,400	10.7 °C	13.7 °C	Negative
Mean Minimum Annual Temperature	5,218	-1.4 °C	1.8 °C	Negative
Snowfall	3,976	2,876 mm	1,730 mm	Positive
Precipitation	543	1,126 mm	1,063 mm	Positive
Relative Humidity	221	69%	68%	Positive
Elevation	109	366 m	322 m	Positive

Not significant = % Slope, Transformed Aspect, and Curvature.

Table 7.—Environmental factors significantly linked to red spruce occurrence based on single-factor analysis of variance for the Southern group (P <0.01; 11,366 total grid cells; 57 grid cells with red spruce).

Factor	F-Value	Average Value with red spruce	Average Value w/o red spruce	Relationship with red spruce
Snowfall	598	1,691 mm	420 mm	Positive
Elevation	376	1,110 m	335 m	Positive
Relative Humidity	263	73%	69%	Positive
Precipitation	260	1,551 mm	1,184 mm	Positive
Mean Maximum Annual Temperature	246	16.0 °C	19.8 °C	Negative
Mean Annual Temperature	238	9.5 °C	13.3 °C	Negative
Mean Minimum Annual Temperature	210	2.9 °C	6.7 °C	Negative
% Slope	118	28%	11%	Positive

Not significant = Transformed Aspect and Curvature landscape (i.e., red spruce is usually absent, requiring favorable factors to generate positive values) (Table 9). Snowfall and elevation were the only predictive factors to sequentially enter the predictive equation.

DISCUSSION

The current distribution of red spruce is consistent with E. Little's classic maps (Little 1971) that are still in use today (Burns and Honkala 1990). The distribution of red spruce has a funnel-like shape when viewed along its main southwest-northeast axis—spreading widely across New England and the Adirondacks before tapering to form a narrow shaft along the Central and Southern Appalachians. This imbalanced distribution probably explains why red spruce has more tree associates in the North relative to the South, which is contrary to the general theory of decreasing species richness with latitude (Pianka 1966, Hillebrand 2004, Lomolino et al. 2006). Indeed, red spruce spans a myriad of growing sites in the Northeast (coastline to interior; low to high elevation; wet to dry), mixing with a greater array of species than in its exclusive montane position in the South (White and Cogbill 1992).

Consistent with its distribution, the density of FIA plots harboring red spruce changed appreciably among regions. Red spruce had a rather contiguous presence over New England and the Adirondacks (Fig. 1), becoming increasingly scattered southward before disappearing altogether in the low mountains of southern Pennsylvania (the "Pennsylvania Saddle"). Further southward, red spruce reappears in clusters on high ranges of the Central and Southern Appalachians (Fig. 2). The distribution and continuity of red spruce basically reflects its preference for seasonally cool, moist, fog-shrouded, snow-laden sites (Siccama 1974), conditions that are widespread from coast to mountaintop in the far Northeast but increasingly restricted to the highest elevations southward (Cogbill and White 1991, White and Cogbill 1992).

Among regions, red spruce attained its highest average importance in the Southern Appalachians. This distinction

Table 8.—Environmental factors, equation coefficients, and Chi-square values of the best-fit model explaining red spruce occurrence in the Northeast based on stepwise logistic regression[a]. Final equation: Red spruce logit = 15.0 – 0.66(MATemp) + 0.005(Precip) – 0.002(Elev) – 0.145(RelHum) – 0.0004(Snow) – 0.52(TMax).

Factor	Coefficient	Chi-Square (measure of variance explained)
Intercept	+ 15.0	
Mean Annual Temperature	– 0.66	3,988.6
Precipitation	+ 0.005	219.4
Elevation	– 0.002	158.5
Relative Humidity	– 0.145	27.4
Snowfall	– 0.004	19.2
TMax	– 0.52	27.0

[a] Logistic regression parameters: Red spruce = 1, P level for variables entry/exit was set at 0.001.

Table 9.—Environmental factors, equation coefficients, and Chi-square values of the best-fit model explaining red spruce occurrence in the South based on stepwise logistic regression[a]. Final equation: Red spruce logit = –10.37 + 0.0011(Snow) + 0.0054(Elev).

Factor	Coefficient	Chi-Square (measure of variance explained)
Intercept	–10.37	
Snowfall	+ 0.0011	565.3
Elevation	+ 0.0054	183.3

[a] Logistic regression parameters: Red spruce = 1, P level for variables entry/exit was set at 0.001.

can be attributed to various factors. First, the southern extension of red spruce occurs at latitudes where fewer cool-adaptive species inherently occur. The limited number of competitors would confer a distinct advantage to red spruce in capturing a larger portion of growing space, as reflected in tree density, basal area, and overall importance. Secondly, differences in forest history and land use could also explain high red spruce importance in the Southern Appalachians (Pyle and Schafale 1988, White and Cogbill 1992, Hayes et al. 2007). Here, red spruce was historically distributed over high-elevation mountain tops, side slopes, and coves. Logging operations and associated slash fires generally occurred from valley floor to mountaintop according to accessibility and human presence. As logging operations proceeded, the distribution of red spruce was progressively "squeezed" to higher elevations. Logging operations often ended when slopes became too steep, terrain too rugged, or forests too stunted for financial gain. Thus, the remaining unlogged red spruce stands were concentrated on upper slopes and mountaintops, where it inherently had higher importance. In other words, high importance of red spruce might merely reflect its present-day compressed state whereby mid-elevation stands of low red spruce importance were preferentially logged and converted to hardwoods while those with high red spruce importance remained (Pielke 1981).

Last, balsam woolly adelgid (*Adelges piceae* Ratzeburg) has had a profound effect on red spruce's chief competitor in the South – Fraser fir (Ragenovich and Mitchell 2006). The effects of this exotic insect have been devastating; Fraser fir has experienced extremely high mortality since the 1950s (Beck 1990). High Fraser fir mortality led to the release of substantial growing space, undoubtedly benefiting red spruce (Pauley et al. 1996). Fraser fir might be permanently relegated to a small, understory species as no tree-sized individuals (≥5 in. d.b.h.) were recorded on FIA-based plots harboring red spruce.

Stand basal area progressively decreased across regions from the Southern Appalachians to New England. This pattern is consistent with the notion that site productivity normally decreases with increasing latitude. Apparently, even though red spruce is restricted to high elevations in the South (areas inherently lower in site productivity), growing conditions and site productivity are still higher there than across a broad range of sites encountered in the North. Korstian (1937) points out that red spruce attains its maximum development in the Southern Appalachians, attaining larger sizes than in the Northeast. Likewise, Gibson (1913) mentions that red spruce reaches its highest development in the Southern Appalachians, with larger individuals possessing more clear lumber than that found in New England and the Canadian provinces.

Regional differences in forest history may offer an additional explanation, whereby red spruce stands in the South are largely unlogged remnants or mature second-growth stands possessing higher basal areas compared to younger and intensively managed stands to the north. Indeed, the percentage of mature stands increases southwards (Table 1). A greater proportion of red spruce stands occurs on federally managed lands in the South (e.g., Great Smoky Mountains National Park, TN, NC; Monongahela National Forest, WV), areas where timber harvest is more conservative or prohibited outright.

The trend for tree regeneration moved in the opposite direction from stand basal area, sequentially increasing in density from the Southern Appalachians to New England (Table 4). This reciprocal relationship demonstrates that growing space not used by the overstory will be available for understory development. This relationship is not new information as foresters have long known about overstory-understory relationships and associated trade-offs.

Not surprisingly, red spruce associates changed from principally boreal species in New England (balsam fir, northern white cedar, paper birch) to temperate species southwestward (maples, American beech, and hemlock). Black cherry was a prominent associate only in the Central Appalachians, where its high timber value may provide the financial means for red spruce restoration through release cutting (Rentch et al. 2007). Curiously, shade-intolerant birches (yellow and black) were quite abundant in Southern Appalachian stands, probably a consequence of disproportional increase due to past cutting and fire (Korstian 1937). It is tempting to propose a spruce-birch forest type specifically for this region (Eyre 1980), but this association may diminish as birches wane with time. Interestingly, yellow birch was an important companion tree in all regions and, due to its similar ecophysiology and distributional configuration (Erdmann 1990), may serve as a site indicator for red spruce restoration. In addition, Fraser fir may serve this purpose in the Southern Appalachians, as balsam fir and rhododendron (*Rhododendron maximum* L.) do in the Central Appalachians (Allard and Leonard 1952).

Overall, red spruce populations were remarkably stable when compared across diameter and height classes. When assessed against other shade-tolerant competitors, red spruce did as well if not better (Table 5). Balsam fir, eastern hemlock, and American beech all exhibited increasing trends, although these projected increases may be offset by other limitations, such as an inherently short life span (balsam fir) or possible impacts by introduced insects and diseases (hemlock woolly adelgid, beech bark disease complex [*Cryptococcus-Nectria*]). Unexpectedly, sugar and red maple had decreasing trends across the board, which is in stark contrast to their superior performance in other ecosystems (Lorimer 1984, Nigh et al. 1985, Ebinger 1986, Abrams 1998, Nowacki and Abrams 2008). The projected decrease of maples probably represents a natural retraction following major expansion associated with the Great Cutover and subsequent burnovers of the late 1800s and early 1900s (Pauley 1989). Indeed, the severe, anthropogenic-driven disturbances of this era lay well outside of the prevailing wind-based, gap-phase dynamics of red spruce ecosystems (Brooks 1911, Foster and Reiners 1983, White et al. 1985, Cogbill 1996, Hayes et al. 2007, Fraver et al. 2009). The contrasting response of co-occurring maples (expansion) and spruce (contraction) is a classic hallmark of how angiosperms and gymnosperms typically react to major disturbance (Bond 1989). Thus, without the continuation of the major anthropogenic disturbances of the past, maples and other opportunistic hardwoods seem destined to decline as shade-tolerant conifers (hemlock, red spruce, and firs) re-emerge under a more favorable "natural" disturbance regime.

Red spruce, like most conifers, was disproportionately affected by logging and accompanying wildfires in the late 1800s and early 1900s (Clarkson 1964, Cogbill 1996, Lewis 1998). Red spruce's aversion to logging is evident today when managed landscapes are compared to preserves (see Table 3 of Woodcock and others 2008). Since hardwoods were the principal post-disturbance benefactors, some of the greatest opportunities for red spruce restoration exist where hardwoods currently dominate former red spruce sites (Minckler 1945). As such, the Central Appalachians may be a premier area to pursue restoration based on the high percentage of hardwood-dominated stands with red spruce (Table 3). At present, red spruce seems to be in a favorable position, abundantly regenerating throughout its range (Table 4) and well poised for overstory advancement given the opportunity (Hornbeck and Kochenderfer 1998). Again, silvicultural treatments such as thinning from below (Schuler et al. 2002) and thinning from above (Rentch et al. 2007) should be implemented to facilitate understory red spruce vigor, survivorship, and recruitment to larger size classes. Increasing conifer (red spruce) representation in an otherwise broadleaf-dominated forest provides multiple benefits, including higher tree diversity (and related improvements to forest health and resiliency), increases in total stand volume (through conifer-hardwood differences in resource needs and niche space), and expansion of conifer-based habitats for wildlife.

In conclusion, red spruce seems to be doing well throughout its range. Based on regeneration, recruitment, and overall health, red spruce is actually expanding in many cases (Pauley et al. 1996, Koon 2004). This finding may simply reflect red spruce's natural tendency to recapture its former status on severely disturbed landscapes. Put into a tortoise-and-hare analogy (Bond 1989), opportunistic hardwoods sprinted off quickly after the destructive disturbances of the late 1800s and early 1900s, but shade-tolerant red spruce has slowly gained ground over time as forest floor conditions recover (e.g., increased moisture, shade, and surface organics favorable for red spruce regeneration) and overtopping hardwoods senesce (releasing growing space to understory red spruce). However, the resiliency of red spruce might be tested yet again with atmospheric pollutants and impending climate change. Climate change may have profound and unexpected effects on the entire red spruce ecosystem, including all component species. As such, the favorable outlook projected here for red spruce may not stand under substantial climate change (Iverson et al. 2008), particularly with increasing temperatures and decreasing snowfall. Indeed, climate change, in the form of increasing temperatures, already may have diminished red spruce since the end of the Little Ice Age (Hamburg and Cogbill 1988). However, higher elevations, where a great deal of red spruce resides, may be inherently more resistant to climate warming (Seidel et al. 2009). At these elevations, conditions may continue to support the improving trends of red spruce expressed today.

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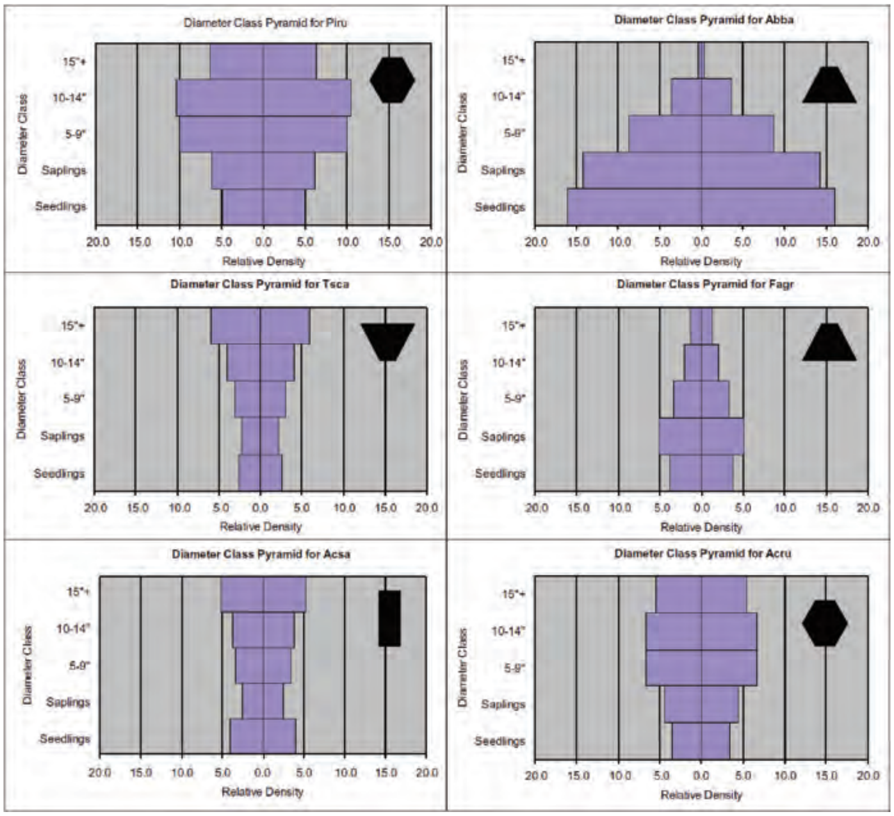
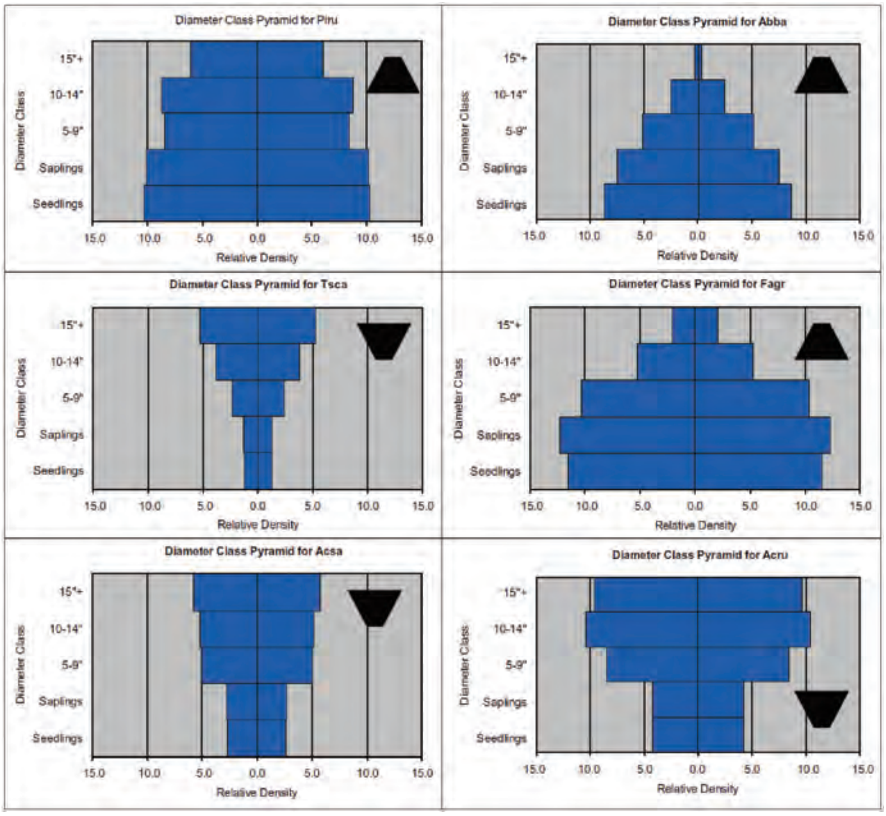
APPENDIX A.

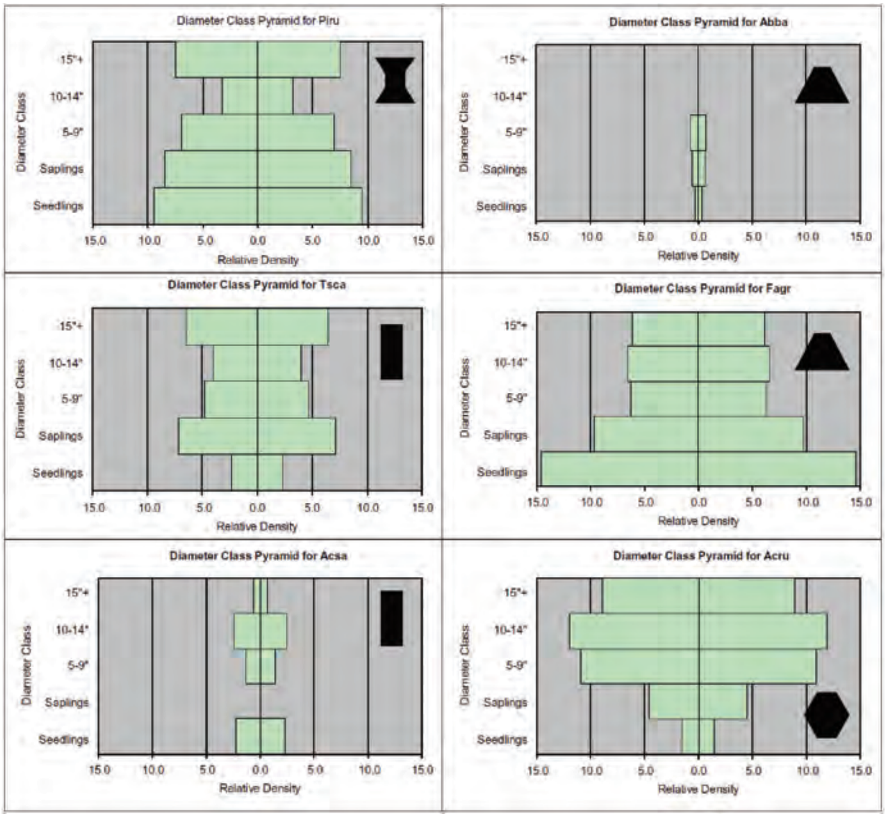
Diameter-class distributions (population pyramid format) based on relative density for six common species. Population trends are designated by black inset symbols: pyramid = increasing population, hourglass-shaped = decreasing then increasing population, linear = stable or indistinguishable population trends, barrel-shaped = increasing then decreasing population, and inverse pyramid = decreasing population. Abbreviations: Piru = *Picea rubens,* Abba = *Abies balsamea,* Tsca = *Tsuga canadensis*, Fagr = *Fagus grandifolia*, Acsa = *Acer saccharum*, and Acru = *Acer rubrum.* These centrally balanced bar graphs are additive, e.g., 5 + 5 = 10 percent relative density.



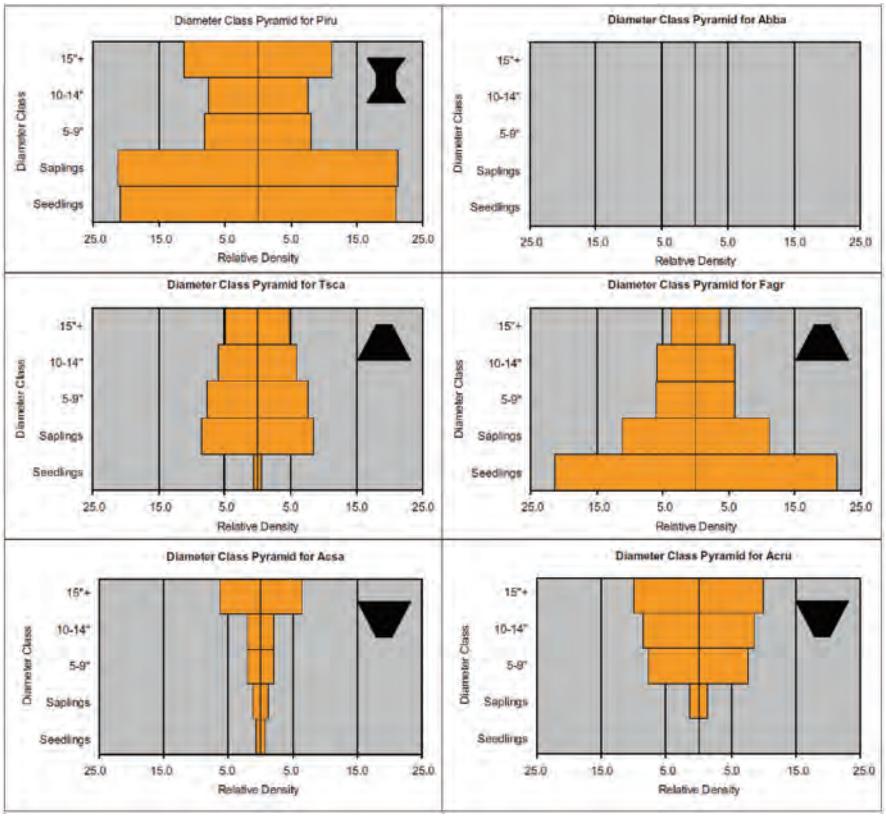
Appendix A1.—The New England Region.



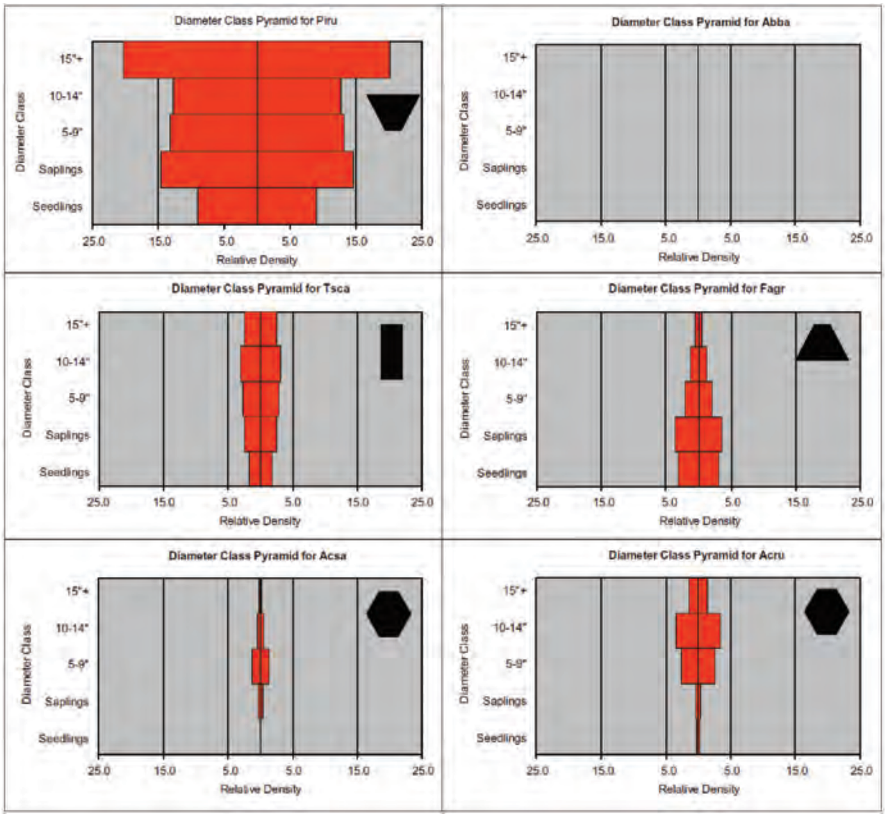
Appendix A2.—The Adirondack Region.



Appendix A3.—The Northern Appalachian Region.



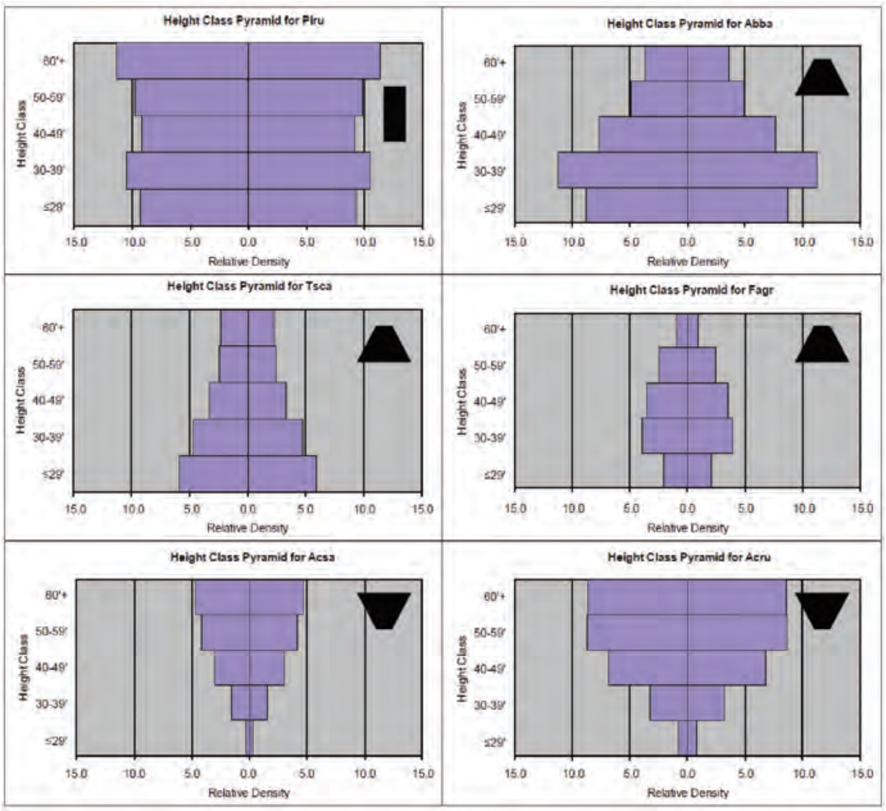
Appendix A4.—The Central Appalachian Region.



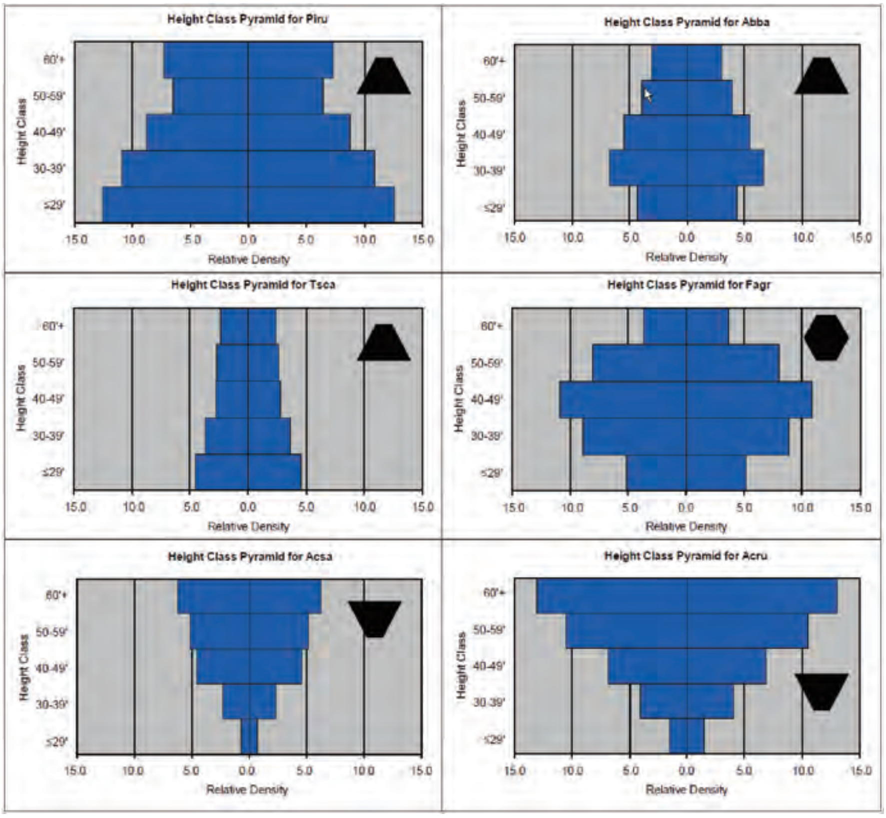
Appendix A5.—The Southern Appalachian Region.

APPENDIX B.

Height-class distributions (population pyramid format) based on relative density for six common species. Population trends are designated by black inset symbols: pyramid = increasing population, hourglass-shaped = decreasing then increasing population, linear = stable or indistinguishable population trends, barrel-shaped = increasing then decreasing population, and inverse pyramid = decreasing population. Abbreviations: Piru = Picea rubens, Abba = Abies balsamea, Tsca = Tsuga canadensis, Fagr = Fagus grandifolia, Acsa = Acer saccharum, and Acru = Acer rubrum. These centrally balanced bar graphs are additive, e.g., 5 + 5 = 10 percent relative density.



Appendix B1. The New England Region.



Height Class Pyramid for Piru

Height Class Pyramid for Abba

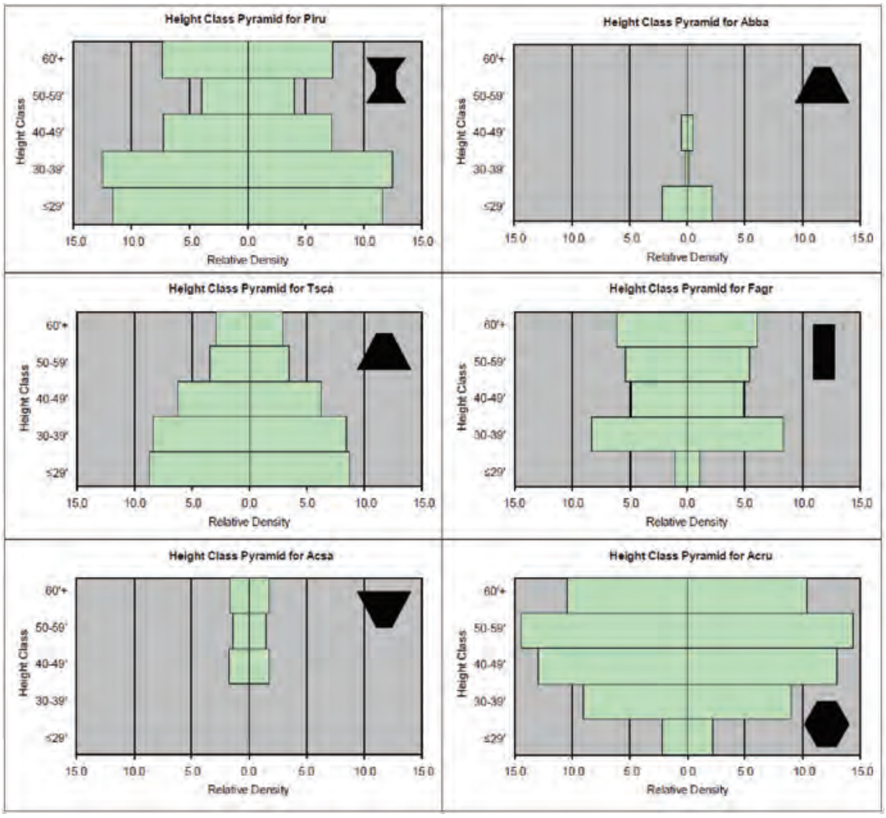
Height Class Pyramid for Tsca

Height Class Pyramid for Fagr

Height Class Pyramid for Acsa

Height Class Pyramid for Acru

Appendix B2. The Adirondack Region.



Height Class Pyramid for Piru

Height Class Pyramid for Abba

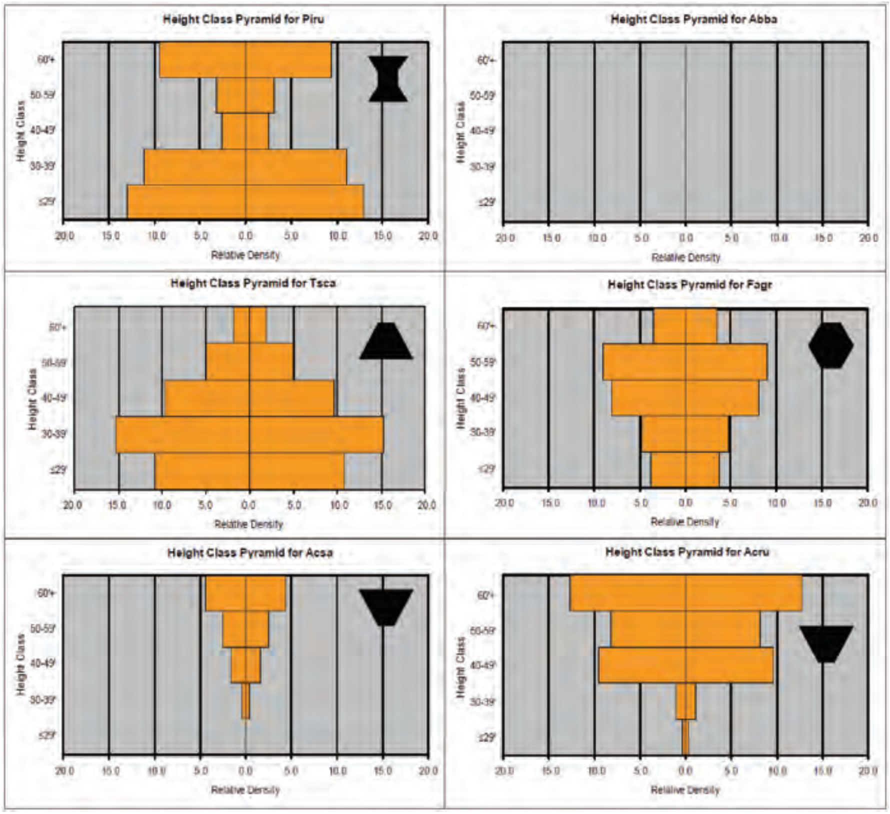
Height Class Pyramid for Tsca

Height Class Pyramid for Fagr

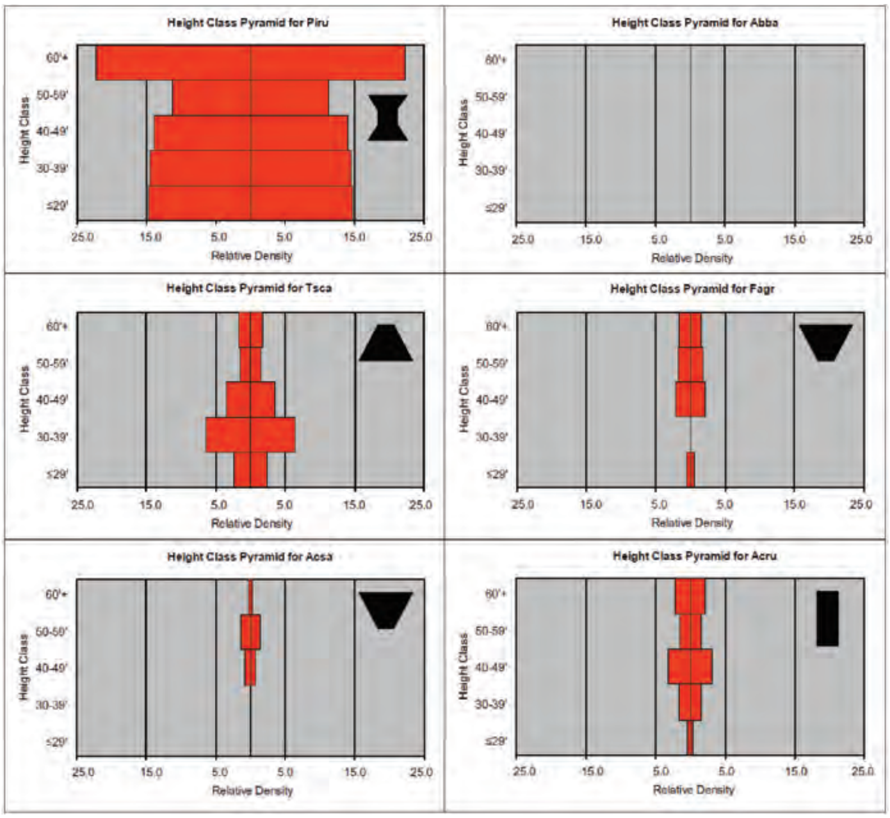
Height Class Pyramid for Acsa

Height Class Pyramid for Acru

Appendix B3. The Northern Appalachian Region.



Appendix B4. The Central Appalachian Region.



Appendix B5. The Southern Appalachian Region.

THE CURRENT DISTRIBUTION, PREDICTIVE MODELING, AND RESTORATION POTENTIAL OF RED SPRUCE IN WEST VIRGINIA

Gregory Nowacki and Dan Wendt[1]

Abstract.—The environmental relationships of red spruce (*Picea rubens* Sarg.) were assessed in east-central West Virginia. Although many significant relationships existed, red spruce was most strongly associated with elevation, climate, and soil moisture factors. Specifically, red spruce was positively associated with elevation, number of frost days, mean annual precipitation, and soil wetness (as expressed by depth to impermeable "fragipan" horizon, depth to water table, and drainage class) and negatively associated with growing degree days and mean annual temperature. A predictive model was built by subjecting the dataset to logistical stepwise regression. Elevation was overwhelmingly the most important predictor of red spruce and explained the majority of variation. A predictive map of red spruce occurrence using a four-factor regression equation (elevation, depth of water table, precipitation, and growing degree days) was created. Opportunities to restore red spruce ecosystems in West Virginia were identified by comparing the actual mapped distribution of red spruce with the predictive model output. Limitations of using current distributional data as input for predictive modeling are discussed.

INTRODUCTION

The forests of the eastern United States experienced sweeping changes at the hands of Europeans and other immigrants (Williams 1982, 1990; MacCleery 1996). Viewed as impediments to western expansion, forests were often indiscriminately logged and burned to make way for agricultural development and settlement (Frederick and Sedjo 1991). Where forests were allowed to regenerate, tree species responded differently based on the type of disturbance (cutting, fire, pasturage), site conditions, and their individual life histories and physiological traits. When occurring in mixed forests, conifers were invariably logged first because their superior timber qualities, ease of transport (floatable down rivers), or other characteristics (e.g., tannin from hemlock [*Tsuga canadensis* (L.) Carr.] bark) made them desirable. Under this scenario, hardwoods typically benefited at the expense of conifers (Nowacki and Abrams 1992, Cole et al. 1998, Schulte et al. 2007). This was indeed the case with red spruce (*Picea rubens* Sarg.) in the Central and Southern Appalachians, especially after wildfires burned through logging slash, consuming regeneration and larger seed trees (Korstian 1937, Allard and Leonard 1952, Clarkson 1964, Lewis 1998). Seedbed and microclimatic conditions favorable for red spruce regeneration (thick moist humus layer; cool, shaded settings) were also badly damaged by wildfire (Brooks 1911, Minckler 1945, Allard and Leonard 1952, Pyle and Schafale 1988, Hayes et al. 2007). Upon drying, thick humus layers became highly combustible, further intensifying fire and its negative effects on biota (Pauley 2008). In some extreme cases, nothing but rubble fields was left behind (Allard and Leonard 1952). All told, red spruce suffered a serious range contraction as it was relegated to the most rugged, inaccessible, and highest portions of its former distribution (Hopkins 1899, Pielke 1981, Pyle and Schafale 1988).

Since the unprecedented level of cutting and burning of the late 1800s and early 1900s, disturbance conditions have stabilized and forests have re-emerged, although with more youthful characteristics (younger and smaller trees; more shade-intolerant species; simplified age-class and stand structures) (Allard and Leonard 1952, Pauley 1989, Fortney

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1993). As such, great potential now exists for red spruce restoration through natural successional processes (Pielke 1981) or active management (planting and thinning; Hornbeck and Kochenderfer 1998). To engage in red spruce restoration effectively, managers must identify and prioritize landscapes where red spruce recovery is most likely to succeed. In this spirit we set forth to identify those environmental factors most closely associated with the current distribution of red spruce and to create a predictive model to support red spruce restoration efforts.

METHODS

The red spruce data layer used in our analysis was generated by the Department of Geography, West Virginia University, in 1988 under contract with the U.S. Forest Service, Northeastern Forest Experiment Station. The Monongahela National Forest, the Northeastern Forest Experiment Station, and the West Virginia Department of Natural Resources set the mapping specifications. Expert opinion and other records were used to focus on those areas of the state where red spruce was the dominant conifer. Color-infrared aerial photographs at a scale of 1:30,000 were interpreted and mapped. The data layer depicted stands having ≥25 percent conifer cover in the overstory. At present, it is considered one of the best maps depicting the red spruce resource in West Virginia (Fig. 1).

Mapped stands of red spruce fell exclusively within eight counties in east-central West Virginia, which thus became our study area (Fig. 2). Using a geographic information system, we created a systematic 500 x 500 meter sampling grid of more than 60,000 points for the eight-county study area (Fig 3). The points were intersected with the red spruce cover (presence/absence) and available climatic, topographic, and soil layers representing 20 different environmental variables (Table 1). Climate data layers were downloaded from the Daymet U.S. Data Center (http://www.daymet.org/). Daymet uses a digital elevation model and ground-based meteorological station data to generate continuous climate surfaces (e.g., temperature, precipitation) at a 1 km resolution. Data layers were based on an 18 year daily record (1980-1997) and included mean air temperature, mean annual precipitation, growing degree days, and number of frost days. Topographic data layers (e.g. aspect, slope,

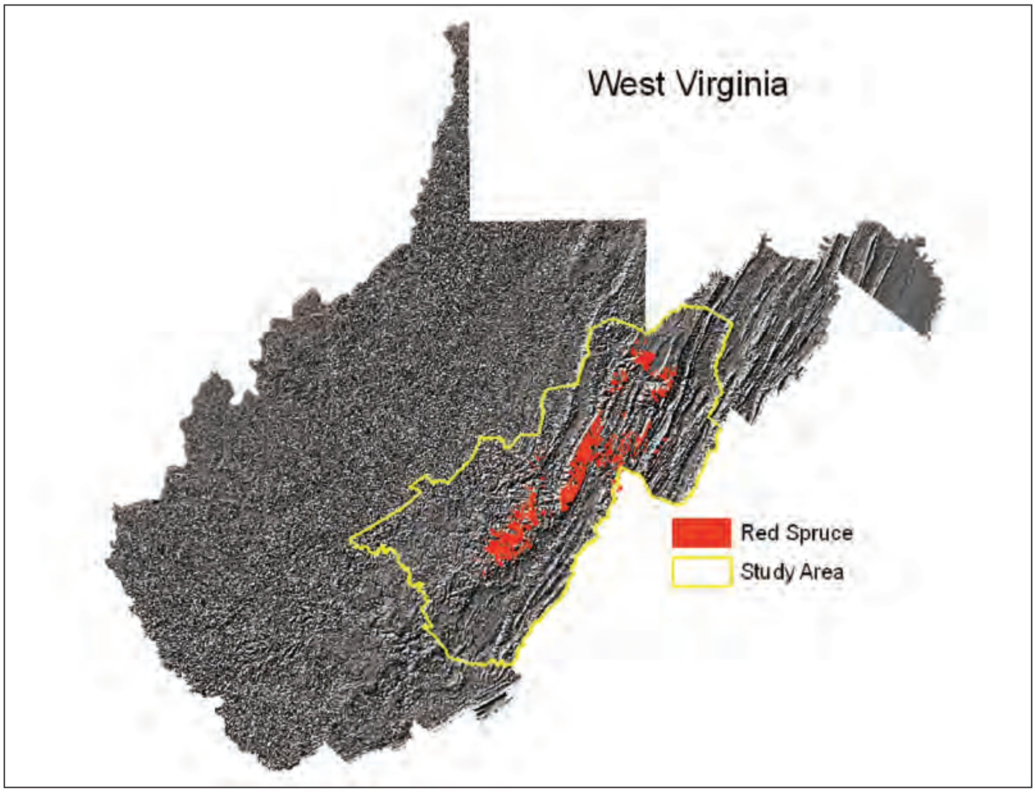

Figure 1.—The occurrence of red spruce stands (red) superimposed on a topographic coverage of West Virginia. The yellow line demarcates the eight-county study area. Note that few stands are located outside of the study area in Virginia.

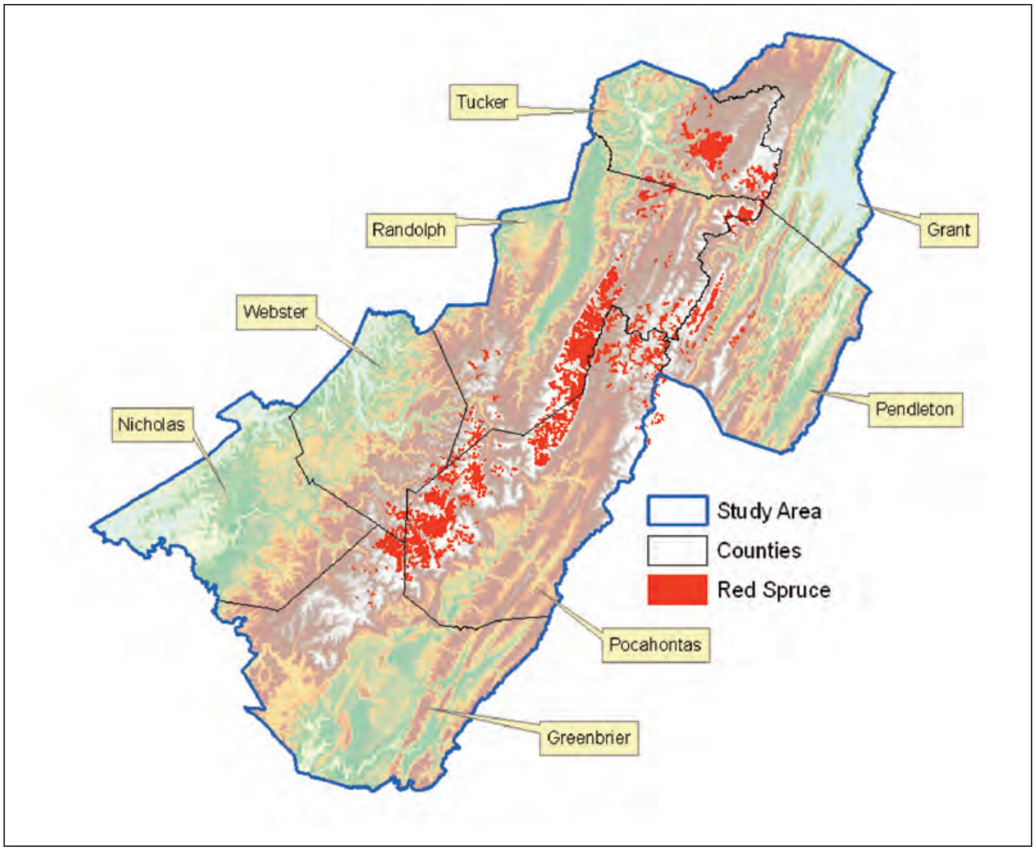

Figure 2.—The distribution of red spruce stands (red) within the eight-county study area in east-central West Virginia. County names identified in call-out boxes. Background colors represent an elevation gradient ranging from 195 to 1,481 m (lowest to highest elevation: green, yellow, dark red, white).

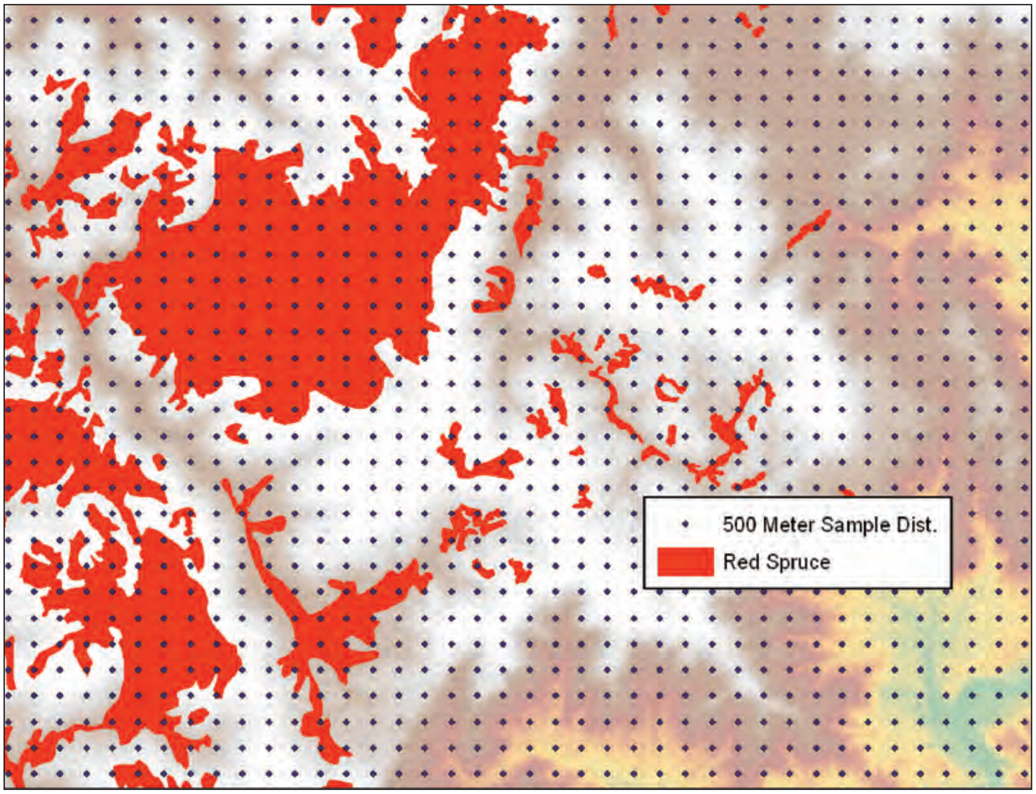

Figure 3.—Close-up illustration of 500-m point locations superimposed on the 1988 West Virginia red spruce layer. Background colors represent an elevation gradient ranging from 195 to 1,481 m (lowest to highest elevation: green, yellow, dark red, white).

Table 1.—Descriptions of 20 soil, climatic, and topographic variables used to analyze and predict red spruce occurrence in east-central West Virginia. The number of points populated with each variable in parentheses (total possible = 60,220).

Climate variables	Acronym[a]	Description
Mean Annual Temperature (59,807)	MAT	Mean °C over an 18-year period of the average air temperature for a 24-hour period.
Growing Degree Days (59,807)	GDD	The 18-year mean of the annual summation of the daily average air temperatures that are >0 °C, expressed in degree-days.
Number of Frost Days (59,807)	FROST	The 18-year mean of the number of days in an annual period when the daily minimum air temperature is ≤0 °C.
Mean Annual Precipitation (59,807)	MAP	The18-year mean of the total accumulated precipitation over 1 yr, expressed in cm.
Topographic variables		
Elevation (60,114)	ELEV	Elevation in meters generated from terrain data.
Slope (60,114)	SLOP	Percent slope generated from terrain data.
Aspect (59,820)	ASP	Aspect degrees generated from terrain data and transformed using Beers' and others (1966) formula.
Soil variables[b]		
pH[c] (58,884)	pH	Soil reaction: a measure of acidity or alkalinity.
Cation Exchange Capacity[c] (58,132)	CEC	The total amount of extractable cations held by soil, expressed in milliequivalents/100g of soil at pH 7.
Available Water Capacity[c] (46,436)	AWC	The quantity of water that the soil is capable of storing for plant use expressed in cm of water/ cm of soil.
Bulk Density[c] (58,583)	BULK	The oven-dry weight of soil at 1/3 bar water tension expressed in g/cm^3.
Organic Matter[c] (59,008)	OM	The amount of plant and animal residue in the soil expressed as a %, by weight, of the soil.
% Sand[c] (29,608)	SAND	The amount of mineral soil particles within 0.05 to 2 mm in diameter expressed as a %, by weight, of the soil.
% Silt[c] (29,608)	SILT	The amount of mineral soil particles within 0.002 to 0.05 mm in diameter expressed as a %, by weight, of the soil.
% Clay[c] (29,608)	CLAY	The amount of mineral soil particles <0.002 mm in diameter, expressed as a %, by weight, of the soil.
Drainage Class (58,924)	DRAIN	Numeric portrayal of natural soil drainage as interpreted from soil polygon data: 1 = excessively drained 2 = somewhat excessively drained 3 = well drained 4 = moderately well drained 5 = somewhat poorly drained 6 = poorly drained 7 = very poorly drained
Depth to Lithic (60,075)	LITHIC	Inches to bedrock (R horizon).
Depth to Fragipan (60,198)	FRAG	Inches to a dense soil layer that restricts water movement.
Depth to Paralithic (60,198)	PARA	Inches to a paralithic (Cr horizon).
Depth to Water Table (60,198)	WATER	Inches to a saturated zone in the soil based on redoximorphic features.

[a] Acronyms used in Table 3.

[b] Interpreted from SSURGO soil polygon data.

c Data represented a combined average across all soil layers.

elevation) were derived from a seamless raster elevation dataset from the U.S. Geological Survey's National Elevation Dataset (NED). The NED uses a diverse set of source data that is processed to a common coordinate system and unit of vertical measure. The resolution of this dataset was 1 arc-second (about 30 meters). Soils data were obtained online for the eight-county study area from the USDA Natural Resources Conservation Service's Soil Survey Geographic (SSURGO) Database (http://soils.usda.gov/survey/geography/ssurgo/). More than 100,000 polygons were mapped in the eight-county study area, ranging from 0.4-2,575 ha, averaging 1.6 ha, and representing 493 unique soil map units. Point data were derived from mapped soil polygons for all soil variables (Table 1).

The resulting dataset, comprising 60,220 points, was subjected to single-factor analysis of variance (ANOVA) to identify significant environmental differences between spruce and non-spruce locations. Correlation analysis was used to understand interrelations among all factors, with Pearson's r of ±0.80 being considered strongly correlated. Since red spruce data were represented in terms of presence or absence (binominal), stepwise logistic regression was used in SAS Version 9.1 (SAS Institute Inc., Cary, NC) for predictive modeling. All environmental factors were included in the regression procedure, which ultimately generates an equation composed of a set of factors that best explains the variation of the dependent variable (red spruce). This procedure is done in an iterative fashion, whereby the factor that captures the most variation is selected first. The variation explained by the selected factor is removed before the remaining factors are evaluated for entry (or removal). The stepwise analysis continues until the critical P level for parameter entry is reached, which was set at 0.0001. The resultant equation produces what are called "logits," which in turn are converted to probabilities using the following equation:

Red spruce probability = $e^x / (1 + e^x)$,
where e = natural logarithm, x = red spruce logits

The probability of red spruce occurrence was calculated at each point and displayed in raster format (500 x 500 m grid cells) by probability class (0-0.1, 0.1-0.25, 0.25-0.50, >0.50).

RESULTS

Locations harboring red spruce differed in many environmental aspects from those without spruce (Table 2). The most conspicuous difference was elevation, with red spruce heavily skewed towards higher altitudes (Fig. 4a). Red spruce distribution was largely confined to elevations above 900 m (mean = 1,171 m), as opposed to 803 m for nonspruce locations. Several climatic variables were strongly correlated with elevation (Table 3) and, in turn, also displayed significant differences between sites with and without red spruce. The number of growing degree days and mean annual temperatures were generally lower for red spruce sites (Figs. 4b and 4c), whereas the number of frost days and precipitation were higher (Figs. 4d and 5a). Red spruce was associated with sites having <4,000 growing degree days, >140 frost days, mean annual temperatures ≤8 °C, and mean annual precipitation ≥140 cm. Red spruce's propensity for wetness was reflected in its preference for soils with shallow fragipans (a soil horizon that restricts water percolation), high water tables, inherently poorer drainage (Fig. 5b), and higher available water capacities (Table 2). This preference is further reinforced by red spruce's increased frequency on less steep slopes (slower runoff; greater water infiltration) compared to non-spruce sites (Fig. 5c). Red spruce lived up to its reputation as an acidophile by occurring more frequently on sites that had lower pHs relative to nonspruce locations (Fig. 5d).

Since red spruce was represented by binomial (presence/absence) rather than continuous data, stepwise logistic regression in SAS was used for predictive modeling. All 20 environmental "predictor" variables were used in the initial run (Table 1), but the resultant analysis was greatly restricted by the limited number of observations associated with percent sand, percent silt, and percent clay data (29,608 points). Since these factors explained a very small amount of variation in the resultant regression equation, a second run was performed after their removal, greatly increasing the number of observations (45,177) and thus improving the analysis. Nine predictor variables were placed in the final equation before the variable-entry cutoff was met (Table 4). No variables were removed during the stepwise procedure. The vast amount of variation of red spruce was explained by the first parameter entered, which was elevation (ELEV)

Table 2.—Descriptive statistics of variables significantly linked to red spruce occurrence based on Analysis of Variance (ANOVA)[a].

Factor	No. of points without spruce	No. of points with spruce	Mean of points without spruce[b]	Mean of points with spruce[b]	ANOVA F-Value
Elevation	58,574	1,540	803	1,171	4,542
Growing Degree Days	58,266	1,541	3,732	3,169	4,135
Mean Annual Temperature	58,266	1,541	8.8	6.8	4,067
# of Frost Days	58,266	1,541	146	163	3,196
Mean Annual Precipitation	58,266	1,541	131	148	1,539
Depth to Fragipan	58,657	1,541	187	158	671
Depth to Water Table	58,657	1,541	179	143	622
Drainage Class	57,456	1,468	3.2	3.6	615
% Slope	58,574	1,540	27	19	370
pH	57,418	1,466	4.9	4.6	263
Available Water Capacity	45,036	1,400	0.22	0.31	242
Organic Matter	57,512	1,496	30	22	96
Depth to Paralithic	58,657	1,541	153	167	73
% Silt	28,864	744	49	45	59
% Sand	28,864	744	35	38	34
Bulk Density	57,239	1,344	0.74	0.80	10
Depth to Lithic	58,539	1,536	160	164	8

[a] All listed variables were significant at $P < 0.01$.

[b] Units listed in Table 1.

Nonsignificant variables: Cation exchange capacity, % clay, and transformed aspect.

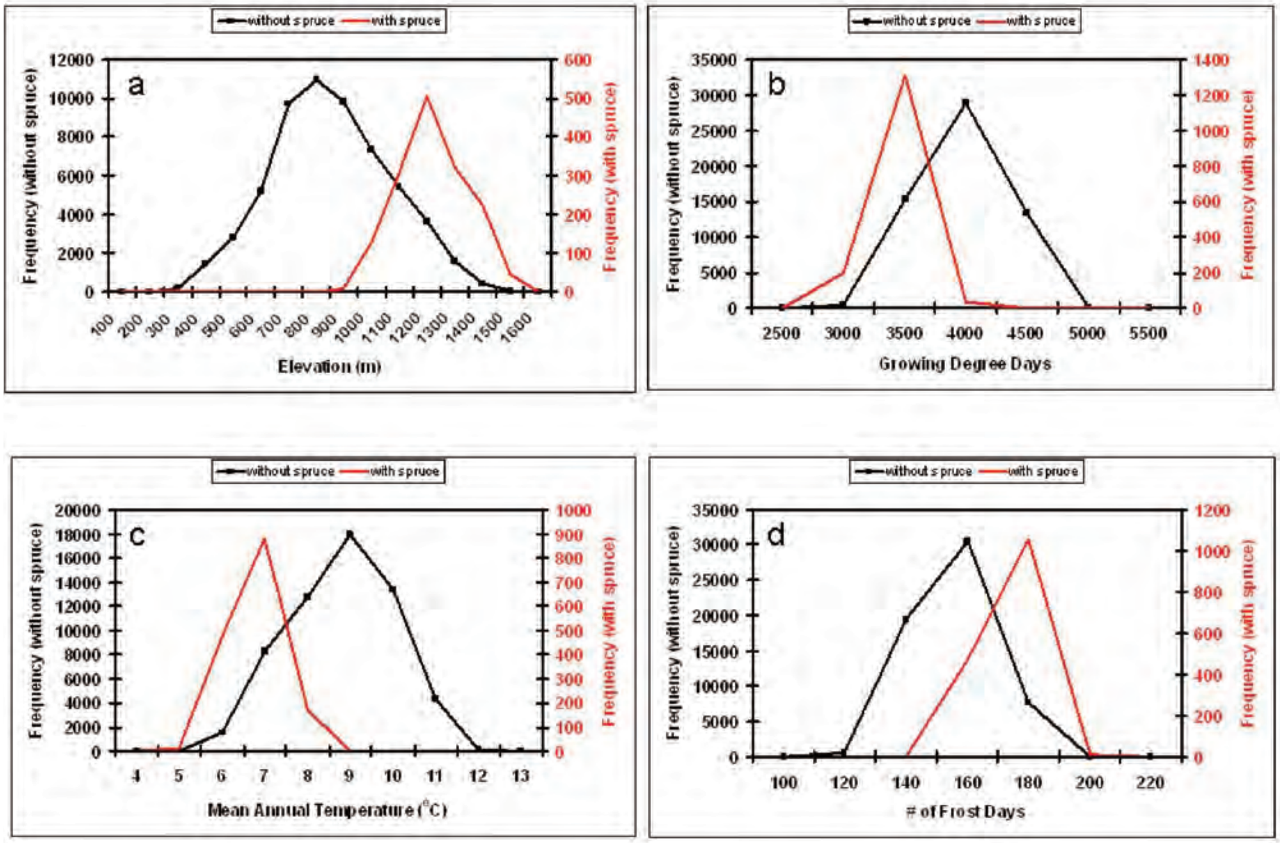

Figure 4.—Frequency distributions of elevation (a), growing degree days (b), mean annual temperature (c), and number of frost days (d) for spruce and non-spruce sites. See Table 1 for variable descriptions.

Table 3.—Correlation analysis of red spruce occurrence and 20 environmental and climatic variables. Highly correlated variables (≥ 0.80; ≤ -0.80) are highlighted in yellow.

Factor	Spruce	MAT	GDD	FROST	MAP	ASP	SLOP	ELEV	pH	CEC	AWC	BULK	OM	CLAY	SAND	SILT	DRAIN	LITH	FRAG	PARA
Spruce	1.00																			
MAT	-0.25	1.00																		
GDD	-0.25	0.97	1.00																	
FROST	0.23	-0.94	-0.97	1.00																
MAP	0.16	-0.60	-0.60	0.49	1.00															
ASP	0.00	-0.01	-0.01	0.01	-0.01	1.00														
SLOP	-0.08	0.05	0.04	-0.04	0.05	0.05	1.00													
ELEV	0.27	-0.88	-0.90	0.84	0.54	-0.01	-0.03	1.00												
pH	-0.07	0.21	0.22	-0.24	-0.04	0.01	-0.03	-0.30	1.00											
CEC	0.01	0.15	0.16	-0.22	0.15	-0.02	0.12	0.02	-0.40	1.00										
AWC	0.07	-0.19	-0.20	0.27	0.04	-0.01	0.07	0.26	-0.49	0.67	1.00									
BULK	0.01	-0.12	-0.13	0.20	-0.13	0.03	-0.12	-0.07	0.51	-0.97	-0.54	1.00								
OM	-0.04	0.24	0.26	-0.36	0.16	-0.02	0.11	-0.07	-0.26	0.89	0.19	-0.91	1.00							
CLAY	0.00	-0.12	-0.11	0.09	0.21	-0.02	0.03	0.08	0.06	0.15	0.56	-0.08	0.15	1.00						
SAND	0.03	-0.04	-0.05	0.05	-0.05	0.03	0.02	0.06	-0.14	-0.17	-0.50	-0.02	-0.14	-0.59	1.00					
SILT	-0.04	0.11	0.12	-0.11	-0.01	-0.02	-0.02	-0.11	0.19	0.18	0.43	0.08	0.12	0.41	-0.95	1.00				
DRAIN	0.10	-0.11	-0.10	0.08	0.11	-0.03	-0.24	0.05	0.11	-0.14	-0.10	0.16	-0.10	0.26	-0.32	0.27	1.00			
LITHIC	0.01	-0.15	-0.16	0.18	0.03	-0.03	-0.08	0.11	-0.32	-0.04	0.20	-0.02	-0.13	-0.05	-0.30	0.30	0.16	1.00		
FRAG	-0.11	0.10	0.10	-0.07	-0.15	0.04	0.16	-0.05	0.00	0.05	0.08	-0.05	0.01	-0.14	0.11	-0.06	-0.52	-0.24	1.00	
PARA	0.03	0.10	0.11	-0.16	0.11	-0.01	-0.13	-0.12	0.38	0.04	-0.31	0.01	0.21	-0.06	0.38	-0.47	0.27	-0.46	-0.28	1.00

Spruce = red spruce occurrence, MAT = Mean Annual Temperature, GDD = Growing Degree Days, FROST = No. of Frost Days, MAP = Mean Annual Precipitation, ASP = Transformed Aspect, SLOP = % Slope, ELEV = Elevation, pH = Soil pH, CEC = Cation Exchange Capacity, AWC = Available Water Capacity, BULK = Bulk Density, OM = Organic Matter, CLAY = % Soil Clay, SAND = % Soil Sand, SILT = % Soil Silt, DRAIN = Soil Drainage Class (1 = excessively drained to 7 = very poorly drained), LITH = Depth to Lithic, FRAG = Depth to Fragipan, PARA = Depth to Paralithic.

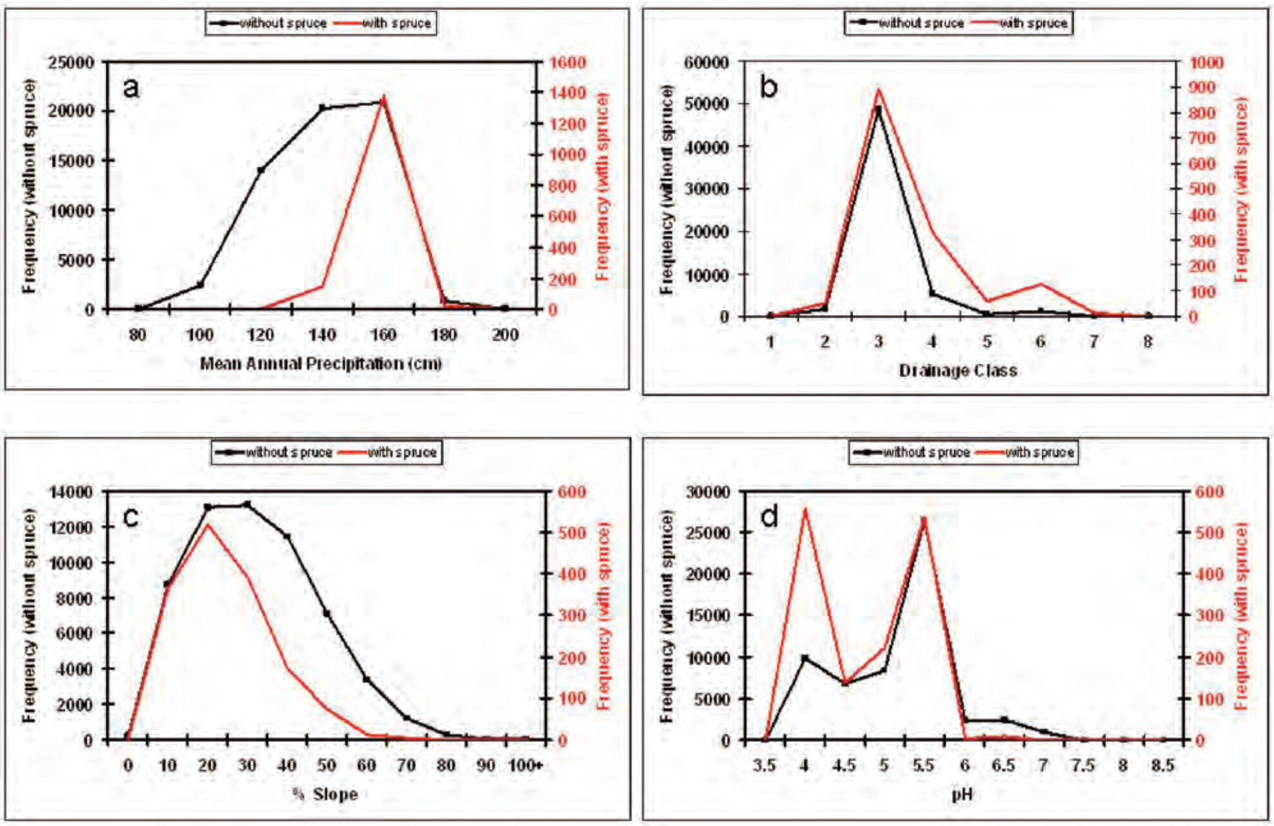

Figure 5.—Frequency distributions of mean annual precipitation (a), drainage class (b), percent slope (c), and soil pH (d) for spruce and non-spruce sites. See Table 1 for variable descriptions.

(chi-square score = 2,830). There was a marked drop in the amount of variation explained by the second variable entry of water table depth (WATER) (chi-square score = 496), followed by mean annual precipitation (MAP) (177), and growing degree days (GDD) (107). Although meeting the variable-entry criterion (thus being significant additions to the equation), the remaining factors explained only small amounts of variation (Table 4).

Trade-offs had to be weighed when selecting a regression equation for mapping as each raster cell (the basis of the map) requires data from all predictor variables to calculate a probability. As the number of variables increased, the number of cells by which a probability could be calculated dropped due to missing input values. Considering this constraint, we ultimately chose a four-variable equation, which explained most of the variation in red spruce with a minimum number of variables. The selected equation to compute and map red spruce probability (Fig. 6) was:

$$\text{Probability of red spruce} = -4.6199 + 0.00513(\text{ELEV}) - 0.00622(\text{WATER}) + 0.0455(\text{MAP}) - 0.00288(\text{GDD}),$$

Visual inspection of the resultant probability map and the base red spruce layer revealed a high level of correspondence (Fig. 7). Our probability map compared favorably to Menzel and others' (2006a) predicted Virginia northern flying squirrel habitat, especially at the >75 percent probability class, and Dillard et al. (2008) predicted occupancy for Cheat Mountain salamander (*Plethodon nettingi*).

Table 4.—The sequential entry of environmental variables predicting red spruce occurrence (dependent variable) based on stepwise logistic regression (P-value for variable entry = 0.0001). The amount of variation explained by each predictor variable is given by the chi-square score.

Step	Variable Entered	Chi-Square Score
1	Elevation	2,829.6
2	Depth to water table	495.8
3	Mean annual precipitation	177.4
4	Growing degree days	107.2
5	% Slope	66.5
6	Number of frost days	34.7
7	Depth to lithic	25.2
8	Available water capacity	43.5
9	Mean air temperature	19.9

Based on our predicted values, three large areas noticeably lacking red spruce occurred along the periphery of red spruce's mapped distribution (see inset maps of Figure 7). These areas were: (a) the mountainous areas around the Kumbrabow State Forest in southern Randolph County, (b) the Cabin Mountain escarpment and Stony River Valley, and (c) the highlands of northern Greenbrier County. These are likely areas of past red spruce occurrence and represent prime areas for future red spruce restoration efforts.

DISCUSSION

The rich array of plant life is due, in part, to the many environmental gradients that span the Earth (Whittaker 1956, 1967). In areas where environmental gradients lie in different directions, geospatial analyses can often successfully isolate the main factors driving vegetation patterns and species distribution. However, where environmental gradients tightly parallel one another, it may be difficult to disentangle and rank factors according to their influence on vegetation (Nowacki and Abrams 1992). This "confounding" is indeed the case in east-central West Virginia, where climatic, geologic, and edaphic gradients tend to align themselves across the rugged terrain, thus all potentially contributing to the presence of vegetation zones (Brooks 1911, Core 1950, Thomas-Van Gundy et al. 2007).

In mountainous regions, elevation is often used as the primary backdrop to analyze, identify, and describe an array of important ecological relationships (Bormann et al. 1970, White and Cogbill 1992). In this respect, elevation is a multifaceted factor (or "complex gradient" per Whittaker 1967) that embodies many interrelated variables, especially those associated with how energy and moisture are captured and processed. From this perspective, it was not surprising that elevation was found to be most explanatory of red spruce occurrence, both through analysis of variation (Table 2) and stepwise logistic regression (first variable selected; Table 4). A strong correlation found between elevation and climatic factors (Table 3) seems to confirm Siccama's (1974) contention that it is climate, as expressed through elevation,

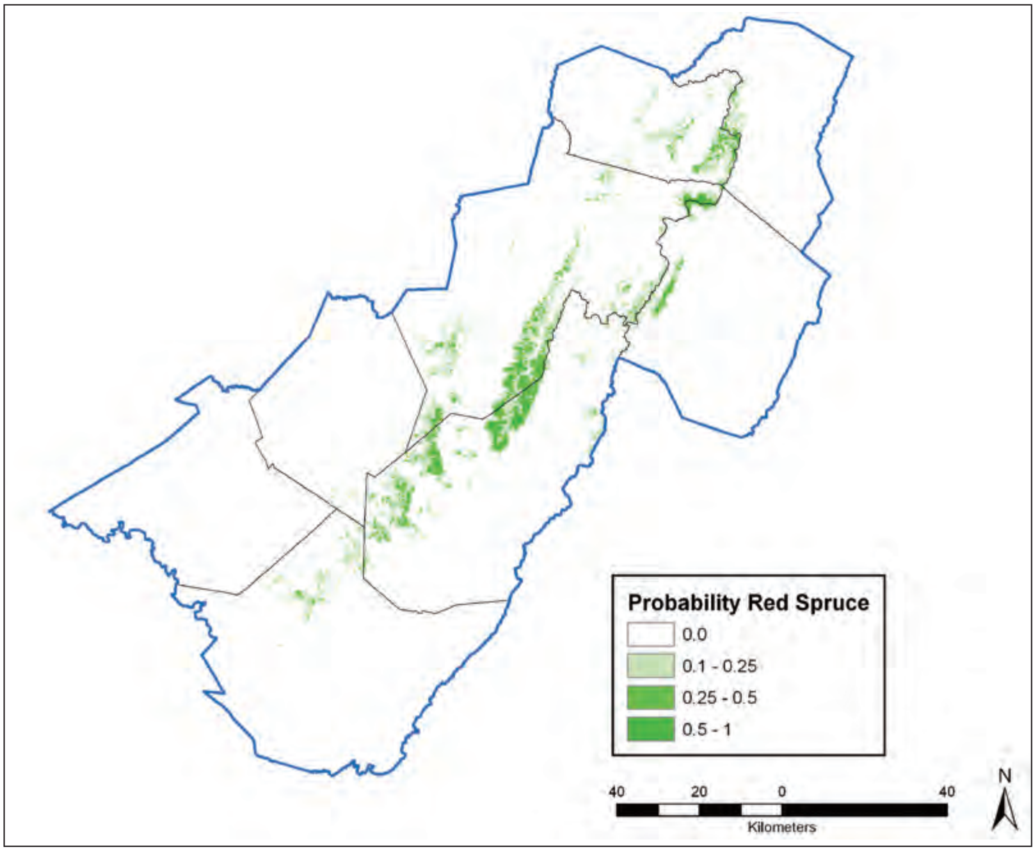

Figure 6.—Probability classes of red spruce occurrence based on the top four factors of stepwise logistical regression.

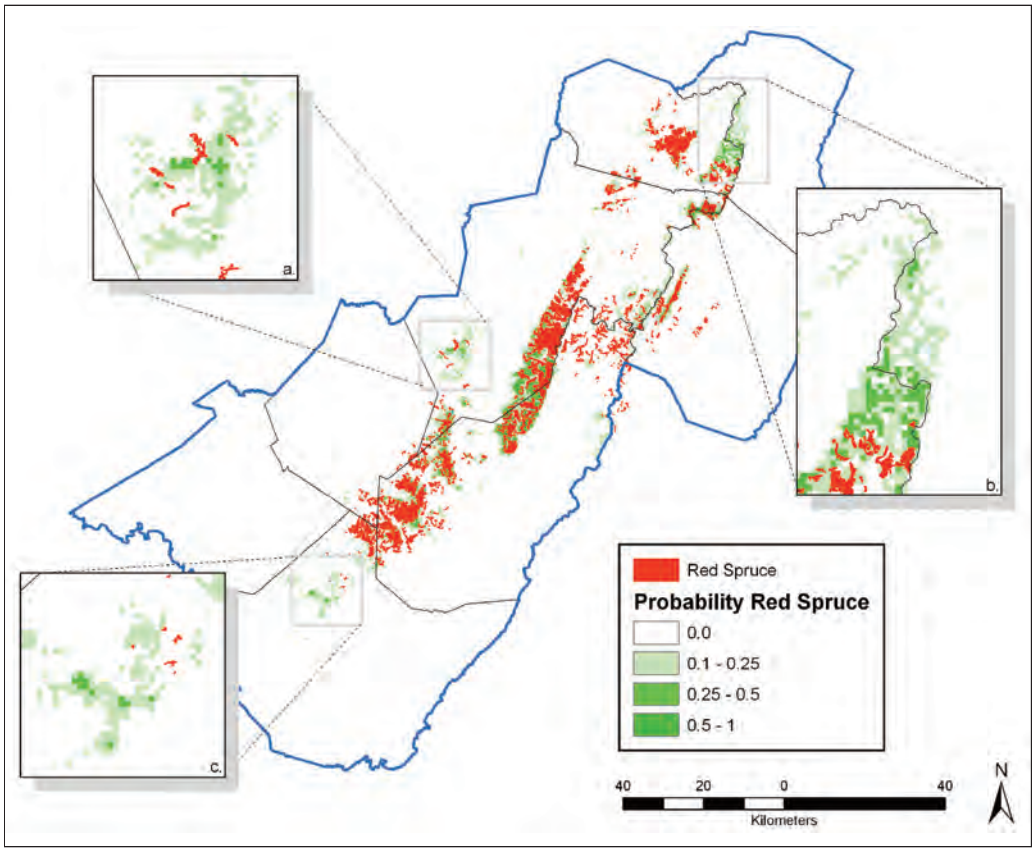

Figure 7.—Actual distribution of red spruce superimposed on probability map. The three inset boxes represent areas of high red spruce restoration potential based on the predictive model.

which is the principal driver of vegetation distribution. According to Siccama (1974), the change from deciduous to conifer dominance along mountain flanks corresponds to marked decline in frost-free (growing) season, increased contact with clouds and associated moisture from fog drip, and increased incidence of rime icing and hoar frost.

Red spruce was found at elevations over 900 m in West Virginia, which corresponds with other studies (Core 1950, Allard and Leonard 1952, Stephenson and Clovis 1983) and projected minimum elevations for the state (Cogbill and White 1991). Here, cool temperatures, short growing seasons, and persistently wet and cloudy conditions prevail. Snowfall may also be an important determinant of red spruce occurrence, especially in the Southern Appalachians (Nowacki et al. 2010). Pielke (1981) postulated that the minimum elevation for red spruce follows a 20 °C mean July temperature isoline, whereas Cogbill and White (1991) found that ecotones between spruce-fir and adjacent lower forests correspond to the 17 °C mean July temperature across the full extent of the Appalachians. Using the same logic, we found that the lower elevation of red spruce occurred at an 8 °C mean annual temperature (MAT) (Fig. 4c). However, this 8 °C MAT isoline may have limited application, as Cogbill and White (1991) found that lower spruce-fir boundaries do not correlate well with mean annual temperature across the Appalachians. Furthermore, attaching temperature limits to present-day red spruce occurrence may be universally flawed as distributions may have been substantially altered by past logging and fire events (Pielke 1981, Pyle and Schafale 1988). For instance, Hopkins (1899) reported presettlement red spruce occurring as low as 700 m. Hayes et al. (2007) found that the lower limits of spruce-fir forests are nearly 200 m higher today on landscapes where past logging took place.

Red spruce seemed to prosper under wet conditions given its positive association with precipitation. Red spruce's propensity for wetness was further reinforced by soil (shallow to restrictive fragipans, high water tables, poorer drainage, and increased available water capacity) and site attributes (more gentle slopes) (Table 2). These wet conditions indicate the perudic moisture regime of soil taxonomy, which may in turn serve as a good predictor of red spruce sites (Jason Teets, Natural Resources Conservation Service, pers. comm.). Alternatively, red spruce's current occurrence on wetter sites may be a mere reflection of land-use history—essentially representing refugia from past fires and/or pasture conversion, which greatly affected much of the West Virginia landscape (Hopkins 1899). Indeed, red spruce has a wider ecological amplitude (i.e., occurs on a greater array of sites) in the Northeast than in the fire-ravaged Southern Appalachians (White and Cogbill 1992, Fraver et al. 2009, Nowacki et al. 2010). In and around Canaan Valley, WV, spruce grew on a greater diversity of sites in presettlement times, from wet valley floors to high, steep, well-drained rocky ridges (Allard and Leonard 1952). The deleterious effects of fire on red spruce are well established in the literature (Brooks 1911, Korstian 1937, Mincker 1945, Pyle and Schafale 1988, Hayes et al. 2007) and need to be considered when using current distributional data as model input. For instance, red spruce's occurrence on less-steep terrain relative to non-spruce locations may simply reflect severe past burns on steep side slopes, thus relegating red spruce to more gently sloped mountain tops and upper shoulders. Pyle and Schafale (1988) mention this very phenomenon in the Black Mountains of North Carolina.

Red spruce's acidophilic tendencies were corroborated by its preference for lower-pH soils (Table 2). Red spruce promotes acidic conditions through its production of acid-rich foliage. These organic acids, combined with spruce needle castings, have a distinct effect on soils. Together they foster the formation of a thick organic surface horizon called the mor layer. Moreover, as organic acids percolate through mineral soils in these well-watered environments, they often leach a zone immediately beneath the mor layer of humus, iron, and aluminum (called the albic or E horizon) and redeposit these materials at lower depths (representing Bh, Bs, or Bhs horizons). Thus, the presence of thick organic surfaces and spodic properties (E and Bh/Bs/Bhs horizons) may be indicative of red spruce sites (Bormann et al. 1970).

Surprisingly, yet consistent with a larger assessment spanning the East (Nowacki et al. 2010), aspect was not significantly related to red spruce occurrence. This finding lends credence to the general observation that aspect may not be as important as previously thought (Leak 1982, White and Cogbill 1992, Menzel et al. 2006a, Hayes et al. 2007). One would expect aspect differences to alter red spruce distributions in a predictable manner (i.e., fostering red spruce at lower elevations on cool northeast-facing slopes and elevating it on warm southwest-facing slopes). Apparently, the high precipitation and perpetual cloudiness offset the expected effects of aspect on temperature and insolation (White and Cogbill 1992). The tendency for afternoon clouds and rain due to orographic effects may temper radiational heating of southwestern slopes. Moreover, physical site conditions (e.g., depth to bedrock, topographic position, soil texture) can easily overshadow the influence of aspect (Leak 1982). Hayes and others (2007) determined that aspect did not strongly influence the presettlement distribution of spruce-fir in the Great Smoky Mountains National Park in Tennessee and North Carolina. However, where logging took place on south-facing aspects, the lower limits of spruce-fir retracted by 122 m. This retraction was likely due to the desiccation of seedbeds through exposure, thus thwarting red spruce regeneration.

Red spruce has been greatly affected by past logging and fire events throughout the Southern Appalachians (Brooks 1911, Korstian 1937, Mincker 1945, Pyle and Schafale 1988, Stephenson 1993). There is ample evidence that post-disturbance soil and site conditions became warmer and drier—a situation that greatly discourages red spruce regeneration (Allard and Leonard 1952, Fortney 1993). Unfortunately, only approximations of anthropogenic impacts can be made as the true extent of presettlement red spruce is unknown in West Virginia. By any account, the reduction of the red spruce resource has been extreme, ranging from 50 to 95 percent depending on data source and time period (Table 5).

Concerns over the wanton destruction and range contraction of the red spruce resource were expressed early (Hopkins 1899). Initial efforts to restore red spruce over its former range date back to the 1920s and 1930s (Minckler 1940, 1945). Interest in red spruce restoration has resurged (Schuler et al. 2002, Rentch et al. 2007), driven in part by increased awareness of threatened and endangered species and their habitat needs (e.g., Cheat Mountain salamander, Virginia northern flying squirrel [*Glaucomys sabrinus fuscus*], delisted in 2008) (Cohen 1994, Mitchell et al. 1999, Ford et al. 2004, Menzel et al. 2006ab, Pauley 2008, Dillard et al. 2008). Recent favorable news that red spruce is recovering naturally (Koon 2004) and that restoration also can be facilitated through silvicultural practices (Hornbeck and Kochenderfer 1998) further buoys enthusiasm for restoration efforts.

In support of impending restoration efforts, a probabilistic model of red spruce occurrence has been tendered for consideration (Fig. 6). The congruence of our map with Menzel et al. (2006a) independent effort that predicted Virginia northern flying squirrel habitat strongly validates

Table 5.—Timeline comparison of estimated red spruce area in West Virginia between presettlement and subsequent periods.

Presettlement red spruce acreage	Red spruce acreage at given year		Percent reduction	Source[a]
607,000 hectares	304,000 hectares	1865	50%	Hopkins 1899
607,000 hectares	91,000 hectares	1895	85%	Hopkins 1899
607,000 hectares	91,000 hectares	1900	85%	West Virginia Board of Agriculture 1900 [Lewis 1998]
190,000 hectares	77,000 hectares	1910	59%	Brooks 1911 [Clarkson 1964, Core 1950]
405,000 hectares	20,000 hectares	1937	95%	Korstian 1937
200,100 hectares	24,000 acres	1975	88%	Adams and Stephenson 1989
180,000 acres	24,300 hectares	1980	87%	Pielke 1981

[a] Literature referring to these areas in brackets.

both models. Dillard et al. (2008) predicted occupancy maps of the conifer-dependent Cheat Mountain salamander provide further support of our work. Altogether these predictive models provide a scientific basis to locate, plan, and execute red spruce restoration activities.

Some of the greatest opportunities for restoration may exist at locations where red spruce has a high predicted probability but is currently sparse or altogether absent (Fig. 7). For instance, the highlands encompassing the Kumbrabow State Forest and the MeadWestvaco Ecosystem Research Forest may be a prime area (Fig. 7a). Here, red spruce occurs in scattered stands, some of which harbor the vulnerable Virginia northern flying squirrel (Menzel et al. (2006b). As suggested by Menzel et al.(2006b), expanding and reconnecting these small, disjunct patches of red spruce may prove beneficial, thus improving habitat conditions for the Virginia northern flying squirrel and other conifer obligates.

Grand opportunities encircle Canaan Valley, especially from the Dolly Sods Scenic Area northward across the headwaters of the Stony River and the Cabin Mountain escarpment (Fig. 7b). Indeed, red spruce was prominent throughout this region prior to cutting (Allard and Leonard 1952). However, restoring red spruce to this landscape might prove extremely difficult as logging and past fires largely destroyed the deep humus layers, leaving behind rock-strewn surfaces (see photos of Allard and Leonard 1952) that greatly deter red spruce regeneration. Encouragingly, enough red spruce habitat remains on Cabin Mountain to still support Virginia northern flying squirrels (Ford et al. 2007). According to Fortney (1993), red spruce has been expanding downslope on the mountains rimming Canaan Valley since the 1940s.

Recovery and expansion of red spruce along its southern boundary in Greenbrier County also have promise (Fig. 7c). This area corresponds with the southern extent of Menzel et al. (2006a) modeled Virginia northern flying squirrel habitat. Ample opportunity exists here as ~13,560 ha of red spruce forests formerly existed in Greenbrier County in presettlement times (Brooks 1911, Clarkson 1964). However, much of this area lies in private ownership, which may limit restoration efforts without effective public outreach.

We consider our predictive map rather conservative since red spruce's original range was much more expansive, possibly occurring as low as 700 m in places (Hopkins 1899). Due to the inherent limitations of using a current red spruce stand map as input data, a certain degree of caution should be exercised when using our probabilistic map. Case in point is the Canaan Valley, home to some of the finest presettlement red spruce forests in the Appalachians (Allard and Leopard 1952, Fortney 1993). Here, our model generated low probabilities for red spruce (Fig. 7b). Clearly the potential for red spruce restoration within Canaan Valley is not captured by our model. Moreover, the model seems to greatly underestimate spruce restoration potential at lower elevations, especially in northern Pocahontas County, southeastern Randolph County, and southwestern Pendleton County (Kent Karriker, U.S. Forest Service, pers. comm.).

In areas where red spruce was formerly known to occur, perhaps the only remaining legacy resides in soils (Stephanie Connolly, U.S. Forest Service, pers. comm.). Historically growing under cool, moist, and acidic conditions, red spruce left distinct signatures in the mor layer and in the development of spodic horizons (E and Bh/Bs/Bhs horizons diagnostic of Spodosols) or soils with spodic materials (Inceptisols). The endurance of these signatures depends on starting conditions (e.g., thicknesses), landscape position, and subsequent disturbance events (cutting, burning, and suite of replacement species). The maintenance of thick O horizons can be quite ephemeral as post-logging burning was widespread and intense, effectively consuming many organic surfaces (Allard and Leopard 1952). As such, their use as red spruce indicators may be limited, being often relegated to wetter portions of the landscape that did not burn. The presence of spodic horizons (or soils with spodic materials) is probably of greater reliability due to their depth (less affected by surface disturbances) and inherent longevity.

Optimally, information on presettlement forest conditions should be used for building a predictive model but, unfortunately, this information is scarce in West Virginia (Stephenson 1993). Moreover, most existing information is nonquantitative, in the form of generalized accounts and anecdotal observations from early explorers and settlers.

Therefore area estimates of presettlement red spruce vary over a wide range (Table 5). Although witness-tree data probably represent the best, most quantitative information on presettlement vegetation, there is a paucity of witness trees in West Virginia, especially at higher elevations (Strahler 1972, Abrams and McCay 1996). As such, data layers depicting existing distributions are probably superior in the end, especially if climate change has occurred over the past century. In that case, models based on current distributions may provide more reliable and realistic predictions for red spruce success.

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PREDICTING CLIMATE CHANGE EXTIRPATION RISK FOR CENTRAL AND SOUTHERN APPALACHIAN FOREST TREE SPECIES

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Abstract.—Climate change will likely pose a severe threat to the viability of certain forest tree species, which will be forced either to adapt to new conditions or to shift to more favorable environments if they are to survive. Several forest tree species of the central and southern Appalachians may be at particular risk, since they occur in limited high-elevation ranges and/or are currently threatened by nonnative insects and diseases. We are beginning an assessment of potential climate change impacts on more than 100 North American forest tree species, using the innovative Multivariate Spatio-Temporal Clustering (MSTC) technique. Combining aspects of traditional geographical information systems and statistical clustering techniques, MSTC statistically predicts environmental niche envelopes to forecast species' geographic ranges under altered environmental conditions such as those expected under climate change. We outline the objectives of this project, present some preliminary results for central and southern Appalachian tree species, and discuss the need for assistance from fellow scientists in the development of this work.

INTRODUCTION

Climate change is expected to result in extensive ecological, social, and economic effects for the forests of the United States (Malmsheimer et al. 2008). Climate change probably will threaten the viability of certain forest tree species, which will be forced either to adapt to new conditions or to shift their ranges to more favorable environments. Animal and plant species, including trees, are already exhibiting changes in phenology and distribution in response to climate change (Parmesan and Yohe 2003, Woodall et al. 2009), and many species are expected to go extinct as their access to suitable habitat becomes more limited (Thomas et al. 2004). Forest tree species with already limited ranges may be at particular risk (Schwartz et al. 2006).

High-elevation species, including those whose distributions include the central and southern Appalachian Mountains, may be at elevated risk from climate change because of their tendency toward naturally small, isolated, and fragmented populations, which, in some cases, may result in lower genetic diversity and/or inter-population gene exchange (e.g., Potter et al. 2008b, Tang et al. 2008). Additionally, some high-elevation endemics may lack suitable habitat in which to move to match changes in climate, especially if changing climate conditions and inter-specific competition force these species to move their distributions toward higher elevations, which may not exist. Delcourt and Delcourt (1998), for example, predict that a 3 °C increase in the mean July temperature would raise climatically limited ecotones by ~480 m. This increase could result in the extinction of red spruce-Fraser fir forests in the southern Appalachians because these forests are already confined to the highest mountain elevations. The potential impacts of climate change on high-elevation species is of particular concern given the high biological diversity harbored by mountain systems, caused by the compression of climatic life zones and by small-scale habitat diversity (Koerner and Spehn 2002, Koerner and Ohsawa 2005).

Evolutionary biologists predict that plant species will respond in one of three ways to changes that push their current habitat out of their climatic tolerance limits: 1)

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adaptation, 2) migration (range shift), or 3) extirpation (Davis et al. 2005).

Although some evidence exists that trees have the capacity to evolve rapidly to new environmental conditions (Petit et al. 2004), adaptation via natural selection may be unlikely in many cases, given the long generation time for forest tree species (St. Clair and Howe 2007). Rehfeldt et al. (1999), for example, predict that tree adaptation to climate change would take 1 to 13 generations, or 100 to 1,000 years.

Tree species successfully migrated long distances during the climate changes of the Pleistocene, but may not be able to match climate shifts anticipated in the near future because they are expected to occur much more rapidly (Davis and Shaw 2001). Even when tree species possess propagule dispersal mechanisms that allow them to shift their ranges, their effective migration may be impeded by forest fragmentation (Opdam and Wascher 2004), they may experience inbreeding-reduced genetic diversity as a result of founder effects (Petit et al. 2004), and their genetically important "trailing edge" populations may be extirpated (Hampe and Petit 2005). It is worth noting that some of the most genetically distinct Appalachian populations of at least one forest tree species, eastern hemlock (*Tsuga canadensis* [L.] Carr.), are located near the very southern end of the range (Potter et al. 2008a).

Forest tree species or populations that are not able to shift their distribution or adapt in response to changing climatic conditions may instead face extinction or local extirpation. This possibility may be a concern particularly for species that have narrow habitat requirements, are located exclusively at high elevations, and/or are not able to disperse their propagules effectively across long distances. Even if not extirpated outright, populations of these and other species could experience significant inbreeding, genetic drift, and decreased genetic variation as a result of reduced population size. Such populations may then become more susceptible to mortality caused both by nonnative pests and pathogens and by the environmental pressures associated with climate change. This susceptibility could generate a cycle of mortality, loss of genetic variation, and inability to adapt to change that could ultimately result in population extirpation (Fig. 1).

Within the central and southern Appalachians, three forest tree taxa likely to be at greatest risk of extinction as a result of climate change are Fraser fir (*Abies fraseri* [Pursh] Poir.), intermediate balsam fir (*Abies balsamea* [L.] Mill. var. *phanerolepis* Fern.), and Carolina hemlock (*Tsuga caroliniana* Engelm.). All three are limited to small, high-elevation populations, and are under siege from exotic pests: the balsam woolly adelgid (*Adelges piceae* Ratz.) in the case of Fraser fir (Dull et al. 1988) and intermediate balsam fir (Bross-Fregonara 2002), and hemlock woolly adelgid (*Adelges tsugae* Annand) in the case of Carolina hemlock (Jetton et al. 2008). Other species, such as Table Mountain pine (*Pinus pungens* Lamb.), red spruce (*Picea rubens* Sarg.), and striped maple (*Acer pensylvanicum* L.) are less likely to experience range-wide extinction, but could have their southern and central Appalachian populations eliminated as a result of changing climate conditions. These populations may contain unique genotypes resulting from long-term biogeographical processes and from selection pressures that may be different from those experienced by these species in their more northerly populations.

We are in the early stages of a large-scale assessment of the risk posed by climate change to the genetic integrity of many North American species. Central to this project is the application of the innovative Multivariate Spatio-Temporal Clustering (MSTC) technique (Hargrove and Hoffman 2005). We are using MSTC to predict the future location and quality of habitat for tree species and, along with consideration of species' biological attributes, will assess whether range-shifting tree species might be able to track appropriate environmental conditions over time and avoid the loss of extensive genetic variation. We here present preliminary results for four southern and central Appalachian forest tree species.

METHODS

The U.S. Department of Agriculture Forest Service Forest Health Monitoring (FHM) program recently identified climate change as a priority area for funding projects through its Evaluation Monitoring grant program. Additionally, attendees at the annual FHM Working Group meeting in 2008 approved a resolution calling for a baseline assessment of the climate change-associated risks of genetic degradation, local extirpation, or species-wide extinction of North American tree species.

That assessment will address three central questions: 1) Given the current distributions of forest tree species, where will the appropriate environmental conditions exist for each species in 2050 and 2100 under two climate change scenarios? 2) What portions of tree species' ranges are most at risk of extirpation because of their distance to expected future habitat, and how likely will they be to traverse that distance given existing forest fragmentation en route? 3) What is the risk of genetic degradation to populations of each tree species, given what we know about the biology of these species and the landscape of change they face?

Much innovative work has predicted the distribution of forest tree species under climate change (Iverson et al. 2004a, b; Rehfeldt et al. 2006; Schwartz et al. 2006). An assessment of the potential genetic impacts of climate change on forest tree species, however, requires a tool that:

- Can predict changes in appropriate habitat for a large number of species (in this case, approximately 200 across all regions of North America).
- Allows for flexible data inputs on the current locations for forest tree species occurrences, including for rare species that do not occur in the USDA Forest Service Forest Inventory and Analysis (FIA) database.
- Generates relatively high-resolution results applicable at the population level.
- Can predict acceptable habitat globally; this capability has the advantage of determining potential suitable habitat for U.S. species in Canada and Mexico, for example, and also allows for investigating any species worldwide for which we have good location information.
- Incorporates the pertinent environmental variables that determine plant distributions.

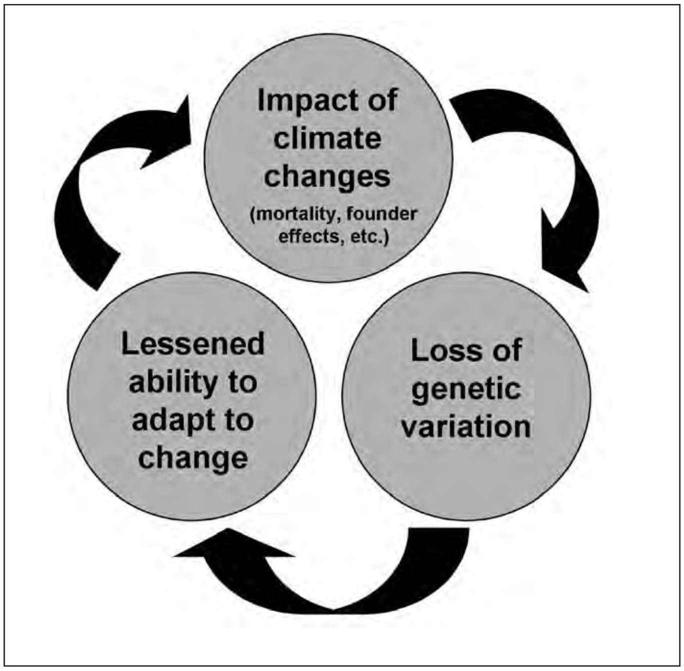

Figure 1.—The potential feedback cycle in which the impacts of climate change result in the loss of genetic variation within declining forest tree populations, which may in turn decrease the ability of those populations to adapt to change. A lessened ability to adapt to change may, finally, magnify additional future impacts of climate change. Note that this cycle would apply to declining species, but that some species may benefit genetically from the effects of climate change.

The MSTC approach developed by Hargrove and Hoffman (2005) meets these requirements. MSTC applies aspects of traditional geographic information systems (GIS) and statistical clustering techniques to statistically predict species' environmental niche envelopes. This approach can be used to forecast a species' geographic range under altered environmental conditions such as those expected with global climate change (Hargrove and Hoffman 2003). Global in scope, it incorporates 16 spatial environmental variables (Table 1) and generates maps at a resolution of 4 km^2.

MSTC employs nonhierarchical clustering on the individual pixels in a digital map from a GIS to classify the cells into types or categories. The technique uses the standardized values of each environmental condition for every raster cell in the map as a set of coordinates that together specify a position for that raster cell in a data space having a dimension for each of the included environmental characteristics. Two raster cells from anywhere in the map with similar combinations of environmental characteristics will be located near each other in this data space. Their proximity and relative positions in the data space will quantitatively reflect their environmental similarities, allowing these cells to be classified into environmentally similar groups or "ecoregions" (Hargrove and Hoffman 2003, 2005). The MSTC process allows the user to determine the coarseness of the output maps, which display each 4 km^2 pixel within an "ecoregion" with other pixels possessing similar environmental conditions. The user can, in other words, choose whether the map contains many small ecoregions, each containing little environmental heterogeneity, or only a few ecoregions, each containing a relatively large amount of environmental heterogeneity. (Within a given map, each ecoregion contains roughly equal environmental heterogeneity; maps depicting coarser divisions contain greater heterogeneity within ecoregions than do maps depicting finer divisions.) The results presented here were generated using a fine division of the 4 km^2 pixels globally into 30,000 ecoregions.

Table 1.—Spatial environmental variables included in the Multivariate Spatio-Temporal Clustering (MSTC) analysis.

Category	Spatial environmental variable
Soil	
	Plant-available water capacity
	Bulk density of soil
	Kjeldahl soil nitrogen
	Organic matter in soil
Temperature	
	In the coldest quarter
	In the warmest quarter
	Diurnal temperature difference
	Biotemperature
	Solar insolation
Precipitation	
	In the driest quarter
	In the wettest quarter
	In the warmest quarter
	In the coldest quarter
	Ratio of precipitation to evapotranspiration
Topography	
	Compound topographic index (convexness or concavity)
Growing season	
	Length in integer months

For the first part of this assessment project, MSTC will predict the location and quality of habitat for at least 100 forest tree species under two climate change scenarios in 2050 and 2100 under the Hadley model and Parallel Climate Model, each under the A1 (higher-emissions) and B1 (lower-emissions) scenarios. Existing FIA data (USDA Forest Service 2009) will be used as training data for most species, providing the location of species and an "importance value" that represents the fitness of the species at each location. For rare tree species not well sampled by FIA, training data will come from other sources. These training data are used to determine the current environmental envelope or niche for each species by selecting the ecoregions containing two or more species occurrences using the FIA data. These current ecoregions are then compared to future ecoregions generated by MSTC under the various climate change scenarios; the future ecoregions most similar to current ecoregions in which the species of interest occurs therefore encompass the future areas with the closest fit to the current environmental niche for that species.

Although somewhat time-consuming in initial implementation, MSTC allows for the relatively rapid testing of many species, unlike the Regression Tree Analysis approaches often used to generate predictions of suitable habitat for tree species. Additionally, unlike Regression Tree Analyses, MSTC is a multivariate approach that includes all the variables simultaneously and that does not require imposing an importance order for the variables included. Finally, MSTC avoids the Regression Tree Analysis tendency to overfit models of suitable species habitat.

The primary products of this work will be an extensive number of large-scale, ~4 km^2 resolution maps for more than 100 North American tree species. These will be packaged and available to the public as part of a new online assessment of North American forest trees' genetic risk induced by climate change.

The current analysis reported here is limited to a handful of forest tree species present in the central and southern Appalachians. FIA occurrence data were used as the training data for three species: red spruce, mountain magnolia (*Magnolia fraseri* Walt.), and striped maple. For the larger species, red spruce and mountain magnolia, these data encompassed plots containing at least one tree greater than 10 inches diameter at breast height (d.b.h.) or 30 feet in height. For striped maple, a smaller species, the plots included were those containing a tree greater than 5 inches d.b.h. or 20 feet tall. Other, more appropriate species location data were used for the rare species included in the study, Fraser fir and Carolina hemlock.

We note that the 4 km^2 resolution of the analysis could miss some important microhabitats for certain tree species. However, the use of coarser resolution data was the tradeoff for being able to use the MSTC approach at a global level, which we believe is an important advantage of MSTC. The goal of the analysis is to be able to predict general areas of current and future habitat suitability, some of which may be unexpected. Other approaches could then be employed to investigate habitat suitability at a finer resolution.

For the second part of the project, MSTC will measure the straight-line Minimum Required Migration (MRM) distance from each 4 km^2 grid cell in each species' existing distribution to the nearest favorable future habitat. The greater this distance, the less likely that the species will be able to reach the nearest future refuge, and the more likely that the species will become locally extinct. Information on the locations of future refuges will be integrated with existing forest fragmentation data to quantify the quality of those refuges and to determine the amount of biotic "resistance" species are likely to encounter as their ranges shift toward those refuges.

During the third part of the project, we will work with forest geneticists and ecologists to assess the risk of genetic degradation, including the susceptibility of extinction in all or part of the current range, for several forest tree species. Revolving around a set of factors that could increase the risk of genetic degradation for a tree species or population (Table 2), this analysis will synthesize results from the first two parts of the project with existing knowledge about the biology and genetic diversity of each species. It will incorporate the MSTC climate envelope maps, the MRM distance maps, information about the biology of individual tree species, knowledge about extrinsic factors impacting those tree species (including forest fragmentation, pest or pathogen infestation, or over-exploitation), and our understanding of population genetic processes.

RESULTS AND DISCUSSION

To demonstrate the utility of this work to predicting the location of appropriate habitat for high-elevation species over time, we generated climate change prediction maps for four species based on the Hadley A1 (higher-emissions) scenario in 2050 and 2100: Carolina hemlock (Fig. 2), mountain magnolia (Fig. 3), red spruce (Fig. 4), and Fraser fir (Fig. 5). Within each figure, the green dots represent the species' occurrence locations used as training points in developing the maps. The red areas are regions environmentally identical to locations in which the species currently occurs, while darker gray shades indicate locations that are increasingly similar to the locations in which the species occurs. It is important to note that darker areas in the map do not necessarily represent suitable habitat, but rather are areas similar to habitat that we know to be suitable based on known existing species locations – the red areas that match current known occurrence locations of the species in question. This approach allows map users to determine the appropriate thresholds of similarity when assessing future suitable habitat for a given species.

The preliminary results presented here suggest that, at least under the Hadley A1 scenario, suitable habitat for several forest tree species of the central and southern Appalachian Mountains could expand somewhat by 2050, and then contract by 2100. For example, MSTC predicts that Carolina hemlock will see a dramatic expansion of matching (red) habitat to the east and west of the Appalachian core by 2050, followed by a contraction to fairly isolated higher-elevation patches by 2100 (Fig. 2). Mountain magnolia (Fig. 3), meanwhile, may have additional matching habitat to the southeast and northeast by 2050, but much of this habitat, as well as currently matching habitat to the west and north, may become less suitable by 2100. Red spruce (Fig. 4) may see a slight advance of matching habitat in the central and southern Appalachians by 2050, but some of this habitat disappears by 2100. It would be difficult to determine specifically which changing environmental conditions might

Table 2.—Factors, both intrinsic and extrinsic to a species or population of forest trees, that increase its risk of extinction, extirpation, or genetic degradation.

Intrinsic factors	Extrinsic factors
Limited range	Extensive fragmentation
Small/disjunct populations	Pest/pathogen infestation
Limited to high elevations	Large shift of range with climate change
Long lifespan	Exploitation
Long time to reproduction	Exposure to atmospheric deposition
Low fecundity	Geographic dispersal barriers[a]
Physical habitat specialization	Anthropogenic dispersal barriers[a]
Limited seed/pollen dispersal	Exposure to sea-level rise[a,b]
Low species-wide genetic variation	
Late successional species	
Dependence on specific disturbance regime[a]	
Reliance on interspecific interactions[a]	
Sensitivity to temperature and precipitation change[a]	
Lack of phenological flexibility[a]	

[a] From Young et al. (2009).

[b] Not applicable to the Appalachian Mountains.

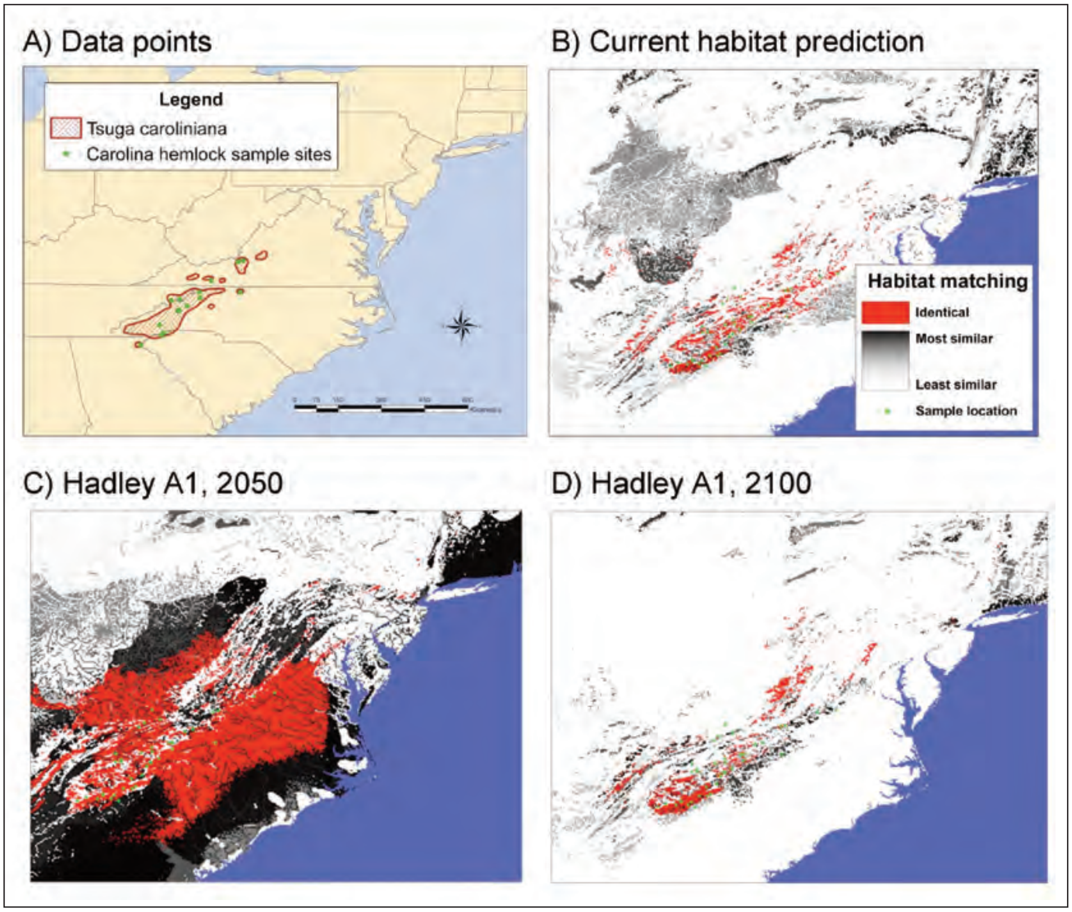

Figure 2.—Multivariate Spatio-Clustering predictions of current and future acceptable environmental conditions for Carolina hemlock. The coordinates of 15 known Carolina hemlock stands (the small green dots) were used along with FIA plot data as training data (A) to predict the location of currently acceptable habitat conditions (B), which was in turn used to predict the locations of acceptable environmental conditions in 2050 (C) and 2100 (D) using the Hadley A1 (higher-emissions) scenario.

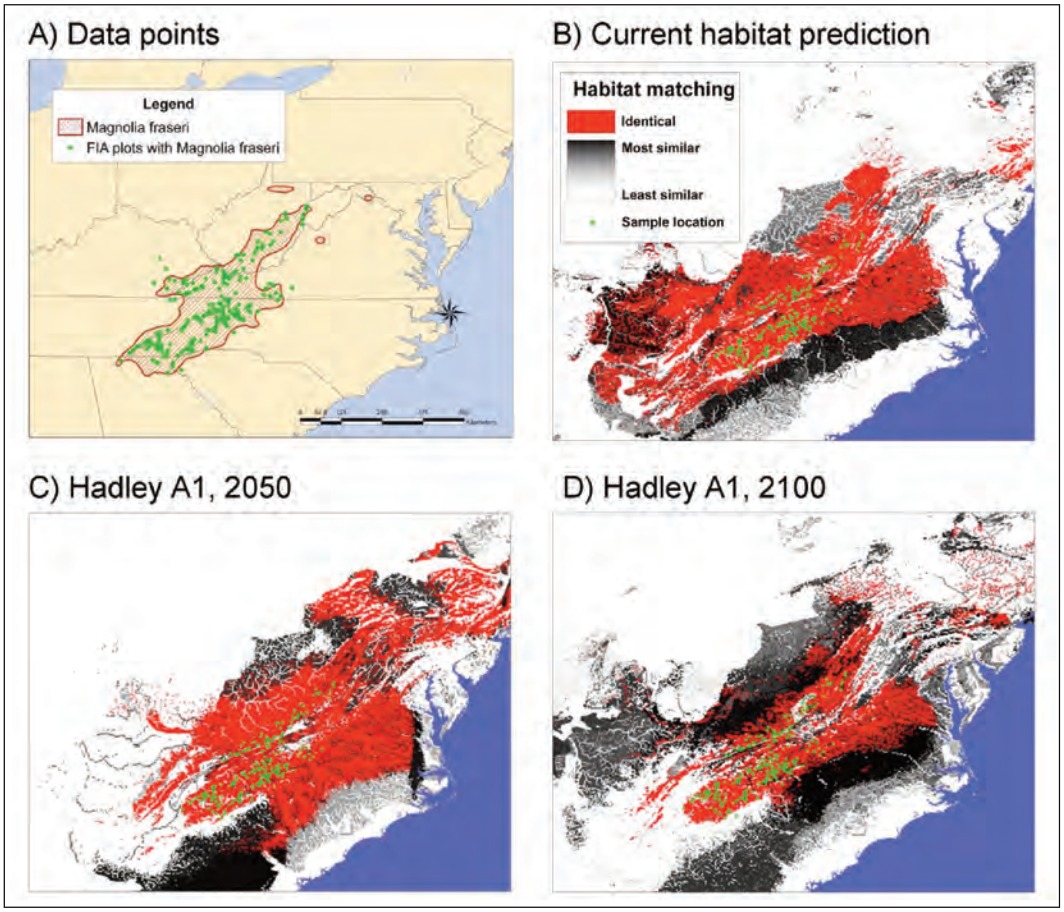

Figure 3.—Multivariate Spatio-Clustering predictions of current and future acceptable environmental conditions for mountain magnolia. The small green dots in all four subfigures depict the 562 Forest Inventory and Analysis plot locations that were used as training data (A) to predict the location of currently acceptable habitat conditions (B), which was in turn used to predict the locations of acceptable environmental conditions in 2050 (C) and 2100 (D) using the Hadley A1 (higher-emissions) scenario.

cause this pattern, but these results suggest that, in general, the climatic and edaphic factors expected to occur under this climate change scenario might result in larger areas of acceptable habitat for red spruce than currently exist.

Somewhat surprisingly, Fraser fir (Fig. 5) showed a pattern of suitable habitat contraction in 2050 and slight expansion into 2100, with the matching habitat at the later date similar in extent to the current predicted matching habitat.

It is important to reiterate here that we are not, in fact, modeling habitat, but rather using an empirical clustering approach to predict habitat suitability in the present and the future based on the environmental characteristics existing at known locations of individual tree species. We are confident that the results are accurately predicting suitable habitat given the environmental variables we are using and the resolution at which these data are available. We acknowledge that in some cases the resolution of the data (4 km^2) may result in missing some microhabitat niches that may be important for certain Appalachian species. In such cases, we believe the results are still useful because they allow for the identification of places where other, finer-resolution analyses could help identify locations for habitat protection, gene conservation efforts, translocations of trees from other locations, and other measures.

Additionally, we plan to use one or more measurements of how well a species is adapted at each location in which it occurs, such as basal area or importance value derived from the FIA data, to further identify not only those areas that match any current habitat, but also those that match the best current habitat. We can then be more confident (given data limitations) that our maps will identify locations with the best current and future habitat suitability.

The results of this work will be valuable for scientists and policymakers attempting to determine which forest tree species and populations, in the face of climate change, should be targeted 1) for monitoring efforts, including

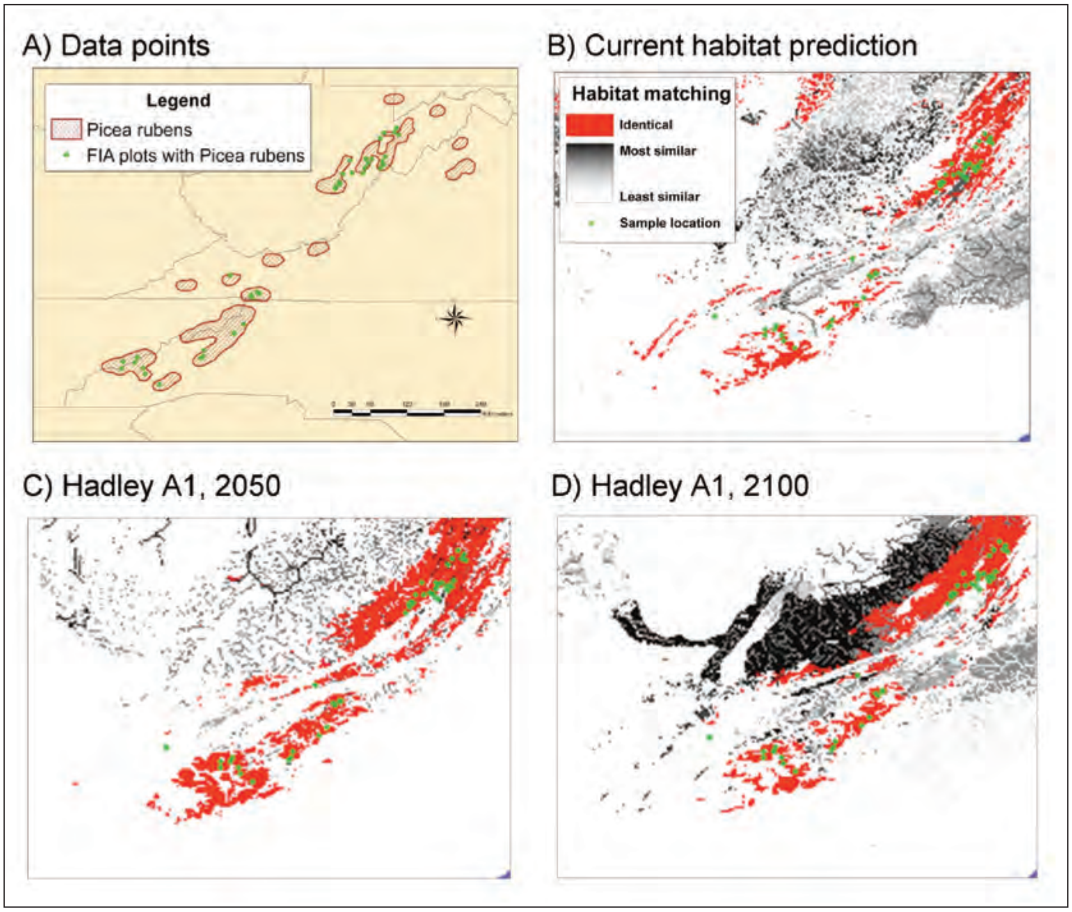

Figure 4.—Multivariate Spatio-Clustering predictions of current and future acceptable environmental conditions for red spruce in the central and southern Appalachian Mountains. The small green dots in all four subfigures depict the Forest Inventory and Analysis plot locations (2,274 plots across eastern United States) that were used as training data (A) to predict the location of currently acceptable habitat conditions (B), which was in turn used to predict the locations of acceptable environmental conditions in 2050 (C) and 2100 (D) using the Hadley A1 (higher-emissions) scenario.

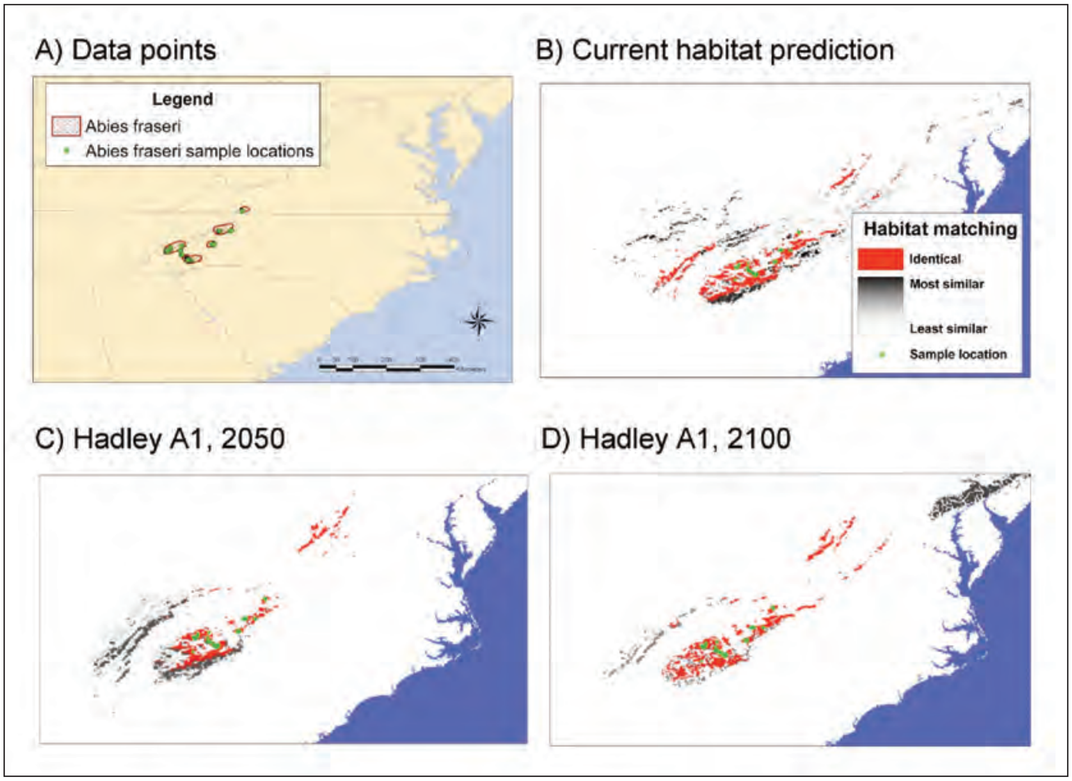

Figure 5.—Multivariate Spatio-Clustering predictions of current and future acceptable environmental conditions for Fraser fir. The coordinates of 302 known Fraser fir locations (the small green dots) were used as training data (A) to predict the location of currently acceptable habitat conditions (B), which was in turn used to predict the locations of acceptable environmental conditions in 2050 (C) and 2100 (D) using the Hadley A1 (higher-emissions) scenario.

FHM Detection Monitoring and Evaluation Monitoring activities; 2) for on-site and off-site conservation actions; and 3) for molecular marker studies that quantify the genetic architecture and diversity of at-risk species. The results also should be useful for land-use planners and conservation organizations interested in identifying geographic locations that could be preserved as important future habitat for at-risk tree species.

FUTURE WORK

This work is merely the beginning of a project that aims to predict suitable environmental conditions for more than 100 North American forest tree species, to quantify the distance between the current locations of these species and their future locations, and to assess whether these changes will negatively affect the genetic integrity of these species and their populations.

As we proceed, we will need assistance from forest ecologists, geneticists, and species specialists. Our most immediate need is to identify coordinate data of rare species and species with ranges that extend into Canada, since the FIA plot grid does not sample rare species well and is limited to the conterminous United States and southern Alaska.

In the longer term, we will need assistance from other scientists to assess the potential genetic impacts of climate change on North American forest tree species. These species-level assessments may be accomplished in the context of a Bayesian Belief Network approach, which is a tool that incorporates expert opinion into models of biological systems useful for making ecological predictions and aiding in resource-management decision-making (Marcot et al. 2006, McCann et al. 2006). Anyone interested in assisting should contact the lead author at the email address listed at the beginning of this paper.

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DISRUPTION OF CALCIUM NUTRITION AT HUBBARD BROOK EXPERIMENTAL FOREST (NEW HAMPSHIRE) ALTERS THE HEALTH AND PRODUCTIVITY OF RED SPRUCE AND SUGAR MAPLE TREES AND PROVIDES LESSONS PERTINENT TO OTHER SITES AND REGIONS

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Abstract.—Pollution-induced acidification and other anthropogenic factors are leaching calcium (Ca) and mobilizing aluminum (Al) in many forest soils. Because Ca is an essential nutrient and Al is a potential toxin, resulting depletions of Ca and increases in available Al may significantly alter the health and productivity of forest trees. Controlled experiments on red spruce (*Picea rubens* Sarg.) and sugar maple (*Acer saccharum* Marsh.) seedlings – species experiencing decline in the field – have documented physiological disruptions specific to Ca deficiency. More importantly, field studies at Hubbard Brook Experimental Forest (HBEF) in New Hampshire have shown that Ca additions that increase soil Ca levels to those estimated to exist prior to pollutant-induced Ca leaching, reverse many of the symptoms of red spruce and sugar maple decline. For example, Ca addition to Watershed 1 at the HBEF increased the Ca nutrition, sugar storage, antioxidant enzyme activity, and cold tolerance of the current-year foliage of mature red spruce trees and dramatically reduced foliar winter injury during a high-injury year. Similarly, soil Ca additions in a replicated plot-based study at HBEF increased foliar Ca concentrations in sugar maple trees and simultaneously alleviated the two characteristic symptoms of maple decline – branch dieback and reductions in woody growth. Improvements in Ca nutrition here also significantly increased levels of stem wound closure. Previous research with red spruce saplings in the Southern Appalachian Mountains and sugar maple trees across the Allegheny Plateau of north central Pennsylvania are consistent with our findings for mature trees at HBEF and suggest that the influence of Ca depletion on tree function and decline are pertinent to many sites and regions. Although species like red spruce and sugar maple may be particularly susceptible to Ca deficiency and related decline, results of studies on other tree species in the laboratory and field suggest a broader influence of Ca deficiency. Because Ca deficiency and Al toxicity particularly disrupt plant carbon (C) relations (i.e., the biochemistry of photosynthesis, respiration, and growth) alterations in the availability of these cations may also disproportionately reduce levels of C sequestration within forest systems.

INTRODUCTION

Growing evidence from around the globe indicates that anthropogenic factors including pollution-induced acidification, associated aluminum (Al) mobility, and nitrogen (N) saturation are disrupting natural nutrient cycles and depleting base cations from forest ecosystems (Lawrence et al. 1995; Likens et al. 1996, 1998; Aber et al. 1998, 2003). Although cation depletion can have varied and interacting influences on ecosystem function (e.g., altering nutrient cycling, species composition, and food webs in forested systems Schaberg et al. 2001, in press), it is the loss of calcium (Ca) that may be particularly limiting to tree health and productivity. Ca plays unique roles in plant metabolic pathways that allow plants to recognize and acclimate to biotic and abiotic stresses (Sanders et al. 1999, Pandey et al. 2000, Roos 2000) and that regulate cellular energy relations (Pan and Dilley 2000, Dilley 2004, Miqyass et al. 2007, Tozawa et al. 2008) – two processes critical to the long-term survival and growth of trees.

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Historically, much of the research regarding the influence of Ca on plant health has involved basic research with herbaceous crops, especially Arabidopsis (e.g., Cheong et al. 2003, Pandey et al. 2004, Liu et al. 2005). However, laboratory-based experiments with red spruce (*Picea rubens* Sarg.) and sugar maple (*Acer saccharum* Marsh.) seedlings – two tree species that are experiencing decline in the field – have also been conducted. For example, experiments with red spruce saplings have shown that the loss of biologically available Ca 1) reduces the stability of foliar membranes and decreases foliar cold tolerance (Schaberg et al. 2000a); and 2) slows the closure of stomata during water stress – predisposing plants to drought damage (Borer et al. 2005). Similar work with pot-grown sugar maple seedlings has shown that photosynthesis and growth are depressed when Ca is limited (St. Claire and Lynch 2005a) and that low cation (especially Ca) nutrition may also reduce levels of mycorrhizal colonization – exacerbating nutritional deficits (St. Claire and Lynch 2005b). Results of these controlled studies lay the foundation for understanding the fundamental changes in physiology that result from pollution-induced plant Ca deficiencies. Nonetheless, complementary experimentation must also occur in the field to evaluate whether laboratory results have bearing under the more complicated conditions that exist in heterogeneous forest systems.

The Hubbard Brook Experimental Forest (HBEF) in New Hampshire is an ideal location to evaluate the broader, real-world risks of Ca depletion to forest health and productivity in the field. HBEF is where acid deposition was first measured and defined in the United States (Likens et al. 1972), and it has provided some of the most convincing evidence connecting acid deposition to Ca depletion (Likens et al. 1996, 1998). Furthermore, once the nature and extent of Ca depletion were known, HBEF established two long-term experiments to assess the influence of ambient Ca depletion on nutrient cycling, forest health, and productivity. One of these experiments involved the replacement of all the Ca estimated to have been lost through acid-induced pollutant leaching back to an entire forested watershed (Groffman et al. 2004). The second was a replicated plot-based experiment that provided a broad spectrum of soil Ca levels (Berger et al. 2001).

Here we describe the results of several studies that evaluated the influence of Ca manipulation of native forest soils on mature red spruce and sugar maple health and productivity in the field. Although the studies described vary in the treatment scale (from entire watershed to replicated 45 m plots), the important commonality is that treatment impacts in both were compared to an ambient control – soils that have been depleted of Ca largely as a result of acid deposition-induced Ca leaching (Likens et al. 1996, 1998). Thus, the subjects of comparison in these experiments are the nutrition, health, and productivity of trees under ambient conditions (Ca partially depleted due to acidic inputs) versus the nutrition and function of trees on sites that received added Ca (intended to bring soil Ca levels to pre-pollution levels). This design helps to identify current deficits in tree status attributable to pollution-induced Ca depletion. The replicated plot study also includes a soil Al treatment. Because Al competes with and reduces Ca uptake, the addition of the Al treatment provides a look at the consequences of further reductions in Ca availability beyond those currently experienced under ambient conditions. Tree assessments focus on foliar nutrition (to verify treatment-induced changes in Ca availability) and physiological/health measures that have previously been shown to be Ca-dependent (i.e., foliar sugar concentrations; the activity of the antioxidant enzyme ascorbate peroxidase [APX]; cold tolerance; winter injury and bud mortality for red spruce; and foliar nutrition, crown vigor and dieback, xylem growth and wound closure for sugar maple).

STUDY AREA

Watershed-level Study of Red Spruce

HBEF is divided into multiple small headwater watersheds which serve as either reference or treatment sites. Watershed 6 is the biogeochemical-reference watershed of the forest for which extensive Ca depletion has been documented (Likens et al. 1996, Likens et al. 1998). Watershed 1 was fertilized in 1999 with 38 g m^{-2} $CaSiO_3$ (wollastonite, a form of Ca that is inherently slow-releasing) to increase the availability of Ca to pre-industrial levels (Groffman et al. 2004). Because red spruce was a common component of the forests at the upper reaches of both the reference and treated watersheds, these locations were used to evaluate the influence of soil Ca depletion on red spruce physiology and health.

Replicated-plot Study of Sugar Maple

We also used the Nutrient Perturbation (NuPert) study comprising 12 forested plots (45 m x 45 m) where sugar maple is the dominant canopy tree species (Berger et al. 2001). In 1995, the 12 plots were equally and randomly divided among three treatments: 1) control (no treatment), 2) soil Ca addition (to boost Ca to pre-pollution levels of availability), and 3) soil Al addition (to compete with and reduce Ca availability), resulting in four replicates of the treatments. Treatment applications of $CaCl_2$ or $AlCl_3$ occurred in fall and spring to coincide with leafless periods. Annual additions of $CaCl_2$ were discontinued in 1999 and replaced with a one-time application of wollastonite pellets (38 g m^{-2}) to provide a slow release of Ca to the soil as done elsewhere at the HBEF (Peters et al. 2004). At the time that nutritional and health measures reported here were made, the NuPert plots had received a total of 48 g m^{-2} of Ca and 8.1 g m^{-2} Al via treatment additions (Huggett et al. 2007).

METHODS

Foliar Winter Injury and Bud Mortality of Red Spruce

Winter injury was assessed in May 2003 on both the Ca-addition and reference watersheds at HBEF. One-tenth-ha circular plots containing dominant or co-dominant red spruce were randomly chosen in each watershed. All red spruce trees in these plots above breast height (1.3 m) were assessed and categorized into the following crown classes: dominant, co-dominant, intermediate, suppressed, and understory. Six plots containing 38 trees were examined for winter injury in the Ca-addition watershed and seven plots containing 44 trees were assessed in the reference watershed. All spruce trees in each plot were visually evaluated for the reddening of current-year foliage and rated on a scale of 0 to 10 by two observers (Lazarus et al. 2004). A score of 1 represented 1-10 percent injury, a score of 2 represented 11-20 percent injury, etc. Bud mortality associated with foliar winter injury was visually assessed on both watersheds using binoculars on 28 October 2003; we used the same 0-10 injury scale as for foliar assessments.

Cation Concentrations in Red Spruce Foliage

To measure cation nutrition, we sampled foliage in late October 2003 from a sub-sample of trees assessed for winter injury in May 2003. We used shotguns to collect current-year, sunlit foliage from dominant and co-dominant trees from six plots from the Ca-addition watershed (31 trees total) and seven plots from the reference watershed (37 trees total). In November 2005 six south-facing plots per watershed were established containing five mature dominant or co-dominant red spruce each (n = 30 per watershed, total n = 60 for all measures). Samples of sunlit, current-year foliage from the upper crowns of trees were collected for the measurement of cation concentration in November 2005. These same trees were used for foliar collections in February 2006 to measure soluble sugar concentrations and APX activity. For both the 2003 and 2005 collections, samples used for cation analysis were sealed in plastic bags for transport and dried for 2 weeks at 65 ˚C upon return to the laboratory. Samples were then ground to pass a 2 mm sieve and digested by heating with nitric acid and hydrogen peroxide using a block digester (adapted from Jones and Case 1990), and analyzed for total foliar Ca, Al, potassium (K), magnesium (Mg), and manganese (Mn) by inductively coupled plasma atomic emission spectroscopy (ICP-AES, PlasmaSpec 2.5, Leeman Labs, Lowell, MA). Eastern white pine needles from the National Bureau of Standards and Technology (SRM 1575), sample duplicates, and blanks were analyzed for procedural verification. Tissue standards were within 5 percent of certified values.

Soluble Sugar Analysis of Red Spruce Foliage

Samples analyzed for soluble sugar concentration were packed in ice in the field, freeze-dried, ground, and ultimately stored at -80 ˚C until ready for assay. Cuticular waxes were removed with hexane, and sugars were extracted with 80 percent ethanol (Hinesley et al. 1992). Methods described by

Schaberg et al. (2002) were followed to analyze concentrations of stachyose, glucose, sucrose, xylose, fructose, and raffinose using a Waters HPLC with a 510 pump, a 410 differential refractometer, and a Waters Sugar-Pak column. Data were analyzed for both individual and total sugar concentrations using Waters Millenium™ 2000 software (Advanced Chemistry Development, Inc., Toronto, ONT), and expressed as milligrams per gram dry mass.

Ascorbate Peroxidase Activity in Red Spruce Foliage

Current-year foliage was packed in ice in the field. In the laboratory, samples were homogenized in extraction buffer modified from Schwanz and Polle (1998) and stored at -80 °C until ready for assay. Enzyme activity was monitored spectrophotometrically with a Beckman DU 800 (Beckman Coulter, Inc., Fullerton, CA). Total soluble protein was analyzed with a brilliant-blue total protein kit (TP0100, Sigma-Aldrich Co., St. Louis, MO). The methods of Nakano and Asada (1981) were followed as samples were spectrophotometrically analyzed at 290 nm, and the linear decrease in absorbance for 2 minutes was recorded to determine the activity of APX as ascorbate scavenged hydrogen peroxide (H_2O_2). Ascorbate oxidase activity was measured via the same methods with the omission of H_2O_2, and subtracted from APX activity to yield APX specific activity.

Cold Tolerance of Red Spruce Foliage

Current-year foliage was collected in February 2006 to measure cold tolerance at the point in winter when red spruce is most vulnerable to freezing injury. Samples were bagged and packed in ice in the field, and stored overnight at 4 °C. The following day, samples were chopped and bulked. Subsamples per tree were exposed to decreasing temperatures at a rate of -6 °C h^{-1} and held at 14 preselected test temperatures ranging from -15 °C to -90 °C for 30 minutes (Halman et al. 2008). Following freezing tests, a 3.0 mL solution of 0.01-percent *v/v* Triton X-100 in deionized water (4 °C) was added and samples were shaken for 8 h at room temperature. Initial conductivity of the effusate was measured with a multielectrode instrument (Wavefront Technology, Ann Arbor, MI). Then samples were dried for 72 h at 45 °C to kill the tissue and soaked in fresh detergent solution for 24 h. Final conductivity was measured. Relative electrolyte leakage (REL), a measure of membrane permeability calculated as the proportion of initial to final conductivity at a given test temperature, was used to calculate T_m, the temperature at the midpoint of a sigmoid curve fit to REL data for all test temperatures (Schaberg et al. 2000b, Strimbeck and DeHayes 2000).

Nutrition of Sugar Maple Foliage

Foliar cations were measured using the methods described above for red spruce foliage, except that peach leaves from the National Bureau of Standards and Technology (SRM 15547) were used as a procedural check rather than white pine needles.

Evaluation of Canopy Health for Sugar Maple

Tree health evaluations were conducted on 27 August 2004 according to methods used by the North American Maple Project (Cooke et al. 1996). Crown vigor was estimated for each sample tree using the scale: 1) healthy (no major branch mortality); 2) light decline; 3) moderate decline; 4) severe decline; and 5) dead. Branch dieback was also estimated for each sample tree using a 12-class system (for complete methods, see Cooke et al. 1996).

Evaluation of Sugar Maple Basal Area Growth

Two increment cores were taken from the main stems of sample trees at breast height in October 2004. Two cores were collected at 180 degrees for each tree. Cores were mounted and prepared according to methods of Cook and Kairiukstis (1989). Radial growth measurements included only the past 10 years of growth (1995-2004) to specifically evaluate treatment impacts. Analyses of growth for each sample tree were based on a ratio of the basal area increment (BAI) of each post-treatment year (1996-2004) divided by the basal area increment of the pre-treatment year of 1995. There was no significant difference in the growth of trees among plots prior to treatment imposition in 1995 (P = 0.349).

Evaluation of Sugar Maple Wound Closure

Each of the five sample trees per plot was initially wounded in July and August 2004 with a 15-mm cork borer. Calipers were used to measure the width of each wound on 1 November 2005. This date was chosen to allow at least one full growing season of response for sample trees.

Statistical Analyses

For almost all the data from the watershed and replicated plots studies, analysis of variance (ANOVA) was used to test for treatment differences. Significance tests utilized a nested design to test treatment differences with plot within treatment, and plot differences with tree within plot (Montgomery 2001). For the replicated plot study, to further assess the differences among Ca perturbation treatments, differences among means were analyzed using two mutually exclusive orthogonal contrasts: 1) Ca vs. Al and Control and 2) Al vs. Control. Sugar maple crown vigor, represented as categorical data, was analyzed using chi-square analysis. Percent branch dieback in sugar maple trees was treated as continuous data but was analyzed using a Wilcoxon/Kruskal-Wallis test because the data were not normally distributed.

RESULTS

Watershed-level Study of Red Spruce

Calcium addition significantly increased the Ca concentration of current-year foliage when measured in 2003 and 2005 (Table 1). Synchronous with these increases in foliar Ca, we detected significant changes in a number of Ca-dependent processes (Table 2). For example, the winter injury of current-year foliage from dominant and co-dominant trees was dramatically reduced for trees from the Ca-addition watershed relative to those on the control (Hawley et al. 2006). Significant reductions in freezing-induced bud mortality were also found for trees on the Ca-addition site compared to the control (Hawley et al. 2006). Ca treatment was also associated with significantly higher foliar sucrose and total sugar concentrations and higher APX activity relative to trees from the control (Halman et al. 2008). These increases in sugar concentration and antioxidant (APX) activity provide physiological explanations for the greater cold tolerance (Halman et al. 2008) and reduced winter injury (Hawley et al. 2006) found for trees on the Ca-treated watershed.

Replicated-plot Study of Sugar Maple

Ca addition increased Ca and reduced Al concentrations in sugar maple foliage at the NuPert site, but we detected no differences in foliar nutrition associated with Al treatment (Table 3). Ca treatment was also associated with an amelioration of the common symptoms of sugar maple decline: crown thinning and xylem growth reductions (Table 4). Relative to trees on Al-addition and control plots, trees on Ca-addition plots expressed greater crown vigor, a lower percent crown dieback, and greater xylem growth (Huggett et al. 2007). Furthermore, wounds imposed on trees on Ca-addition plots were approximately one-half closed 1 year after wounding, whereas wounds on trees from the control and Al-treated plots showed relatively few signs of healing (Huggett et al. 2007).

DISCUSSION

The results of field-based Ca manipulations we report complement the results of previously reported laboratory-based experiments, but extend these findings by verifying that adequate Ca nutrition is needed to support vital stress response and energy relations of mature red spruce and sugar maple trees in native forests.

Results from laboratory studies and correlative data from the field have linked Ca deficiency to reduced foliar cold tolerance, increased foliar winter freezing injury, crown deterioration, and decline of red spruce in the northern portions of its range (DeHayes 1992, DeHayes et al. 1999, Schaberg et al. 2000a, Lazarus et al. 2004), and to impaired energy relations and decline of red spruce saplings in the south (McLaughlin et al. 1991, McLaughlin et al.1993). Our data from long-term Ca additions at the watershed level also emphasize the importance of adequate Ca nutrition in bolstering foliar cold tolerance and reducing freezing injury. However, our data further highlight the broader influence of adequate Ca nutrition to functional

Table 1.—Mean and SE of cation concentration of current-year red spruce (*Picea rubens*) foliage from Ca-addition and reference watersheds at the Hubbard Brook Experimental Forest on two measurement dates. Significant differences between watershed means based on ANOVA are indicated by asterisks: *, P<0.10; ** P<0.05; and ***P<0.001. October 2003 data from Hawley et al. 2006, and November 2005 data from Halman et al. 2008.

	Foliar cation concentration (mg kg^{-1} dry mass)				
Treatment	Ca	Al	K	Mg	Mn
October 2003					
Ca-addition	2,225.8 ***	25.2	6,664.9	901.8	1,715.0
SE	123.4	8.9	632.1	44.4	182.1
Reference	1,704.6 ***	40.7	7,896.1	804.7	1,440.3
SE	108.4	6.8	555.1	39.0	159.9
November 2005					
Ca-addition	2,035.4 **	35.4	5,385	715.4	881.8 **
SE	78.2	1.8	193	17.1	64.0
Reference	1,796.3 **	36.0	5,242	681.0	1,330.8 **
SE	77.0	1.6	178	19.8	106.0

Table 2.—Mean and SE of winter injury, bud mortality, ascorbate peroxidase (APX) activity (expressed per mg of protein), sucrose, total sugars, and cold tolerance (T_m) of current-year red spruce (*Picea rubens*) foliage from Ca-addition and reference watersheds at the Hubbard Brook Experimental Forest on two measurement dates. Significant differences between watershed means based on ANOVA are indicated by asterisks: *, P<0.10; ** P<0.05; and ***P<0.01. 2003 data from Hawley et al. 2006, and 2006 data from Halman et al. 2008.

Treatment	**Winter Injury 2003 (%)**	**Bud mortality 2003 (%)**	**APX 2006 (µmol mg^{-1} min^{-1})**	**Sucrose 2006**	**Total sugars 2006**	**T_m 2006 (°C)**
				--------- (mg g^{-1} dry mass)	**-----**	
Ca-addition	74.3***	6.8***	25.8*	4.00**	84.85**	-43.5**
SE	5.9	1.5	3.9	0.30	2.34	1.4
Reference	24.7***	29.8***	15.1*	2.68**	74.85**	-32.2**
SE	5.4	6.0	2.8	0.29	3.05	1.1

Table 3.—Treatment differences in foliar element concentrations (mean±SE) for sugar maple (*Acer saccharum*) trees in 2004 from Ca-addition, reference, and Al-addition study plots in the NuPert Study at the Hubbard Brook Experimental Forest. Means within element followed by the same letter are not significantly different (P<0.05), based on data from Huggett et al. 2007.

	Foliar cation concentration (mg kg^{-1} dry mass)				
Treatment	**Ca**	**Al**	**K**	**Mg**	**Mn**
August 2004					
Ca-addition	7,959.6 a	30.5 a	6,940.5 a	1,127.9 a	1,107.4 a
SE	477.5	1.4	226.8	70.8	78.7
Reference	5,505.2 b	37.1 b	7,595.7 a	1,006.5 a	1,113.1 a
SE	439.8	1.7	190.5	73.5	107.0
Al-addition	4,506.6 b	40.2 b	7,492.7 a	882.2 a	1,096.8 a
SE	392.3	2.4	278.5	82.2	107.5

Table 4.—Treatment differences in crown vigor, branch dieback, BAI ratio 2002, BAI ratio 2004, and wound closure (mean±SE) for sugar maple (*Acer saccharum*) trees in Ca-addition, reference and Al-addition study plots in the NuPert Study at Hubbard Brook Experimental Forest. Means within measure followed by the same letter are not significantly different (P<0.05), based on data from Huggett et al. 2007.

Treatment	Crown Vigor	Branch dieback (%)	BAI ratio 2002	BAI ratio 2004	Wound closure (mm)
Ca-addition	1.05 a	2.50 a	4.3 a	2.6 a	0.615 a
SE	0.05	0.57	0.5	0.3	0.313
Reference	1.60 b	5.50 b	2.1 b	1.9 b	-0.303 b
SE	0.20	1.08	0.3	0.3	0.260
Al-addition	1.30 b	5.25 b	2.2 b	1.6 b	0.060 b
SE	0.13	0.99	0.2	0.2	0.025

foliar antioxidant systems that protect against a range of oxidative stresses – not just those associated with the cold. Furthermore, Ca addition increased the storage of sucrose and total sugars in red spruce foliage – providing direct evidence of how adequate Ca availability improves the energy relations (here sugar storage) in mature trees in the field. Separate measures of foliar chlorophyll fluorescence for mature red spruce on the Ca-addition and reference watersheds at HBEF also highlight the influence of Ca on carbon (C) relations – here a reduction in photosystem function during summer when Ca is limiting (Boyce 2007).

Sugar maple decline is characterized by a slow loss of crown vigor, the dieback of fine twigs, and reduced radial increment over a period of years, frequently ending in tree death (Horsley et al. 2002). Both reductions and/or imbalances in base cation nutrition and stress imposed by some secondary biotic or abiotic factors have been linked to the onset and severity of decline (Horsley et al. 2002). Here we document that long-term Ca addition reduced the primary symptoms of sugar maple decline and increased crown vigor, reduced the percent of branch dieback, and increased basal area growth relative to trees on ambient (Ca-depleted) and Al-addition plots. In addition, Ca addition significantly improved the rate of stem wound closure – a quality that would benefit sugar maple trees that are regularly wounded for maple syrup production. Deficiencies or imbalances in other cations (e.g., Mg and K) undoubtedly also influence sugar maple health in the field (Horsley et al. 2002, St. Clair et al. 2008). However, our data showing significant reversals in decline symptoms with Ca-specific treatments are consistent with other reports that highlight the particular importance of Ca nutrition to sugar maple growth and survival (Juice et al. 2006, Moore and Ouimet 2006, Schaberg et al. 2006).

Overall, Ca addition to the soils studied was associated with a measurable increase in tree stress response capabilities and increased C storage (expressed as either increased woody growth or elevated concentrations of soluble sugars in foliage). Importantly, because comparisons for Ca treatment for both watershed and plot-based experiments were sites that experienced ambient Ca depletion, the reduced function and vigor of trees on control plots represent the decreased vigor and capacity of native trees due to soil Ca depletion.

Although our data highlight the influence of Ca nutrition on the health and productivity of red spruce and sugar maple trees in native forests in New Hampshire, other data indicate that these same processes have relevance to the vigor of these species in more southern locales. For example, numerous studies have shown that acidic deposition is associated with reduced foliar Ca nutrition and altered C relations (especially increased foliar respiration) among red spruce saplings in the Southern Appalachians (McLaughlin et al. 1990, McLaughlin et al. 1991, McLaughlin and Tjoelker 1992, McLaughlin et al. 1993). In addition, deficiencies of Ca and Mg were associated with the decline in sugar maple trees along the Allegheny Plateau in Pennsylvania (Kolb and McCormick 1992), and additions of Ca and Mg improved growth and crown vigor in these sites (Long et al. 1997). Our data from HBEF show that reversals in sugar maple decline occur with Ca addition alone and that the association of Ca nutrition and tree health is not limited to a specific geographic region. Indeed, new associations between the Ca status and health of trees periodically emerge – particularly in regions that have experienced prolonged pollution-induced Ca leaching (e.g., Europe) or where acid inputs are on the rise (e.g., China) (Schaberg et al. in press).

Because one common consequence of Ca deficiency is a disruption in C storage, our results also highlight a potentially important connection between two pollution-induced threats to forest health and sustainability: acid deposition and climate change. If further testing confirms a general connection between acidic deposition-induced Ca depletion and reduced C sequestration in trees, then the effects of one pollution-based stressor (acidic deposition) would be implicated in exacerbating the driver of another stress agent (climate change) by limiting tree C sequestration and storage. As such, our findings suggest one mechanism through which two anthropogenic stress factors can interact to jeopardize forest health and ecosystem function.

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ABSTRACTS OF ORAL PRESENTATIONS

ACIDIC DEPOSITION AND RED SPRUCE IN THE CENTRAL AND SOUTHERN APPALACHIANS, PAST AND PRESENT

Mary Beth Adams[1]

During the 1980s, the Spruce-Fir Research Program, part of the Congressionally mandated National Atmospheric Precipitation Assessment Program (NAPAP), investigated the links between acidic deposition and decline and mortality of red spruce forests in the eastern United States. The Spruce-Fir Research Program was highly successful in advancing the state of knowledge on spruce-fir ecosystems, particularly in the northern and southern Appalachians and was one of the few to convincingly document the effects of acidic deposition on spruce ecosystems. However, relatively little research was conducted in the central Appalachians at that time. We learned that there was significant mortality of red spruce in the Adirondacks and northern Appalachians and some growth declines documented in the southern Appalachians. A plausible mechanism, changes in cold tolerance resulting from changes in soil and tissue chemistry resulting from acidic deposition, was identified for the northern Appalachian and Adirondack mortality, and much excellent research furthered our understanding of these important forest ecosystems. The results of this research were documented in the 1992 book, "Ecology and Decline of Red Spruce in the Eastern United States."

Since publication of the book, research effort has continued, at a significantly lower level of activity, in the northern and southern Appalachians. Trends in air quality in the eastern U.S. have improved significantly since the passage of the Clean Air Act Amendments in 1990, but the central Appalachians still receive some of the most acidic deposition in the United States on a chronic basis. Relatively little effort has focused on the central Appalachians since 1992, although the scarce evaluations of the health of spruce forests in the central Appalachians have revealed few problems. Our understanding of the structure and importance for habitat of spruce forests in the central and southern Appalachians has improved since the NAPAP days, but significant research needs still exist relative to acidic deposition, particularly related to soil calcium levels, and to interactions with climate change.

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EVIDENCE OF MONTANE SPRUCE-FIR FOREST RECOVERY ON THE HIGH PEAKS AND RIDGES OF THE BLACK MOUNTAINS, NORTH CAROLINA: RECENT TRENDS, 1986-2003

Todd Allen Bowers and Robert I. Bruck[1]

Decline in high elevation red spruce (*Picea rubens* Sarg.) and Fraser fir (*Abies fraseri* (Pursh) Poir.) forests throughout the southern Appalachians was shown following extensive surveys conducted during the 1980s. We resurveyed four permanent, 0.1 ha, spruce-fir forest plots installed in 1986 at 1,980 m in the Black Mountains of North Carolina; remeasured basal area, stem density, tree crown damage and noted insect and disease occurrences. A large significant ($p < 0.10$) increase in live fir stem density of 3,237 stems/ha was evident. Results also show large increases in basal area and stem density for live fir and spruce populations with a corresponding decrease in dead fir stems. Additionally, we observed crown condition improvements for fir on most sites. Data suggests rapid regeneration of dense, healthy fir at 1,980 m, especially where severe mortality and overstory collapse was previously observed. The progression toward a climax high-elevation fir forest is highly variable and very patchy. Balsam woolly adelgid (*Adelges piceae* Ratz.) was rarely encountered suggesting that adelgid populations are currently low, thus allowing for fir recovery. Long-term recovery is uncertain, as fir stems will soon reach adelgid-susceptible age and size classes.

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STATUS AND CONSERVATION OF NORTHERN GOSHAWKS IN THE CENTRAL APPALACHIAN MOUNTAINS: HAS THE POPULATION TREND REVERSED SINCE 2001?

David F. Brinker and Kevin P. Boyle[1]

Prior to European settlement, northern goshawks (*Accipiter gentilis*) were a regular component of the high-elevation Appalachian breeding bird fauna, possibly as far south as the Great Smoky Mountains in North Carolina. As a result of extensive 19th century logging in the Appalachians, goshawks were extirpated from Maryland south by the beginning of the 20th century and greatly reduced in Pennsylvania and the northeastern United States. During the late 20th century, the higher elevations of the central Appalachians were gradually reoccupied by breeding northern goshawks as the population increased throughout the northeast in response to improving habitat conditions. Satellite telemetry studies demonstrate that central Appalachian adult goshawks are permanent residents. Reproductive output from central Appalachian goshawks is correlated with autumn counts of dispersing juvenile and nonbreeding sub-adult goshawks at Hawk Mountain and Waggoner's Gap. Counts of goshawks from 1991 through 2001 show a nonsignificant increase (P~0.32), but are consistent with observations of late 20th century breeding expansion southward. During 2001-2008, counts of dispersing goshawks show a nearly significant decline (P~0.07). This coincides with loss of recent breeding pairs in Maryland and West Virginia and declines in Pennsylvania and New York (BBA data). This recent trend reversal may be the result of increased adult mortality from West Nile virus and lower adult female survival rates (during the incubation and brooding periods) coupled with reduced nesting success rates from depredation by an expanding fisher (*Martes pennanti*) population. South of Pennsylvania, conifers appear to be an important component of northern goshawk nesting habitat. Loss of eastern hemlock (*Tsuga canadensis*) to hemlock woolly adelgid (*Adelges tsugae*) would seriously impact goshawk nesting habitat in the central and southern Appalachians, especially in the absence of any significant recovery of red spruce (*Picea rubens*) and white pine (*Pinus strobus*) dominated forest communities which were decimated by past logging. Restoration of native conifers in high elevation Appalachian forests is critical to the long-term recovery of northern goshawks in the central and southern Appalachians.

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AMERICAN CHESTNUT PERSISTENCE IN SOUTHWESTERN VIRGINIA 80 YEARS AFTER CHESTNUT BLIGHT INTRODUCTION

Katie L. Burke[1]

Forest disease noticeably alters spatial patterns of a species' distribution and this alteration is complex when host mortality is affected by site qualities. In the 1930s, chestnut blight (*Cryphonectria parasitica*) spread through southwestern Virginia, after its introduction to New York in 1904. This pandemic completely altered Appalachian forests, where a native host, the American chestnut (*Castanea dentata*) was dominant. Today, some chestnuts continue to persist in the forest understory as resprouting root stocks. Understanding the current distribution of chestnut is necessary for the management of the American chestnut, for the reintroduction of blight resistant chestnuts, and for control of invasive forest diseases in general. This project determined whether preblight chestnut density predicts current, post-blight chestnut density, and, if not, the site factors that contribute to chestnut persistence. This project was conducted at Mountain Lake Biological Station in southwestern Virginia. Sites (n=24) that were sampled before the blight pandemic were resampled using regularly spaced circular plots (1/25 ha). At each plot, aspect, slope, elevation, soil pH, and stand age were determined. Preblight chestnut and post-blight chestnut were significantly positively correlated ($p = 0.042$, $F = 4.64$, $df = 23$), but the relationship was weak ($r^2 = 0.17$) due to high variation in post-blight chestnut density. To explain this variation, an ordination using nonmetric multidimensional scaling was used to understand the relationship of site quality to chestnut loss. This analysis showed that chestnut persistence was favored on sites with low soil moisture, high heat load (southern to western exposures), steeper slopes, and acidic soil. These environmental variables may affect the prevalence or virulence of the disease. Conditions that once favored chestnut do not necessarily favor chestnut today as an understory shrub with the blight, and sites that once harbored many chestnuts before the blight may not harbor large numbers of chestnuts today.

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NATURAL COMMUNITIES OF THE CENTRAL APPALACHIAN RED SPRUCE ECOSYSTEM AND THEIR CONSERVATION SIGNIFICANCE

Elizabeth A. Byers[1]

Natural communities within the red spruce ecosystem of the central Appalachians are characterized by exceptionally high biodiversity and conservation value. This ecosystem stretches in a southwest – northeast trending band for 250 km along the high elevations of the Allegheny Mountains, from Greenbrier County, WV to Garrett County, MD. The region contains some of the highest concentrations of globally rare plant and animal species within the northeastern states. At the state level, a remarkable 240 rare species have been documented within West Virginia's red spruce ecosystem. Its high conservation value stems from a) its location south of the maximum extent of Pleistocene glaciations; b) its complex topography and geology; and c) the relatively large remaining tracts of natural vegetation compared to other areas in the northeast. Spruce forests are estimated to have originally covered more than half a million acres in West Virginia. Logging and burning from 1880-1920 reduced the spruce forest to a fraction of its former size. Now the region is a patchwork of red spruce, northern hardwoods, and cleared habitats in various stages of succession. Nestled in among the uplands are flat-lying headwater basins that accumulate moisture to form wetland habitats. These wetlands function as frost pockets, catching and pooling both water and cold air that drains from the surrounding uplands. The red spruce ecosystem as a whole occupies the highest, coldest, and wettest environmental niche in the central Appalachians. It is extremely vulnerable to the expected stresses of global climate change.

The National Vegetation Classification has been recently updated to include the full range of red spruce upland forest, woodland, and wetland communities, including six upland associations and 41 wetland associations. Twelve of these associations are new to the national system. More than half of the 47 types have high global conservation priority, and the remaining types have high state conservation priority. The highest conservation priorities at both the global and state levels are forested conifer and mixed swamps, upland spruce-dominated forests, ancient peatlands, and an ice-scour community.

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WET FEET AND SAPPY FINGERS: LESSONS LEARNED FROM RESTORATION WORK IN THE WEST VIRGINIA HIGHLANDS

Amy Cimarolli and David W. Saville[1]

This presentation summarizes our practical experiences from a decade of working with state and federal agencies and private landowners to protect, conserve, and restore the spruce forests and fir swamps of West Virginia. We present case studies that demonstrate the collaborative planning processes, site selection techniques, and restoration activities used in our partnerships to bring about successful projects. The presentation recounts some of our experiences and share some of the lessons we've learned working at two unique restoration sites, each with their own set of challenges and participants – Canaan Valley and Blister Swamp.

The key projects include the following:

- West Virginia's balsam fir genetic diversity conservation: To protect the genetic diversity within WV's balsam fir swamps, we collect seed from each key swamp and seed bank it through partners like the Natural Resources Conservation Service (NRCS). Fir seedlings have been grown and planted back into their respective swamps to boost the numbers where balsam woolly adelgid mortality has occurred.
- West Virginia balsam fir swamp forest restoration: To support natural balsam fir regeneration in the swamps where deer browsing prevents sapling development, we construct various types and sizes of deer exclosures. Some become research and demonstration sites on the impacts of deer to swamp vegetation; others simply are deer-free 'refuges' for fir and other companion plants.
- Red spruce forest restoration across the high-elevation WV landscape: To expand and connect fragmented stands of native red spruce forests we; collect significant amounts of seed with volunteers; this seed is not available commercially; seed bank and have seedlings grown at commercial nurseries as well as at the State Nursery and NRCS Plant Materials Center; work with federal and state agencies, researchers, and private landowners to develop innovative and collaborative restoration plans that identify priority sites and applications. Since 2002 more than 100,000 red spruce have been planted in West Virginia primarily by volunteers.

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FOLIAR AND SOIL CHEMISTRY AT RED SPRUCE SITES IN THE MONONGAHELA NATIONAL FOREST

Stephanie J. Connolly[1]

In 2005, soil and foliar chemistry were sampled from 10 sites in the Monongahela National Forest which support red spruce. Soils were sampled from hand-dug pits, by horizon, from the O-horizon to bedrock or 152 cm, and each pit was described fully. Replicate, archived samples also were collected. Analyses of air dried soil samples were performed at three laboratories. Chemical analyses were performed at the University of Maine. Aluminum extractions by strontium chloride, to estimate plant-available aluminum, were determined at The Pennsylvania State University soil testing laboratory, and soil taxonomy, mineralogy, chemical properties, and physical properties were analyzed at the Natural Resources Conservation Service (NRCS) soil survey laboratory in Lincoln, NE. Foliar samples were collected from 10 trees per site by shooting out upper sun-exposed branches with a shotgun. Ends of spruce branches containing current year's growth were excised and collected by tree. These air-dried samples were analyzed for chemistry at the University of Maine's analytical laboratory. Not surprisingly, average soil pH across the 10 sites was typically in the pH range of mid 4 or lower. The average pH through the entire mineral soil pedon at each site was almost always greater than that of the pH from the O-horizon – by as much as 1.1 pH units. Potassium was consistently the dominant base cation in foliar tissue; it was two to six times greater than calcium levels. By comparison, calcium levels in mineral soil were almost always at least twice as great as potassium, and the two had approximately equal concentrations in the organic horizon. Foliar aluminum concentration across all 10 sites averaged 39.8 ppm, which is greater than those typically reported in the literature. By contrast, average foliar manganese concentrations (718 ppm) were less than reported values. At almost all sites, the average aluminum concentrations were greater in the mineral soil than in the O-horizon. Calcium to aluminum (strontium chloride extraction) ratios in the organic layers for all sites were greater than 3, and averaged approximately 24. However, calcium to aluminum ratios in mineral soil were much less. Except for one site, calcium to aluminum ratios in the upper mineral zone (A and B horizons) ranged from 0.16 to 0.59. The differences between organic and mineral soil Ca/Al ratios raise questions about whether red spruce might shift its rooting zone more toward the organic layers to exploit less toxic Al conditions, and what associated physiological changes may occur.

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DETECTING AND MONITORING ACIDIC DEPOSITION EFFECTS ON SOIL CHEMISTRY AND FOREST GROWTH ON THE MONONGAHELA NATIONAL FOREST

Patricia Elias, James Burger, Stephanie Connolly, and Mary Beth Adams[1]

The Monongahela National Forest (MNF) lies downwind from many sources of acid deposition (AD) pollution. Therefore, managers are concerned about the possible deleterious effects of AD on the forest ecosystem. To address the needs of MNF managers, we used Forest Inventory and Analysis (FIA) sites to evaluate forest growth patterns on the MNF to determine the relationship between growth and key indicators of soil acidity. We then used those relationships to create a map of site resistance to acidification across the MNF. To develop a monitoring protocol, we assessed several sampling approaches for their suitability for monitoring AD-related changes in soil and foliage chemistry. Across all FIA sites on the MNF, periodic mean annual volume increment (PMAVI) ranged from -9.5 m^3 ha^{-1} yr^{-1} to 11.8 m^3 ha^{-1} yr^{-1}, suggesting lower-than-expected growth on two-thirds of the sites. Growth was compared to soil indicators of acidity on 30 FIA sites. In the surface horizon, effective base saturation (+), Ca concentration (+), base saturation (+), K concentration (+), Fe concentration (-), Ca/Al molar ratio (+), and Mg/Al molar ratio (+), were correlated with PMAVI ($p \leq 0.1$). Site resistance to acidification was mapped based on site parent material, aspect, elevation, soil depth, and soil texture. There was a significant ($p \leq 0.1$) positive correlation between PMAVI and a resistance index developed using these soil and site factors. Mapped resistance index was also compared with key soil indicators of AD-induced decline on 28 sites across the MNF, and pH, effective base saturation, and Al content were found to be the best indicators related to resistance index. Across the MNF, 14 percent of land area was highly resistant ($RI \geq 0.7$), 57 percent was moderately resistant ($0.7 > RI > 0.45$) and 29 percent was slightly resistant ($RI \leq 0.45$). Soil pH, effective base saturation, Ca/Al molar ratio, and sum of bases varied significantly when sampled by soil horizon versus fixed depths. Sampling by horizon was the better method. A second monitoring approach evaluated the relationship between foliar and soil chemical indicators. Across FIA plots, nutrient concentrations varied by tree species. Results from a potted-seedling study suggest that soil acidity influences growth and foliar concentrations are related to growth rates. This evaluation of the effects of AD on the MNF can be used to develop adaptive management plans and a monitoring program that will meet the AD-related objectives of the 2006 Forest Management plan.

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EASTERN HEMLOCK DECLINE IN RIPARIAN AREAS FROM MAINE TO ALABAMA

D.E. Evans[1], W.M. Aust, C.A. Dolloff, and B.S. Templeton

Eastern hemlock (*Tsuga canadensis*) is an integral component of Appalachian forest ecosystems and is valued for its ecological functions and aesthetic qualities. It is a foundation tree species in riparian systems and is known to moderate steam temperatures and base flow. The hemlock woolly adelgid (*Adelges tsugae*) has the potential to decimate *T. canadensis* populations across its range, which may have negative impacts on ecosystem function in riparian management areas (RMAs). Research efforts addressing eastern hemlock decline have focused on local or state scale outbreaks. Wider scale regional research has been limited to *A. tsugae* trapping and mapping with little research on the condition of *T. canadensis* in RMAs across its range.

We initiated a long-term project to measure *T. canadensis* decline and stand replacement in riparian areas with permanent plots located from Maine to Alabama in the summer of 2008. Forty-nine hemlock stands were randomly located within publically owned RMAs. At each hemlock stand, we measured overstory and understory vegetation, and estimated *T. canadensis* decline. Additionally, we measured coarse woody debris (CWD) in the RMAs.

Preliminary results indicate strong gradients of eastern hemlock decline across its range with states above Massachusetts generally unaffected by *A. tsugae*. Mid-Atlantic and southern states had the highest decline levels. Virginia and North Carolina had the greatest mean decline levels, followed by New Jersey, West Virginia, and Massachusetts. Analysis will include evaluation of site and location factors that are associated with eastern hemlock decline. Additional analysis will focus on replacement of *T. canadensis* in stands with moderate to severe decline, with a focus on identifying possible conifer replacements.

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25+ YEAR CHANGES IN FOREST STRUCTURE AND TREE-RING PATTERNS IN THREE OLD-GROWTH RED SPRUCE STANDS IN WEST VIRGINIA

Eric Heitzman, Sean Dougherty, James Rentch, Steve Adams, and Steve Stephenson[1]

The extent of red spruce (*Picea rubens*) forests in West Virginia has dramatically declined from an estimated 1.5 million acres in 1865 to 30,000 acres today because of widespread logging and forest fires during the late 1800s and early 1900s. Remaining old-growth (i.e., unlogged and unburned) spruce forests are particularly rare. In 1982, field plots were established for the first time in the only three old-growth spruce forests known in West Virginia to describe the vegetation of these unique communities. In 2007, we remeasured these stands to describe changes that occurred over 25+ years. The three case studies indicate that standing dead trees are a common feature of old-growth spruce stands. Spruce regeneration naturally regenerates under small- and large-scale disturbances, but can be inhibited by dense thickets of rhododendron. Declining radial growth trends characteristic of the 1980s were not always observed among current spruce trees.

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BIRD CONSERVATION ISSUES IN HIGH-ELEVATION (RED SPRUCE-FRASER FIR-NORTHERN HARDWOOD) FORESTS OF THE SOUTHERN BLUE RIDGE

William C. Hunter[1]

The highest elevations in North America east of the Mississippi River are in the southern Blue Ridge of Virginia, North Carolina, and Tennessee. This area supports fauna and flora more characteristic of Canada than anywhere else in the southeast United States. The high-elevation forests are within the High Peaks Region to distinguish them from similar forests of the central Appalachians (Allegheny Mountains of West Virginia and Pennsylvania) and boreal forests of the northeast United States and eastern Canada. Specifically, the spruce-fir dominated forests of the High Peaks Region are considered the second most endangered ecosystem in the United States. They range today in elevation from 1,350 to about 2,000 m high and total less than 28,000 ha. They remain today in widely isolated patches from Mount Rogers to the Great Smoky Mountains. Historically, the extent of spruce-fir may have been closer to 56,000 ha, with red spruce dominated forests extended down to 1,000 m on north and east facing slopes, but much of this was cut out by the early 1900s before public lands were established to protect the remaining stands. Most of cut-over areas support northern hardwood forests today with scattered red spruce. At the highest elevations, mature stands of Fraser fir (*Abies fraseri*) have all but been eliminated by exotic insect pests. Both the spruce and fir are apparently affected by air quality (and potentially acid deposition), while all forests in the High Peaks Region are subject to future losses due to global climate change. When glaciers receded many of the species associated with spruce-fir forests became restricted to the southern Appalachians in the southeast United States and genetic data suggests that these same species in the central Appalachians and further north radiated from populations now restricted to the southern Blue Ridge. These and other issues discussed in the southern Blue Ridge Bird Conservation Plan (http://www.partnersinflight.org/bcps/pl_23sum.htm) are discussed with respect to the conservation of locally high-priority species, including northern saw-whet owl (*Aegolius acadicus*), olive-sided flycatcher (*Contopus cooperi*), black-capped chickadee (*Poecile atricapilla*), and red crossbill (type 1, *Loxia curirostra*).

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VEGETATION CONTROLS ON CARBON AND NITROGEN CYCLING AND RETENTION: CONTRASTS IN SPRUCE AND HARDWOOD WATERSHED BUDGETS

Charlene N. Kelly, Stephen H. Schoenholtz, and Mary Beth Adams[1]

Anthropogenic sources of nitrogen (N) have altered the global N cycle to such an extent as to nearly double the rate of N that enters many terrestrial ecosystems. However, predicting the fate of N inputs continues to present challenges, as a multitude of environmental factors play major roles in determining N pathways. This research investigates the role of specific vegetation and subsequent soil and forest floor characteristics in the production and export of C and N within two adjacent watersheds at 730 to 850 m elevation in the Fernow Experimental Forest, near Parsons, WV. These watersheds have identical management histories, varying only in vegetation cover, where one watershed is a planted monoculture of Norway spruce (*Picea abies*) following clearcut felling 40 years ago and the other has regenerated to native Appalachian hardwood also following clearcut felling 40 years ago. Long-term stream chemistry indicates that the hardwood stand has approached N-saturation, with a very large stream export of N (15 kg NO^{3-}-N/ha/yr), whereas the spruce stand exhibits virtually no export of N to the stream. Soil lysimeters were installed at two depths and at several distances from the streams to investigate spatial and temporal patterns of soil solution chemistry and the dynamics of dissolved C and N. Water chemistry throughout the primary stream length in each watershed was analyzed monthly, along with multiple soil and forest floor characteristics, including C and N pools, N mineralization rates, pH, and exchangeable base cations. Stream, soil water, and soil chemical analyses indicate that pH, NO^{3-}, and total N are much lower in the spruce watershed than in the hardwood watershed. Soil aluminum (Al^{+3}) is significantly higher in the spruce watershed, though calcium (Ca^{+2}) concentrations in spruce soil are nearly a third that of the hardwood watershed (110 mg Ca/kg soil vs 290 mg Ca/kg soil, respectively). The forest floor in the spruce watershed has accumulated nearly twice the biomass and N per ha compared with the hardwood watershed. Thus, the forest floor in the spruce watershed may be a large sink for both C and N, through either biotic uptake of N or abiotic immobilization into humic compounds. The differences in C and N cycling observed within these two contrasting forest systems, which experience high N loads, may have implications for native spruce ecosystems at high elevations in the central Appalachians. These results suggest that spruce plays an important role in regulating water quality in high elevation forests impacted by high N deposition.

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MOUNTAIN BIRDWATCH: DEVELOPING A COORDINATED MONITORING PROGRAM FOR HIGH-ELEVATION BIRDS IN THE ATLANTIC NORTHERN FOREST

John D. Lloyd[1], Julie Hart, and J. Dan Lambert

Birds occupying high-elevation forests in the northeast are perceived to be at risk from a variety of external forces, most notably the potential loss and alteration of habitat associated with global climate change and the increased deployment of wind-energy facilities. However, the Breeding Bird Survey (BBS), a standardized national monitoring scheme widely used to monitor trends in the size of bird populations, does not adequately sample populations in high-elevation forests. Furthermore, ad hoc monitoring efforts intended to address the lack of high-elevation BBS routes, each using different sampling methods, have yielded only site-specific information and were of limited use in drawing regionwide inference about the status of birds in high-elevation forests. As a consequence, estimates of population size and trend are lacking for nearly all of the species occupying this habitat type. Mountain Birdwatch was created to address these information gaps. In its initial incarnation, Mountain Birdwatch enlisted volunteers to conduct bird surveys at high-elevation sites throughout the northeastern United States. This effort produced valuable information about occupancy rates for a suite of species, including the endemic Bicknell's thrush, but its value as a monitoring tool was limited by a nonprobabilistic sampling scheme and an inability to account for variation in the detectability of birds. An effort to refine Mountain Birdwatch and address these shortcomings was begun in 2006. Major challenges in the creation of Mountain Birdwatch version 2.0 included defining an appropriate sampling frame, identifying measurable goals, evaluating alternative approaches for sampling bird populations, and analyzing the resultant data, standardizing data management protocols, and envisioning tools and applications for broadly disseminating results, all while working with a diverse, international group of stakeholders. The process of producing a refined Mountain Birdwatch, ready to implement in 2009, offers valuable lessons and insight that may prove useful in implementing rigorous monitoring schemes for high-elevation birds in other regions.

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FRASER FIR STAND STRUCTURE IN THE BLACK MOUNTAINS OF NORTH CAROLINA

Rachael H. McManamay, Lynn M. Resle, and James B. Campbell[1]

Over the past several decades, naturally occurring populations of Fraser fir (*Abies fraseri* [Pursh.] Poir) have experienced devastating mortality rates due to attack by the exotic insect, balsam woolly adelgid (BWA) (*Adelges piceae* Ratz.). The decline in Fraser fir is particularly concerning because its natural geographic distribution is limited to seven disjunct mountaintop regions in the Southern Appalachians. Fraser fir is ecologically valuable and unique because it plays a crucial role in maintaining the integrity and composition of the spruce-fir forest ecosystem. Objectives of this study were to: 1) characterize Fraser fir stand structure 60 years after BWA infestation; 2) use current stand structure to make inferences about whether or not Fraser fir trees are following a cycle of regeneration-mortality that could lead to eventual decline of the population; 3) determine what role, if any, slope, elevation, aspect, and past land use history have on stand structure, mortality, and infestation level; and 4) use high-resolution aerial photography to visualize changes in spruce-fir cover in the Black Mountains over a 50-year period. Forty-four circular plots, ranging from 3.0 m to 8.5 m radius, were sampled in the Black Mountains, North Carolina, from June through September 2008. We found a significant difference between the mean diameter at breast height (d.b.h.) of live trees and dead trees over 4 cm. Mean d.b.h. of live trees was 9.89 cm. Mean d.b.h. of standing dead trees was 5.44 cm. Fraser fir mortality per plot ranged from 0 to 65.7 percent. Elevation was the only geographic variable found to significantly influence Fraser fir mortality. Forty-four percent of trees exhibited symptoms of BWA infestation but did not have BWA present at the time of sampling. Analysis of aerial photographs from 1954 and 1988 revealed that Fraser fir dominated forests with canopy cover greater than 50 percent, decreased nearly 80 percent over the time period, while spruce-fir codominated forests with canopy cover greater than 50 percent increased 209 percent. Preliminary results indicate that Fraser fir is not following a cycle of regeneration-mortality in the Black Mountains. Changes in spruce-fir cover over time can be linked to human induced disturbance factors and the invasive BWA.

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CRITICAL ACID LOAD LIMITS IN A CHANGING CLIMATE: IMPLICATIONS AND SOLUTIONS

Steven G. McNulty[1]

The federal agencies of the United States are currently developing guidelines for critical nitrogen load limits for U.S. forest ecosystems. These guidelines will be used to develop regulations designed to maintain pollutant inputs below the level shown to damage specified ecosystems. By traditional definition, an ecosystem is considered to be at risk when nitrogen loads exceed a critical level. The excess over the critical load is termed the exceedance, and a larger exceedance is often considered to pose a greater risk of damage to an ecosystem. This definition of critical loads applies to acute or chronic individual stress impacts, but does not work well when an ecosystem is subjected to multiple environmental stresses. For example, the mountains of western North Carolina received some of the highest rates of nitrogen deposition in the eastern United States, but these nitrogen deposition levels are still considered to be below the critical load rate. The area experienced a moderate three year drought from 1999-2002. In 2001, white pine and spruce trees began to die in large numbers in the area. The initial evidence confirmed that the affected trees were killed by the southern pine beetle (SPB). This insect species is not normally successful at colonizing these tree species because heavy oleoresin production exudes the boring beetles from impacted trees. Subsequent investigations revealed that the relative ratio of aboveground to belowground biomass was high compared to ratios of same species from lower nitrogen deposition areas. I believe that elevated nitrogen deposition reduced the root biomass, reduced the tree water-uptake potential, reduced oleoresin production, and caused the trees to become more to susceptible to insect colonization during the drought period. If multiple stress (i.e., drought and insects) impacts are included, then the forests in this area were in exceedance of their critical nitrogen threshold. Recent advances in ecosystem modeling of multiple stress impacts on forest ecosystems allow for more complex analysis of multiple stress scenarios. This paper explores how multiple environmental stress impacts can be assessed using computer models to determine variable critical load limits. The implications for improved forest management and pollutant regulation will also be presented.

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POTENTIAL IMPACTS OF CLIMATE CHANGE ON BIRD AND TREE HABITATS WITHIN THE APPALACHIAN MOUNTAINS

Stephen Matthews, Louis Iverson, Anantha Prasad, and Matthew Peters[1]

The habitats associated with the distributions of bird and tree species vary with the resolution of investigation and regional context, and especially within high-elevation forests. Our understanding of how bird distributions may shift with climate change was advanced by our understanding of how climate shapes the boundaries of a species' range. As our knowledge about how tree habitats may respond to climate change improves, we can begin to consider how birds, in turn, might respond to the changes in climate and vegetation. To accomplish this, we modeled the impact of climate change on the importance values of 134 tree species based on climate, elevation, soil, and landscape features. We then developed models of bird species distributions in the eastern United States, using climate, elevation and the previously modeled tree habitat importance values. We selected 147 representative bird species and generated predictive maps of their contemporary habitat associations. As with the tree species models, the bird models were then projected onto three models of climate change under high and low emissions scenarios The resulting bird models indicate that potential suitable habitat will decrease by at least 25 percent for 60 (high emissions) to 43 (low emissions) species and increase for 43 (high) to 18 (low) within the eastern United States. The importance that the Appalachian Mountains play in shaping future distributions of birds and trees, as they have done for millennia, will likely continue. The changes in habitat for birds and trees are characterized by a northeastern directional shift, which is greatly influenced by the Appalachian Mountains. In addition, for many bird species currently occupying this region, we see the habitat suitability decline but not disappear, possibly due to the birds' associations with both climate and tree species. The climate conditions may become less suitable or even unique, but the bird may still be able to occupy parts of the region because of suitable tree habitat, creating refugia for birds within the region. It is important to note that these results represent potential changes in habitat, and consideration of species specific life histories, landscape characteristics, and regional context are important components of model interpretation. Managers may be faced with unique combinations of bird habitat, making it necessary to consider objectives that include maintaining habitat for species vulnerable to projected changes and, in some cases, providing suitable habitat for species that may establish into new regions.

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OVERVIEW OF THE STATUS OF THE CHEAT MOUNTAIN SALAMANDER

Thomas K. Pauley[1]

Plethodon nettingi, the Cheat Mountain salamander, is endemic to the high elevations of the Allegheny Mountains in eastern West Virginia. In 1938, N.B. Green named the species from specimens collected at Barton Knob, Randolph County, in honor of his friend and colleague Graham Netting. Highton and Grobman considered *P. nettingi* a subspecies of the ravine salamander, *P. richmondi*, but subsequently Highton and Larson assigned it full species status. In 1989, the U.S. Fish and Wildlife Service listed *P. nettingi* as a threatened species.

Approximately 80 disjunct populations have been located throughout the total range, which extends about 93 km from Blackwater River Canyon (Tucker County) in the north to Thorny Flat on Snowshoe Mountain (Pocahontas County) in the south. The west to east range varies in distance from less than 0.8 km at the southern tip of the range to 30.5 km near the northern end. Vertically, populations tend to reach lower elevations in the northern part of the range than in the southern part. The highest elevation with *P. nettingi* is Spruce Knob (1,482 m) and the lowest is Blackwater River Canyon (609 m). Seasonally, the earliest date *P. nettingi* has been found on the surface is March 24 (1979 at Stuart Knob) and latest is October 19 (1943 at Gaudineer Knob). Mating occurs in late April or May, but there may be an abbreviated mating period in late September and early October. Females lay eggs in late April or May in well decayed red spruce logs or under rocks and logs. Females attend the nest and eggs hatch in about 4 months.

The disjunct distribution of *P. nettingi* appears to be the result of forest and ground fires that occurred between 1870 and 1930. These fires were, for the most part, the result of careless actions of lumbermen when the original forest was cut. Today, *P. nettingi* has a tenuous existence. Of the approximately 80 known populations, 60 are located on state or federal lands, which afford them more protection than those on private lands. Unfortunately, many populations on public lands are bisected into subpopulations by roads, hiking trails, utility rights-of-way, or ski slopes. Given these disturbances and competitive stress from *P. cinereus* (eastern red-backed salamander) and *Desmognathus ochrophaeus* (Allegheny Mountain dusky salamander), many of these disjunct populations could be imperiled.

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COMPOSITION OF HIGH-ELEVATION BREEDING BIRD ASSEMBLAGES AND ENVIRONMENTAL CORRELATES IN THE SOUTHERN BLUE RIDGE PROVINCE

Scott M. Pearson[1]

Climatic and landscape change threaten to alter the distribution, abundance, and quality of wildlife habitats in the Appalachians. Knowledge of habitat associations and potential responses to these forces of change will be necessary for informed management and conservation of high-elevation communities. The Blue Ridge Parkway provides a transect of over 750 km through the mountains of western North Carolina and Virginia and passes through the major elevation zones, vegetative types, and landscape settings representative of the southern Appalachian mountains. Breeding bird communities were sampled using point counts for 2 years. Topography and land cover around each point were assessed using spatial data from U.S. Geologic Survey and Southeast Gap Analysis Project to model species habitat relationships. The assemblage of bird species found in spruce-fir, northern hardwoods, and high elevation red oak forests, and open habitat types were determined. The degree of similarity and uniqueness among these assemblages was measured among vegetation types and among mountain regions of North Carolina and Virginia. At the local scale, avian diversity and the habitat occupancy of some species was influenced by the composition of the landscape surrounding each sampling point. At a broader scale, elevation and landscape composition were strong correlates of species composition and diversity; however, the influence of these factors varied geographically.

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EVOLUTIONARY HISTORY AND POPULATION GENETICS OF FRASER FIR AND INTERMEDIATE FIR, SOUTHERN APPALACHIAN ENDEMIC CONIFERS IMPERILED BY AN EXOTIC PEST AND CLIMATE CHANGE

Kevin M. Potter, John Frampton, Sedley Josserand, and C. Dana Nelson[1]

Two *Abies* (true fir) taxa are endemic to high elevations of the Appalachian Mountains, where both are restricted to small populations and are imperiled by the same exotic insect. Fraser fir (*Abies fraseri*) exists in a handful of island-like populations on mountain ridges in the southern Appalachians of North Carolina, Tennessee and Virginia. Intermediate or Canaan fir (*Abies balsamea* var. *phanerolepis*) occurs in scattered high-elevation bogs in West Virginia and on mountaintops in Shenandoah National Park in Virginia. Morphological and genetic similarities among Fraser fir, intermediate fir, and the northern, widespread balsam fir (*Abies balsamea*) have raised questions regarding the origin of the Southeastern fir taxa and have provoked debate about their taxonomic status. We used 10 microsatellite molecular genetic markers developed from Fraser fir to quantify genetic variation within Fraser fir and intermediate fir, and to examine the evolutionary relationships among Fraser, intermediate, and balsam fir. We found little genetic differentiation among these three taxa, suggesting that Fraser fir might better be classified as a variety of balsam fir (*Abies balsamea* var. *fraseri*) rather than as a separate species. The results further appear to reject the hypothesis that intermediate fir was of hybrid origin between balsam fir and Fraser fir. Intermediate fir and Fraser fir had lower genetic diversity than balsam fir by several measures, indicating that they have undergone at least some genetic degradation since they were fragmented and isolated from balsam fir at the end of the Pleistocene. Somewhat surprisingly, both intermediate fir and Fraser fir were most closely related to balsam firs from the Maritime provinces of Canada. The results help clarify how North American tree species have responded to the dramatic distributional shifts caused by long-term climate changes since the end of the last glaciation. The results may also prove important for *in situ* and *ex situ* gene conservation efforts for Fraser fir and intermediate fir. Fraser fir has experienced severe mortality across much of its range as a result of infestation by the balsam woolly adelgid (*Adelges piceae*), an insect from Eurasia, while intermediate fir stands in West Virginia have become infested more recently. Both Southeastern fir taxa face extirpation in the face of global climate change, which could make them unable to persist in their current natural stands while isolating them by great distances from the nearest suitable environments.

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IMPACTS OF CLOUD IMMERSION ON MICROCLIMATE, PHOTOSYNTHESIS AND WATER RELATIONS OF FRASER FIR IN A TEMPERATE MOUNTAIN CLOUD FOREST

Keith Reinhardt and William K. Smith[1]

The red spruce-Fraser fir ecosystem (*Picea rubens* Sarg.-*Abies fraseri* [Pursh] Poir.) of the southern Appalachian mountains is a temperate zone cloud forest immersed in clouds for 30 to 40 percent of a typical summer day, and experiencing immersion on about 65 percent of all days annually. We compared the microclimate, photosynthetic gas exchange, and water relations of Fraser fir trees in open areas during cloud-immersed, low-cloud, or sunny periods. In contrast to sunny periods, cloud immersion reduced instantaneous sunlight irradiance by 10 to 50 percent, and midday atmospheric vapor pressure deficit (VPD) was 85 percent lower. Leaf surfaces were wet for up to 16 h per day during cloud-immersed days compared to <1 h for clear days. Shoot-level light-saturated photosynthesis (A_{sat}) on both cloud-immersed (16.0 μmol m^{-2} s^{-1}) and low-cloud (17.9 μmol m^{-2} s^{-1}) days was greater than A_{sat} on sunny days (14.4 μmol m^{-2} s^{-1}). Daily mean A_{sat} was lowest on cloud-immersed days due to reduced sunlight levels, while leaf conductance (g) was significantly higher, with a mean value of 0.30 mol m^{-2} s^{-1}. These g values were greater than commonly reported for conifer tree species with needle-like leaves, and declined exponentially with increasing leaf-to-air VPD. Daily mean transpiration (E) on immersed days was 43 and 20 percent lower compared to sunny and low-cloud days, respectively. As a result, daily mean water use efficiency (A_{sat}/E) was lowest on cloud-immersed days due to light limitation of A_{sat}, and high humidity resulted in greater uncoupling of A_{sat} from g. Thus, substantial differences in photosynthetic CO_2 uptake, and corresponding water relations, were strongly associated with cloudy sky conditions.

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EARLY RED SPRUCE REGENERATION AND RELEASE STUDIES IN THE CENTRAL AND SOUTHERN APPALACHIANS

James Rentch[1]

The aftermath of exploitative harvesting and destruction by fire during the 1920s was first encountered by forest researchers employed by the Appalachian Forest Experiment Station (AEFS) based in Asheville, NC. Two of the more productive researchers were Clarence F. Korstian and Leon S. Minckler, and their studies remain instructive today. This presentation will review their primary conclusions.

Clarence F. Korstian was employed as a silviculturist by the AFES in 1922. His first assignment was to describe conditions on cut-over and burned red spruce stands on the newly formed Monongahela National Forest (WV) and Pisgah National Forest (NC), to outline the reproductive potential of these stands, and to give practical guidance for restoration of this forest type. He compared naturally released, partially released, and unreleased red spruce on cutover stands and found that even for stems that had been suppressed for more than 50 years, fully released red spruce seedlings and saplings could increase annual basal area by as much as 161 percent after 35 years, comparable to stems that had never been suppressed. Trees with large, well formed, pointed crowns and dense foliage responded more quickly and attained higher growth increases than trees with small, rounded crowns and thin foliage. Between 1923 and 1931, Korstian, along with E.F. Frothingham, also initiated a series of planting trials to determine the best species combinations for reforestation of cutover lands. Initially, 20 native and exotic species were tested, and four (red spruce, red pine, balsam fir, and Norway spruce) were considered suitable for reforestation efforts.

Leon Minckler completed and reported on much of this work. In 1945, he presented 3-year results of additional planting trials. Minckler recognized that competing vegetation constituted the biggest obstacle to planting success, and he delineated three common types of sites: 1) those with dense (≥ 80 percent) herbaceous (e.g., bracken, hay-scented fern) and shrubby (blackberry) vegetation, often the best growing sites; 2) young stands of brushy hardwoods (pin cherry, red maple); and 3) burned rocky sites with thin pockets of soils and sparse (< 40 percent) vegetation. Of the 10 treatments tested on type 1 sites, seedling release during the first growing season yielded the greatest survival and growth. For brushy hardwood stands, overhead release again yielded the greatest success. Depending on vegetation density, additional releases were required during the third and potentially the fifth summers, however small openings (5 ft) were as successful as larger openings (10 ft). On severely burned sites, direct seeding of red spruce and balsam fir were relatively successful, however use of normal planted 2-1 nursery seedlings were as successful as super planting stock, fertilizer, rooting hormones, or plant growth regulators. On these sites, the immediate objective was establishment of future seed trees, not reforestation. Ten-year results summarized by Wahlenberg (NC) and Clark (WV) were consistent with Minckler's earlier observations. Practitioners engaged in red spruce restoration should carefully review the results of these and other early researchers.

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THE NATIONAL AUDUBON SOCIETY'S EASTERN FOREST CONSERVATION INITIATIVE: EXAMINING OPPORTUNITIES FOR BIRD CONSERVATION AT A REGIONAL SCALE

Curtis Smalling and Mary Elfner[1]

The forests of the east are under tremendous pressure from a variety of sources, including increasing development and fragmentation, declining air quality, declining water quality, and global climate change. Many priority bird species depend on these forested habitats, including a high percentage (75 percent) of neotropical migrant breeding species. The Eastern Forests Initiative within the National Audubon Society is a new focus of an Eastern States Alliance for Bird Conservation undertaken by Audubon in 2008. Utilizing the backbone of the Important Bird Areas program (IBA), Audubon is identifying those areas within priority habitats (including high-elevation forests) for maximum bird conservation value. Using the methods of the Open Standard for the Practice of Conservation (Conservation Measures Partnership, 2007), Audubon is identifying conservation actions within those forests for birds where there are shared biological resources, shared threats to those resources, and opportunities for shared conservation outcomes. This program will highlight this process and inform potential partners of the status of the project.

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A FRAMEWORK FOR ADDRESSING BIRD CONSERVATION PRIORITIES IN HIGH-ELEVATION VEGETATION COMMUNITIES OF THE APPALACHIAN MOUNTAINS

Brian W. Smith, Dean Demarest, and Ed Laurent[1]

The Appalachian Mountains Joint Venture (AMJV) is a self-directed, nonregulatory bird conservation partnership with the mission of restoring and sustaining native bird populations and their habitats throughout Appalachia. In 2008, the AMJV formed an ad hoc "high-elevation" technical working group to identify and address conservation priorities of bird species reliant on spruce-fir, northern hardwood, and other vegetation communities typically associated with the highest elevations of the Appalachian Mountains. We outline specific goals and guiding principles that frame the working group's activities and discuss initial efforts to spatially and thematically define "high-elevation" bird conservation issues within the Appalachian Mountains. Additionally, we identify conceptual and practical approaches that the AMJV is using to achieve our conservation goals, and define critical data needs that must be fulfilled to ensure success. Finally, we will use this forum to engage new partners in our efforts, and solicit input from on-the-ground managers to gain a better understanding of what information they need to improve conditions for populations of priority birds in the region.

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ECOPHYSIOLOGY OF SEEDLING ESTABLISHMENT IN CONTRASTING SPRUCE-FIR FORESTS OF SOUTHERN APPALACHIAN AND ROCKY MOUNTAIN ECOTONES, USA

William K. Smith, N.C. Keith Reinhardt, and Daniel M. Johnson[1]

Fraser fir (*Abies fraseri* [Pursh] Poiret) and red spruce (*Picea rubens* Sarg.) occur as codominant trees in six relic, mountain-top populations that make up the high-elevation forests of the Southern Appalachian Mountains (SA). These two relic species of the former boreal forest have experienced a significant decline over the past century, most likely due to an introduced insect and/or air pollution. There also appears to be accumulating evidence that natural seedling regeneration appears to be inadequate for replacing these relic spruce-fir forests. Survival in young seedlings of *A. fraseri* and *P. rubens* was increased most (>90 percent) by a facilitated reduction in sky exposure, which was not negatively influenced by water competition with the surrounding plants that reduced sky exposure. Current year seedlings of *A. fraseri* had the least first-year seedling mortality under canopy gaps, compared to the relatively high values found in both closed-canopy and entirely open microsites. Similar trends in photosynthesis occurred and have also been reported for *Abies lasiocarpa* and *Picea engelmannii* in the more xeric spruce-fir forests of the western United States. Avoidance of sky exposure enables warmer needle temperatures at night due to less long-wave radiation exchange to the cold night sky, as well exposure to high levels of incident sunlight the following morning. This combination of stress factors that causes a substantial limitation to annual photosynthetic carbon gain associated with a high mortality (>90 percent), decreased root growth, and low ectomycorrhizal colonization, both of which appeared critical for preventing lethal water stress during the high-mortality in pre-established seedlings. Different modes of adaptation to this combination of stress factors included (i) avoidance mechanisms related to microsite facilitation and phenotypic adjustments in plant architecture, as well as (ii) differences in physiological tolerance that varied between the fir and spruce seedlings. Thus, survival of establishing seedlings in spruce-fir forests may be strongly dependent on microsite protection from sky exposure (e.g., surrounding plants and inanimate structures, plus canopy openness). This sky exposure may be greatest in ecotones between the forest and higher altitude communities such as grass balds in the southern Appalachians or the alpine zone in the Rocky Mountains. Moreover, these ecotonal boundaries could also serve as early indicators global change impacts such as warming temperatures and changing precipitation patterns.

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ALTITUDINAL GRADIENTS OF BRYOPHYTE DIVERSITY AND COMMUNITY ASSEMBLAGE IN SOUTHERN APPALACHIAN SPRUCE-FIR FORESTS

Sarah E. Stehn, Christopher R. Webster, Janice M. Glime, and Michael A. Jenkins[1]

Ground-layer plant communities in spruce-fir forests of the southern Appalachians have likely undergone significant change since the widespread death of canopy Fraser fir (*Abies fraseri*) caused by the exotic balsam woolly adelgid (*Adelges piceae*). Bryophytes comprise an important part of the ground-layer flora in the spruce-fir zone, with an average cover of 26 percent and richness and diversity values rivaling those of the herbaceous layer, yet few contemporary studies have given them significant attention. In attempts to quantify post-adelgid bryophyte community composition, structure, and distribution, we randomly selected 60 plots within spruce-fir forests on the high peaks of Great Smoky Mountains National Park. At each plot, we quantified ground-layer bryophytes by recording species and cover by the line-intercept method along every other meter of three 20 m transects, for a total sampling distance of 1,800 m.

A nonmetric multi-dimensional scaling ordination revealed that, of the environmental variables measured, elevation, deciduous basal area, and cover of ground-layer vegetation had the greatest influence on bryophyte community composition. We attribute altitudinal gradients of bryophyte diversity and community composition to variation in deciduous basal area and thus litter quality, the prevalence of herbaceous plants, and the degree of canopy balsam woolly adelgid infestation. Bryophyte species groups (acrocarpus mosses, pleurocarpus mosses, and liverworts) respond differently to deciduous litter accumulation and competition from ground-layer vegetation based on substrate preference and growth characteristics of the individual species within those groups. We conclude that although disturbance caused by the balsam woolly adelgid creates valuable substrate for bryophyte colonization, it also may contribute to an increase in light availability and deciduous basal area due to the decline of conifers and thus has the potential to have a profound effect on bryophyte diversity and community assemblage.

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SEEING THE BIGGER PICTURE: MULTI-PARTNER SPRUCE RESTORATION IN THE CENTRAL AND SOUTHERN APPALACHIAN MOUNTAINS

Jack Tribble, Thomas Minney, Catherine Johnson, and Ken Sturm[1]

Habitat-based ecosystem partnerships are necessary for implementing strategic forest restoration plans. Overwhelming environmental threats such as climate change and invasive pests and pathogens could have traumatic and devastating effects to our native forests. Additionally, past land-use history has left existing forests isolated, fragmented and in some cases extirpated from the historic landscape. Effective strategies for dealing with these threats can only be built if they are addressed at a broad spatial scale and across public-private ownerships. Habitat-based conservation requires a cohesive group working across boundaries in order to achieve the scale, connectivity, and coordinated management that lead to a sustainable ecosystem. The multi-partner High Elevation Conservation Working Group strives for the return of a functioning red spruce-northern hardwood forest ecosystem across both public and private lands. Seeking common ground and overlapping perspectives was essential to the proactive group planting more than 35,000 trees last year. This presentation and panel discussion explored successful partnership building and issues for landscape-scale restoration. It focused on building a broad-scale, long-term vision for the resource, and an effective, inclusive partnership, as well as how to move from talk to implementation through cooperation.

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UPDATE ON TERRESTRIAL ECOLOGICAL CLASSIFICATION IN THE HIGHLANDS OF WEST VIRGINIA

James P. Vanderhorst[1]

The West Virginia Natural Heritage Program (WVNHP) maintains databases on the biological diversity of the state, including species and natural communities, to help focus conservation efforts by agencies and organizations. Information on terrestrial communities (also called vegetation, or habitat, depending on user or audience focus) is maintained in two databases. The Plots2-WV database now contains standardized vegetation and environmental data from more than 3,000 plots sampled by WVNHP ecologists, contractors, cooperators, and outside contributors. These plot data form the basis for vegetation and ecological system classifications which are applied as conceptual and mapping tools to serve as coarse filters for conservation. The Biotics database contains information on known occurrences of rare species and natural communities and on exemplary occurrences of more common natural communities. Biotics, centrally administered by the nonprofit NatureServe, also relates occurrence information gathered by individual state and provincial programs to provide continent-wide information on taxonomy, distribution, and conservation status of species and natural communities. Both Plots2-WV and Biotics represent cumulative efforts; they are undergoing constant development as new data are collected and entered, as new analyses are performed, and as classification systems are refined and revised.

Attribution of 1,286 West Virginia plots from elevations above 773 m (the state median) to NatureServe's ecological systems provides a broad-scale, low-resolution picture of vegetation patterns in the highlands of the state. Nineteen ecological systems are documented including Allegheny-Cumberland Dry Oak Forest and Woodland, Appalachian (Hemlock)-Northern Hardwood Forest, Appalachian Shale Barrens, Central and Southern Appalachian Montane Oak Forest, Central and Southern Appalachian Spruce-Fir Forest, Central Appalachian Alkaline Glade and Woodland, Central Appalachian Dry Oak-Pine Forest, Central Appalachian Pine-Oak Rocky Woodland, Central Appalachian Stream and Riparian, High Allegheny Wetland, North-Central Appalachian Acidic Cliff and Talus, North-Central Appalachian Circumneutral Cliff and Talus, Northeastern Interior Dry-Mesic Oak Forest, South-Central Interior Large Floodplain, South-Central Interior Mesophytic Forest, South-Central Interior Small Stream and Riparian, Southern and Central Appalachian Cove Forest, Southern Appalachian Grass and Shrub Bald, and Southern Appalachian Oak Forest.

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RED SPRUCE RESTORATION MODELING IN LANDIS

Melissa Thomas-Van Gundy[1]

Scenarios for the restoration of red spruce (*Picea rubens*)-dominated forests on the Monongahela National Forest were created in the landscape simulation model LANDIS. The resulting landscapes were compared to existing habitat suitability index models for the Virginia northern flying squirrel (VNFS) and Cheat Mountain salamander (CMS) as a measure of successful restoration. Four restoration scenarios were included: 1) succession without active management; 2) active management of red spruce only in low probability VNFS or CMS habitat; 3) active restoration of red spruce on all feasible sites; and 4) active management in spruce and spruce-northern hardwood dominated forests only. In scenario 2, direct effects to rare wildlife species will largely be avoided. Although scenario 3 represents a maximum restoration scenario, planting of red spruce is not included in the model. In scenario 4, restoration efforts avoid forested stands with substantial components of high-value hardwood timber species such as black cherry.

The objectives of this research are to develop feasible restoration scenarios involving active and passive management and compare the resulting landscape structure and composition. With a landscape-level analysis, an assessment can be made of the ability of the restoration scenarios to benefit endangered species, including the length of time to reach restoration goals.

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CHARACTERIZATION OF THE ECOLOGICAL REQUIREMENTS FOR THREE PLETHODONTID SALAMANDER SPECIES

Jessica A. Wooten, William B. Sutton, and Thomas K. Pauley[1]

Increased availability of habitat and climate data has facilitated much research concerning the influence of these characteristics on the structure of salamander communities. We aimed to outline environmental requirements influencing the distribution of three sympatric plethodontid salamander species, including *Plethodon cinereus, Desmognathus ochrophaeus,* and the federally protected *Plethodon nettingi.*

To examine differences in microhabitat use, we collected a series of microhabitat variables at "present" and "absent" sites for each species. We tested multiple microhabitat models with logistic regression followed by Akaike's Information Criterion to select the most parsimonious microhabitat model based on logistic regression results. Akaike's Information Criterion is advantageous for studies of microhabitat use because multiple working hypotheses can be evaluated simultaneously. Each hypothesis is ranked with the top model representing the most parsimonious solution. We found that *P. nettingi* was positively associated with sites possessing emergent rock cover and historic fire, while *D. ochrophaeus* and *P. cinereus* were negatively associated with these site attributes.

To better understand the geographic distribution of these salamanders, we used abiotic variables to predict species' distributions via ecological niche modeling (ENM) with the maximum entropy algorithm. Ecological niche modeling uses point locality data combined with environmental data to make spatially explicit predictions concerning geographic areas that are suitable for a particular taxon. These environmental data can then be used to define abiotic requirements of taxa, explore speciation, compare diversity gradients, and investigate concordant phylogeographic patterns. Furthermore, predictions made by ENM allow for identification of new geographic areas where there is suitable climate for organisms; this has important conservation and management implications. Not surprisingly, we revealed that *P. cinereus* was predicted to inhabit a larger geographic area than either *P. nettingi* or *D. ochrophaeus.* This indicates that *P. cinereus* individuals can tolerate a wider range of abiotic variables than *P. nettingi* or *D. ochrophaeus.*

Collectively, our analyses attempted to predict the fundamental niche for each of these salamander species. Our analyses suggest that the current distribution and microhabitat associations of *P. nettingi* are due to a series of drastic habitat disturbances and resulting competitive interactions between these species. Although *D. ochrophaeus* and *P. cinereus* were undoubtedly affected by these disturbances, these two species appear to tolerate broad microclimate and microhabitat characteristics and have a less restricted distribution than *P. nettingi*. Our results indicate that it is imperative to protect remaining red spruce forests to ensure the long term survival of disjunct *P. nettingi* populations.

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ABSTRACTS OF POSTER PRESENTATIONS

USING ENVIRONMENTAL AND SITE-SPECIFIC VARIABLES TO MODEL CURRENT AND POTENTIAL DISTRIBUTION OF RED SPRUCE FOREST HABITAT IN WEST VIRGINIA

Nathan Beane and James Rentch[1]

With the extensive loss of presettlement habitat for red spruce, this species is a high priority for restoration in West Virginia. The advent of climate change caused by human activity and the uncertainty of future environmental changes has also raised interests in the protection and restoration of red spruce ecosystems. Red spruce forests are considered preferred habitat for the endangered Cheat Mountain salamander (*Plethodon nettingi* Green) and provide optimal habitat for the recently delisted Virginia northern flying squirrel (*Glaucomys sabrinus fuscus* Miller). In addition, the ability of red spruce to grow on high-elevation, nutrient-poor soils is beneficial for carbon sequestration. The expansion and/or recovery of red spruce forest habitat are needed for conservation of the valuable resources which these forests offer. The objective of our research is to use environmental and site-specific variables to model the current distribution of red spruce habitat in West Virginia. Specifically, we wish to model habitat along abundance gradients of low, medium, and high, using red spruce importance values derived from plot data (~250 samples) collected in summers 2008 and 2009 throughout the Appalachian Mountain Region of West Virginia. Finally, we wish to perform a risk assessment using hypothesized climate change scenarios. This assessment will be done by manipulating climatic variables of the models to simulate expected changes in climate. Modeling efforts will be performed using Maximum Entropy (MAXENT), a species distribution modeling technique used to characterize a species' niche in environmental space. This analysis will allow us to model future distribution of red spruce habitat in West Virginia, identifying areas where red spruce would likely occur under select climate change scenarios. This research will make a valuable contribution to the conservation and restoration efforts for threatened red spruce ecosystems in West Virginia.

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BALSAM FIR CONSERVATION AND RED SPRUCE ECOSYSTEM RESTORATION INITIATIVES IN THE WEST VIRGINIA HIGHLANDS

Corey A. Bonasso and David W. Saville[1]

The West Virginia Highlands Conservancy has been working for more than a decade to protect, conserve, and restore the spruce-fir forests in West Virginia. Beginning in the mid 1990s an effort was initiated to conserve balsam fir in West Virginia where it reaches its southern most extent in North America. This work led to further efforts which have focused on the restoration of the broader red spruce ecosystem that was once prevalent in the West Virginia Highlands.

The project initially sought to protect the genetic diversity of the various stands of balsam fir around the state that were coming under threat from the exotic insect pest the balsam woolly adelgid. Research by Ohio State University and others suggested that there were significant genetic trait differences between West Virginia stands and with those of balsam fir located further north. Conservation actions ensued to protect this diversity by fostering regeneration of existing stands of balsam fir. Volunteers were organized to collect cones from each of the known stands of balsam fir in West Virginia. Seed was extracted and stored separately at the NRCS Plant Materials Center in Alderson, WV.

Stand regeneration in many areas was not occurring because of heavy deer browse. Through cooperative efforts with state and federal land managers, as well as private land owners, numerous deer exclosures are being constructed in natural balsam stands to allow both natural regeneration and careful restoration activities using seed and seedlings grown from the locally collected cones. Seedlings have since been grown annually for over 10 years for use in restoration projects.

Efforts have been undertaken to restore the red spruce forests and the ecosystem associated with it. Once covering as much as 500,000 acres of the West Virginia Highlands they provide a unique habitat for numerous rare, threatened and endangered species. Logging, fires and development have significantly reduced and fragmented these forests. Cones have been collected and seed banked at the NRCS Plant Materials Center. Landscape-scale restoration plans have been developed focusing on the expansion and connection of patches of red spruce forest. Over 100,000 red spruce seedlings have been planted implementing these plans in numerous restoration and reclamation projects across the highlands. The Highlands Conservancy has also been working on an educational outreach program to build awareness of the historical as well as the current and future ecological importance of the high elevation red spruce forests in West Virginia.

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MANAGEMENT OF GRASSY BALD COMMUNITIES IN THE ROAN HIGHLANDS

James T. Donaldson, N. Schubert, and Lisa C. Huff[1]

No place better exemplifies that which is rare and unique within high-elevation communities of the Appalachian Mountains than the highlands of Roan Mountain. The Roan Highlands are protected through a landscape-level conservation initiative originally established by the Southern Appalachian Highlands Conservancy and the U.S. Forest Service in 1974. The Roan massif rises more than 6,000 ft above mean sea level and straddles the border of North Carolina and Tennessee in the Pisgah and Cherokee National Forests, respectively. Among its unique aspects, the Roan supports 800 known plant species, 27 rare plant communities, and 33 federally or state-listed threatened and endangered species, 27 of which are globally rare. Its threatened community types include: heath balds, seeps, red spruce-Fraser fir forests, grassy balds, and rocky summits, of which the latter three are deemed in need of restoration, in addition to preservation. The grassy balds have been a focus of management in the Roan Highlands, largely due to their iconic status within these high elevation communities. To wit, the grassy balds provide splendid, panoramic views of the high-elevation landscape; they predate European settlement and their origins are enigmatic; the Roan's grassy balds represent the highest quality and the longest linear stretch of this community type remaining in the southern Appalachians; they provide habitat for 10 regionally rare species and numerous locally rare species. The Roan's grassy balds currently occupy less than 25 percent of their historic extent. Trees, shrubs, and blackberries have encroached into the grassy balds due to a lack of natural and anthropogenic disturbances and inadequate levels of management. With so much biodiversity at stake, the scientific and conservation communities determined that broad management partnerships must be formed to sustain the rare elements of the Roan; multiple governmental and nongovernmental organizations have worked together toward mutual conservation goals since the early 1970s. Currently known as the Roan Stewardship Committee, these managing entities collaborated with the Forest Service to establish a restoration goal of approximately 2,000 ac of the Roan's grassy balds in 1991, but that goal has not been met. In this study, we present information recently gathered by members of the Roan Stewardship Committee on efforts to maintain and restore grassy balds communities in the Roan Highlands, emphasizing recent summaries of historic and current adaptive management efforts, as well as data from the first year (2008) of a browsing study known as the Baa-tany Goat Project.

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MAPPING THE CURRENT AND POTENTIAL DISTRIBUTION OF RED SPRUCE IN VIRGINIA: IMPLICATIONS FOR THE RESTORATION OF DEGRADED HIGH-ELEVATION HABITAT

Heather Griscom, Helmut Kraenzle, and Zachary Bortolot[1]

The objective of our project is to create a habitat suitability model to predict potential and future red spruce forest distributions. This model will be used to better understand the influence of climate change on red spruce distribution and to help guide forest restoration efforts. We also anticipate creating a procedure that uses freely available remotely sensed data to locate new red spruce stands and improve the accuracy with which known stands are mapped. In order to accomplish our two objectives, we will integrate remote sensing analysis, GIS analysis, field surveys, and experimental field research. Few studies have used GIS and remote sensing technology to create habitat suitability models and even fewer models have been created to identify restoration sites for forest ecosystems at a large scale. Red spruce was selected as our model species because it is one of the most threatened forest ecosystems in the United States. Many previously forested areas that were historically dominated by red spruce appear to be in a state of arrested succession in the form of stunted, species-poor forest stands or shrub-dominated glades. We anticipate identifying all current red spruce stands in Virginia and potential restoration sites with our proposed methodology. Degraded areas for red spruce restoration will be prioritized based on land-use data. The information will then be disseminated to forest restoration organizations to increase the effectiveness in restoring this critical habitat, either to offset carbon emissions or to conserve biological diversity.

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HERMIT THRUSH BREEDING RANGE EXPANSION AND HABITAT PREFERENCES IN THE SOUTHERN APPALACHIAN HIGH-ELEVATION FORESTS

Andrew J. Laughlin[1]

The hermit thrush (*Catharus guttatus*) is a wide-ranging migratory songbird that is found throughout much of North America. In eastern North America, the hermit thrush spends the winter months in the southeastern states. During the summer breeding season, it migrates north and breeds across much of Canada, New England, and down the ridge of the Appalachian Mountains south of Pennsylvania. Over the last several decades, this bird has been expanding its breeding range further south along the chain of the Appalachian Mountains into the spruce/fir and spruce/northern hardwood forests of Virginia, Tennessee, and North Carolina. Though no nest has yet been discovered in Tennessee or North Carolina, evidence of breeding exists from the banding of fledglings on Roan Mountain over the last several years, and other reports of fledglings found near attending parents.

No formal study of the habitat preferences of the hermit thrush in the spruce/fir and spruce/northern hardwood forests has yet been conducted. For my master's thesis at East Tennessee State University, I will compare the habitat preferences of the hermit thrush and its closely related congener, the veery (*C. fuscescens*). The veery has been a breeding resident in these high-elevation forests since bird surveys began over a century ago, but the hermit thrush is a relatively new arrival. Comparing the habitat preferences of these two forest thrushes will shed light on the local ecology of the hermit thrush, and delineate any habitat partitioning occurring between them. This study will also indicate how these birds are responding to the changes that are taking place in these highly fractured forests.

The forests in which this study will take place are under major stress due to several factors, including acid deposition, the balsam woolly adelgid, and perhaps climate change. Preliminary data indicates that the hermit thrush may be taking advantage of the recent canopy openings and subsequent understory development occurring from the massive Fraser fir die-off. It is important to document how birds that are area-sensitive like the forest thrushes are utilizing different levels of the forest structure. This is especially relevant for forest managers in the dynamic environment of the Southern Appalachian high-elevation forests.

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SPECIES DISTRIBUTION AND RICHNESS PATTERNS OF AVIAN COMMUNITIES IN THE HIGH-ELEVATION FORESTS OF VIRGINIA

Heather Lessig, William J. McShea, and Jeffrey R. Walters[1]

The southern Appalachians support a unique forest ecosystem at higher elevations in which the breeding distribution of several bird species of conservation concern extends to unusually southern latitudes. The dual threats of rising global temperatures and potential wind energy development may impact these forests by reducing or fragmenting preferred habitat. A better understanding of which bird species are sensitive to change and how habitat composition and configuration drive species richness across all elevations is essential for deriving local management plans and preserving regional diversity. We conducted bird surveys and corresponding site and landscape level habitat surveys at multiple high elevation sites on public forests in Virginia from 2005-2007. We detected 101 species at 1,341 points, including 12 species of state or federal conservation concern. We generated multiple models using 10 species whose presence increased with elevation to determine the relative contribution of habitat characteristics at the local and landscape levels. These models indicate that elevation sensitive species respond to multiple habitat scales in a species-specific manner and that management plans should consider more than habitat type. In addition, we show that species richness declines with increasing elevation throughout the region until the highest elevations, where the trend reverses and richness begins to increase. This pattern is driven by differences between migratory guilds and may be caused by more than habitat associations alone. Results highlight the importance of considering scale when determining species distribution and richness and the need to consider multiple habitat factors in conservation planning and management of high-elevation forests.

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GROWTH OF AMERICAN CHESTNUT AND INCIDENCE OF CHESTNUT BLIGHT IN THE FOREST UNDERSTORY

Amy Milo[1]

Three hundred individuals of American chestnut, *Castanea dentata,* at Mountain Lake Biological Station, elevation 1,160 m, were monitored over two field seasons for incidence and growth of cankers caused by the fungus *Cryphonectria parasitica*. Basal disks were collected from 150 individuals that died over the study period and their growth rings were measured for dendrochronological analysis. All individuals were understory trees, and all showed evidence of suppression with a release event occurring in the mid-1990s. Most trees exhibited significantly lower than normal growth for 1 to 3 years before death. Growth histories will be compared with individual disease histories for *C. parasitica* to see if reduced growth is an indicator of disease. Results will show whether local stem density, seasonality, or rate of tree growth affect infection probability, canker growth rate, and tree mortality.

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MODELING THE BREEDING HABITAT DISTRIBUTION OF THE APPALACHIAN YELLOW-BELLIED SAPSUCKER IN NORTH CAROLINA

Scott M. Pearson and John Gerwin[1]

The breeding range of the yellow-bellied sapsucker (*Sphyrapicus varius*) includes forested habitats across northern North America as well as a portion of the southern Appalachian Mountains. Southern populations may be disjunct and ecologically distinct from northern populations, and additional information is needed about their geographic range and preferred habitats. Presence/absence data, GIS maps of elevation and topography, and four quantitative modeling techniques (logistic regression, linear discriminant analysis, Mahalanobis distance, and classification tree) were used to produce habitat maps for this species in North Carolina. Sensitivity and specificity of the quantitative models were compared to each other and to an expert opinion map developed by the NC GAP Analysis Program. The classification tree and a composite model, which combines results from several approaches, had the highest levels of specificity and accuracy. Quantitative models revealed that sapsucker occupancy was greatest on submesic mid-slopes, plateaus, and rounded knobs and slopes at elevations between 1,160 to 1,400 m. These topographic positions are occupied by high-elevation red oak forests as well as some northern hardwood and cove hardwood forests. The modeling results agree with field studies of habitat use in the study region. The elevation range of all occurrences (900 to 1,600 m) disagrees with anecdotal records which list the lower elevation limit for these populations at 1,065 m. Quantitative models can be used to refine the coarse-grained GAP models and guide future studies of habitat selection and population dynamics. Related website: http://biology.mhc.edu/ybsa

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DYNAMICS OF MID-APPALACHIAN RED SPRUCE-HARDWOOD ECOTONES

Adam W. Rollins, Harold S. Adams, and Steven L. Stephenson[1]

Ten belt transects, each consisting of a series of contiguous 10 x 10 m (100 m^2) quadrats were established between 1992 and 1994 at seven study sites in the mountains of southwestern Virginia and eastern central West Virginia. All of the study sites occurred in areas where a relatively distinct and narrow ecotone existed between a forest community dominated by red spruce (*Picea rubens* Sarg.) and one dominated by hardwoods. Each transect was positioned so that it extended from the red spruce community, across the ecotone (the transition zone between hardwood and red spruce community), and into the hardwood community. Eighteen quadrats occurred in the hardwood community, 31 in the ecotone, and 18 in the red spruce community. In 2004 and 2005, all transects were resampled to assess the changes that had taken place. Results indicate that all strata of vegetation had exhibited compositional changes in such a way that both the ecotone and hardwood portions of the transect are becoming more similar to the red spruce portion. In general, red spruce either maintained its ecological status or increased in numbers in all size classes, with a noticeable expansion into the surrounding hardwood community at some study sites.

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INFLUENCE OF ACID DEPOSITION ON REGENERATION DYNAMICS ALONG A DISTURBANCE INTENSITY GRADIENT

Sarah E. Stehn, Christopher R. Webster, Michael A. Jenkins, and Shibu Jose[1]

Now considered one of the most threatened vegetation communities in North America, spruce-fir forests of the southern Appalachians have been devastated by the combined impacts of the exotic balsam woolly adelgid (*Adelges piceae,* BWA) and chronic acid deposition. Endemic Fraser fir (*Abies fraseri*), the dominant overstory species in these forests, has experienced near complete overstory mortality as a result of the adelgid. Forest regeneration patterns indicate high spatial variability, with dense patches of *Rubus* spp., fir, and deciduous regeneration repeating across the landscape. To quantify the spatial variability and density of fir, spruce, and deciduous regeneration in spruce-fir forests, we sampled 60 randomly selected plots within Great Smoky Mountains National Park. As a measure of local variability of regeneration, we used regeneration density of thirty 1-m^2 subplots per plot to calculate a coefficient of within-plot variation for each species.

Despite the impacts of the BWA and chronic acid deposition, fir remains an important part of southern Appalachian spruce-fir forests in all size classes at elevations above 1,750 m. Density of fir in all size classes was associated with time since disturbance. On plots where fir regeneration was present, its local variability was significantly greater than that of spruce or deciduous regeneration. Regression models attributed local variation in fir to the influence of elevation, *Rubus* spp. cover, B-horizon nitrogen concentration, and O-horizon calcium to aluminum ratio. We propose that concurrent influences of BWA infestation and acid deposition may have cultivated the development of soil nutrient hotspots that foster increased competition from nitrophilous ground-layer vegetation such as *Rubus* spp. Additional or co-occurring aluminum hotspots may also exclude sensitive plants by toxicity, further influencing ground-layer competition. Given that full recovery of this imperiled ecosystem remains uncertain, the persistence of this forest type may hinge on the response of ground-layer species and woody regeneration to continued disturbance.

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RED SPRUCE AS WITNESS TREE ON THE MONONGAHELA NATIONAL FOREST

Melissa Thomas-Van Gundy[1]

A digital database of witness tree locations has been created from the earliest deeds of the area now within the Monongahela National Forest. These locations were used to describe the distribution, environmental gradients, and associated tree species of red spruce (*Picea rubens*) in eastern West Virginia from between 1771 and 1889. Contingency table analysis and analysis of standardized residuals were used to assess environmental gradients underlying observed tree species distributions. Indicator kriging was used to create continuous tree species probability coverage of the study area. The distribution of red spruce from witness trees was compared to the current distribution.

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The proceedings includes 18 peer-reviewed papers and 41 abstracts pertaining to acid deposition and nutrient cycling, ecological classification, forest dynamics, avifauna, wildlife and fisheries, forests pests, climate change, old-growth forest structure, regeneration, and restoration.

http://www.nrs.fs.fed.us/