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

Gregory Nowacki, Robert Carr, and Michael Van Dyck[1]

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

[1] Regional Ecologist (GN), GIS Analyst (RC), and Timber Measurement Specialist (MVD), respectively U.S. Forest Service, Eastern Regional Office, Milwaukee, WI. MVD has since transferred to the Forest Management Service Center in Fort Collins, CO.

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

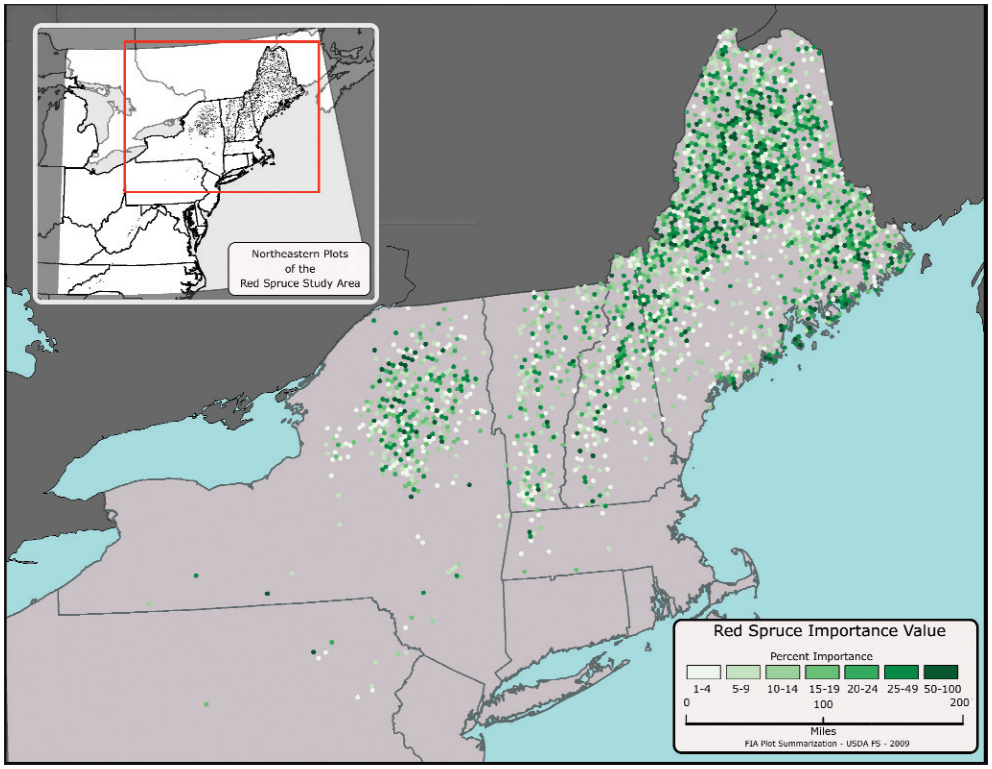

Figure 1.—Spatial projection of red spruce importance in the Northeast using the Forest Inventory and Analysis hexagon grid. Dots represent approximate plot locations.

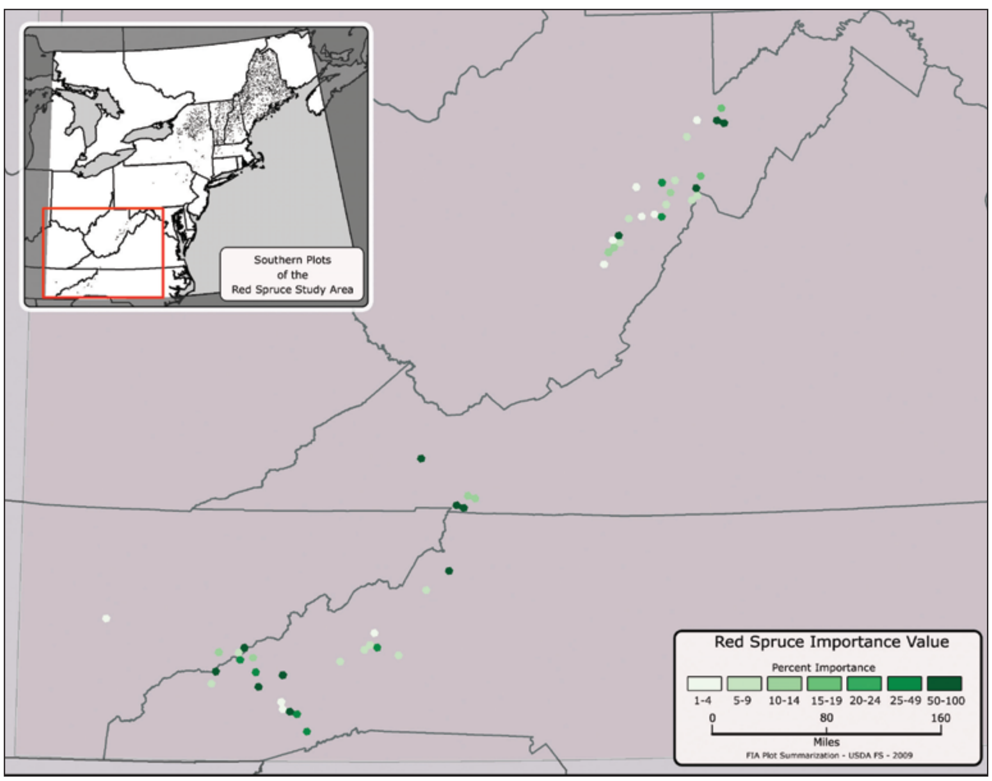

Figure 2.—Spatial projection of red spruce importance in the Central and Southern Appalachians using the Forest Inventory and Analysis hexagon grid. Dots represent approximate plot locations.

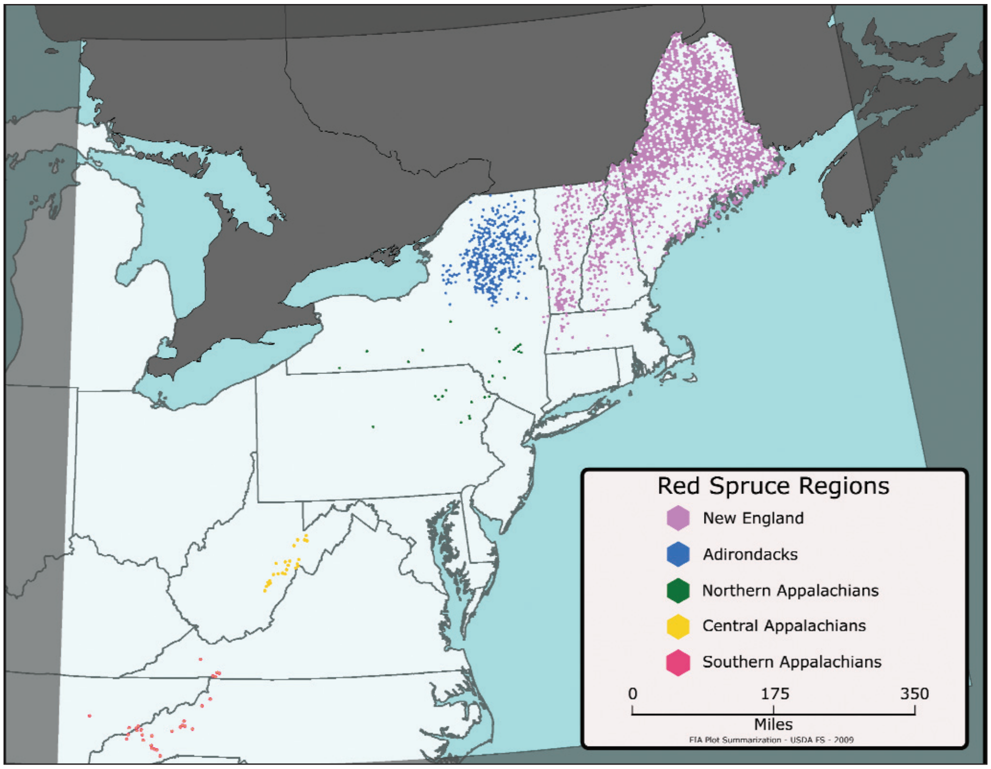

Figure 3.—Regional grouping of red spruce plots based on the Forest Inventory and Analysis hexagon grid.

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

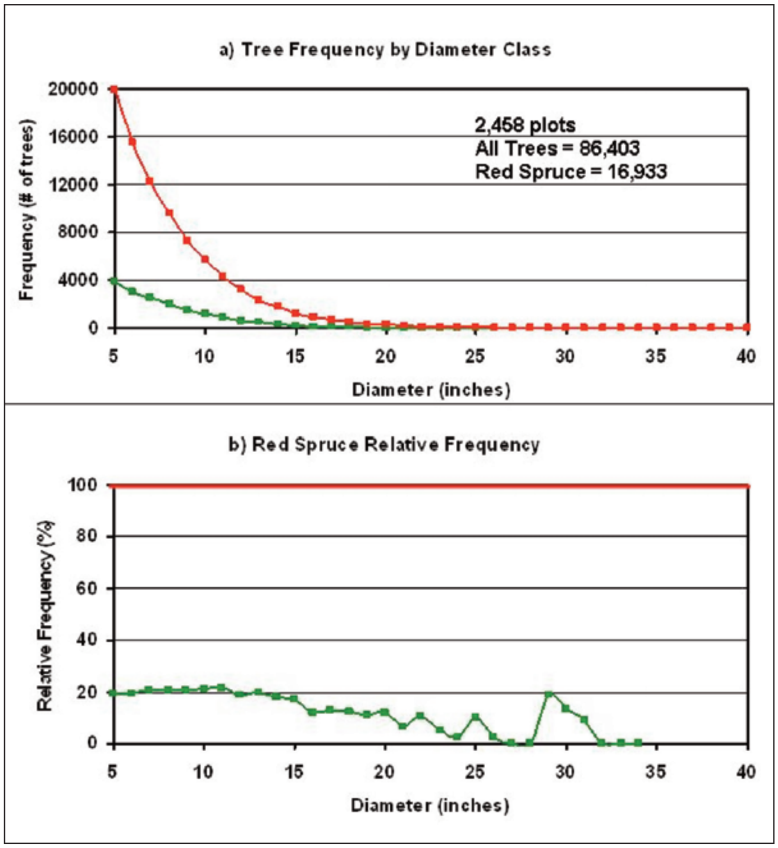

Figure 4.—Diameter-class frequency of all trees (red) and red spruce (green) (a) and relative diameter-class frequency of red spruce (b) based on 2,458 FIA plots.

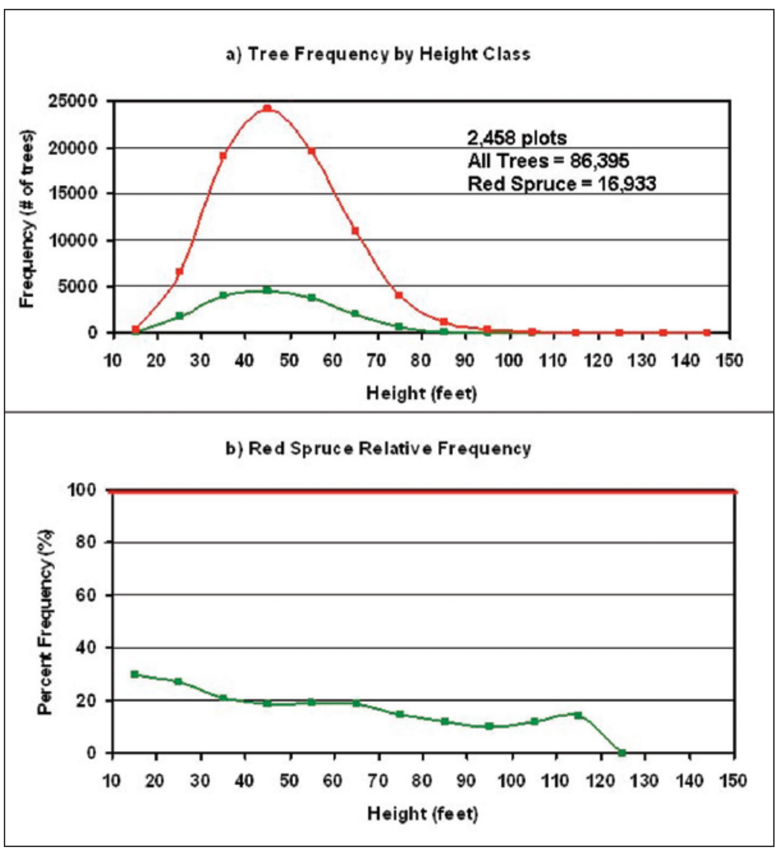

Figure 5.—Height-class frequency of all trees (red) and red spruce (green) (a) and relative height-class frequency of red spruce (b) based on 2,458 FIA plots.

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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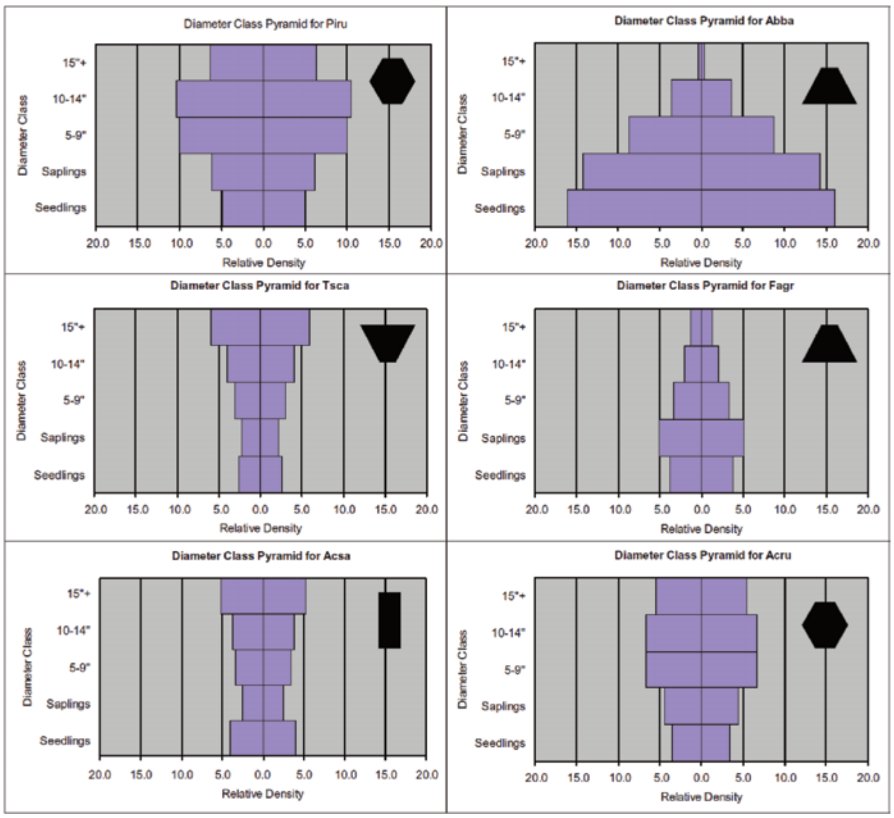
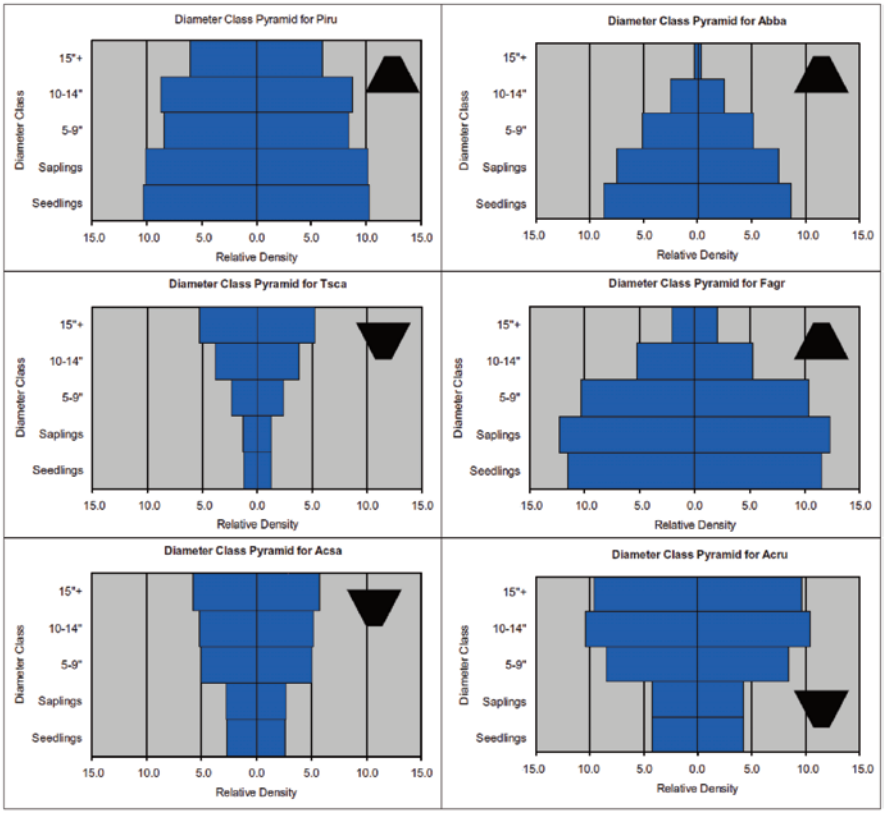
The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein.

APPENDIX A.

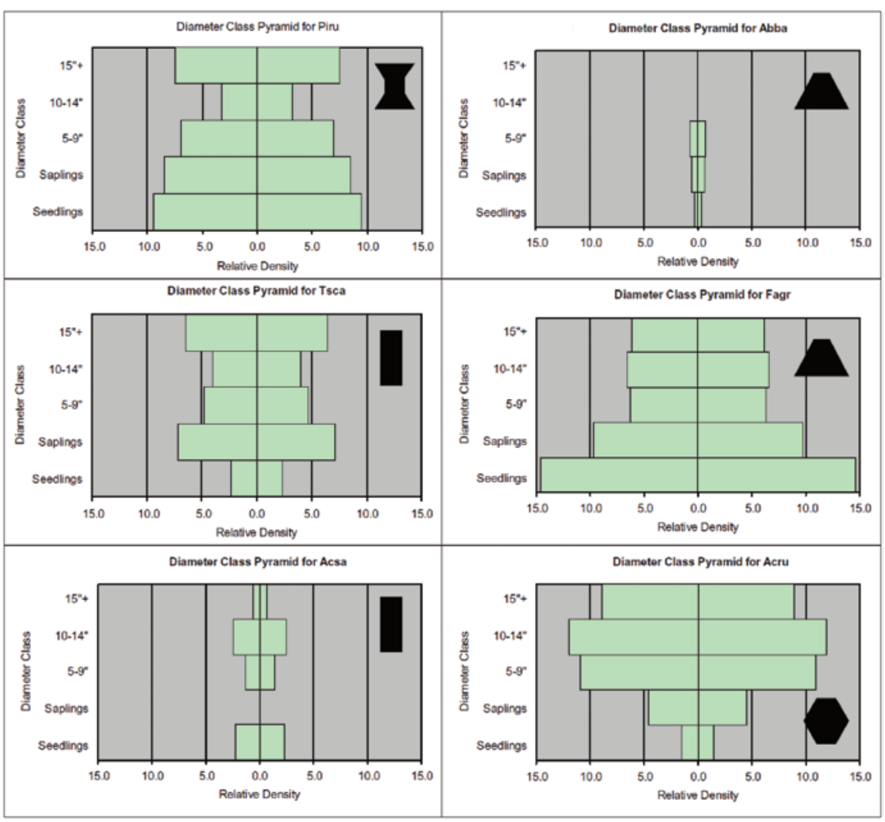
Diameter-class distributions (population pyramid format) based on relative density for six common species. Population trends are designated by black inset symbols: pyramid = increasing population, hourglass-shaped = decreasing then increasing population, linear = stable or indistinguishable population 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.



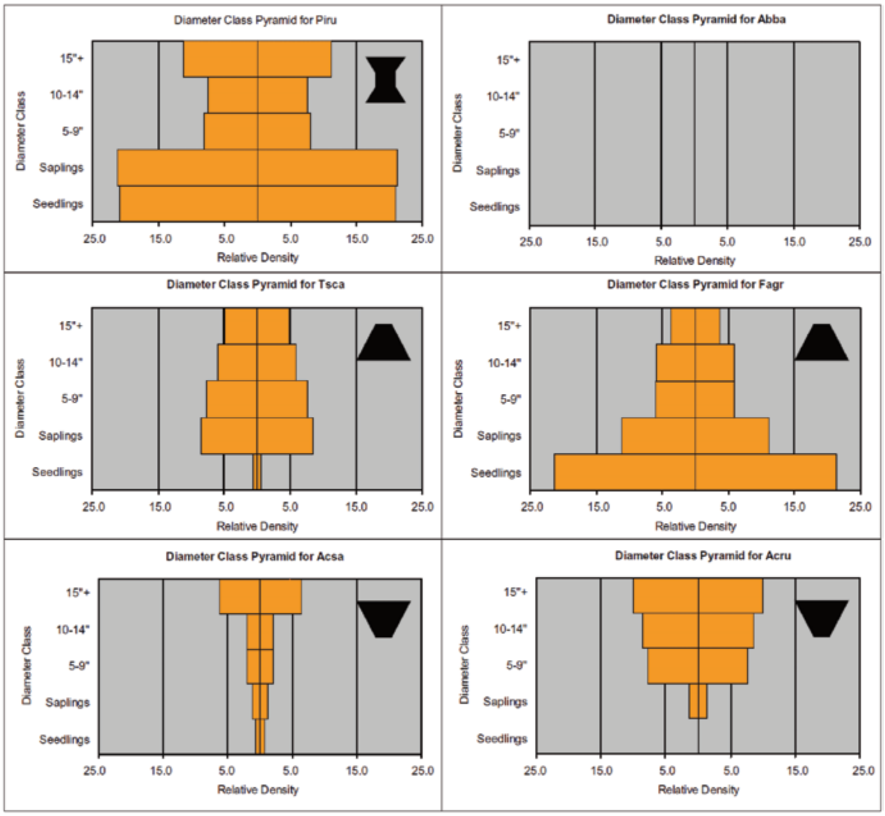
Appendix A1.—The New England Region.



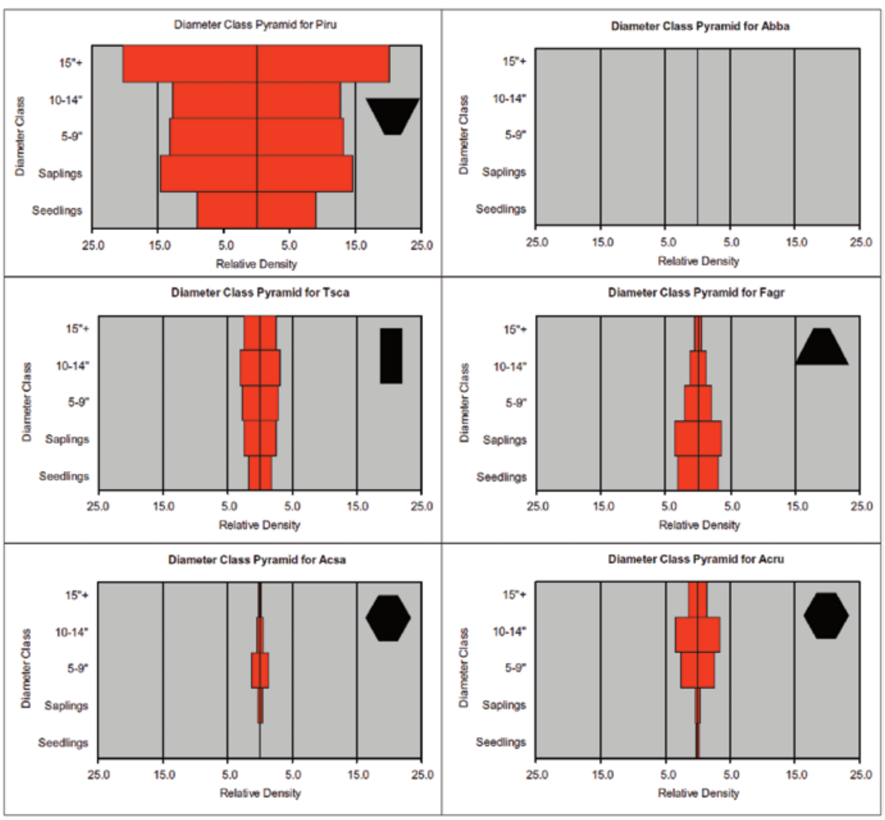
Appendix A2.—The Adirondack Region.



Appendix A3.—The Northern Appalachian Region.



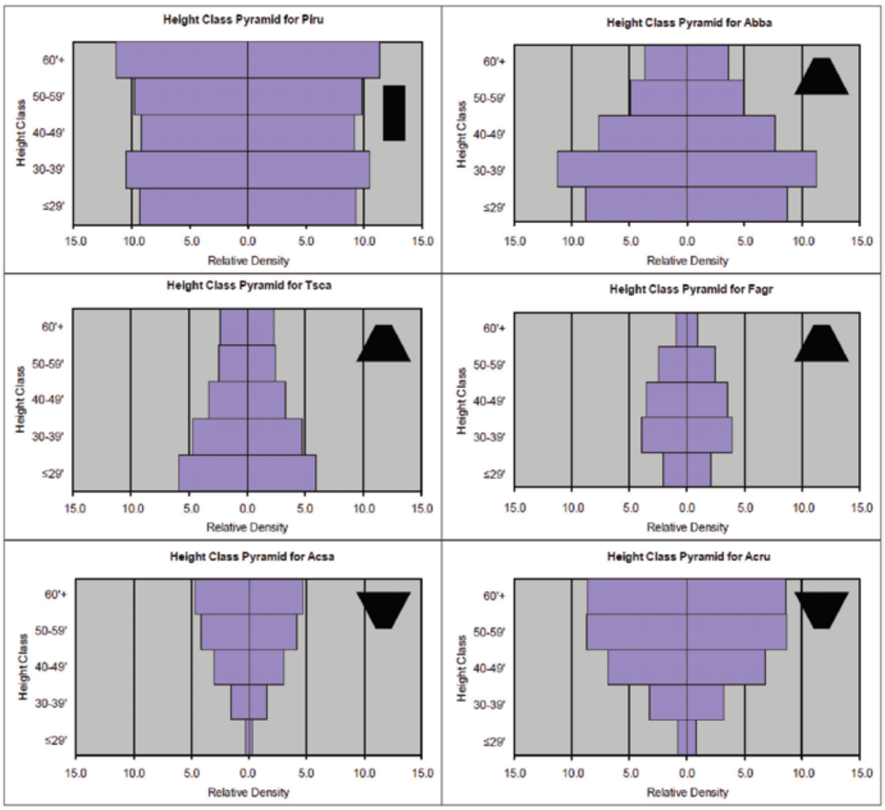
Appendix A4.—The Central Appalachian Region.



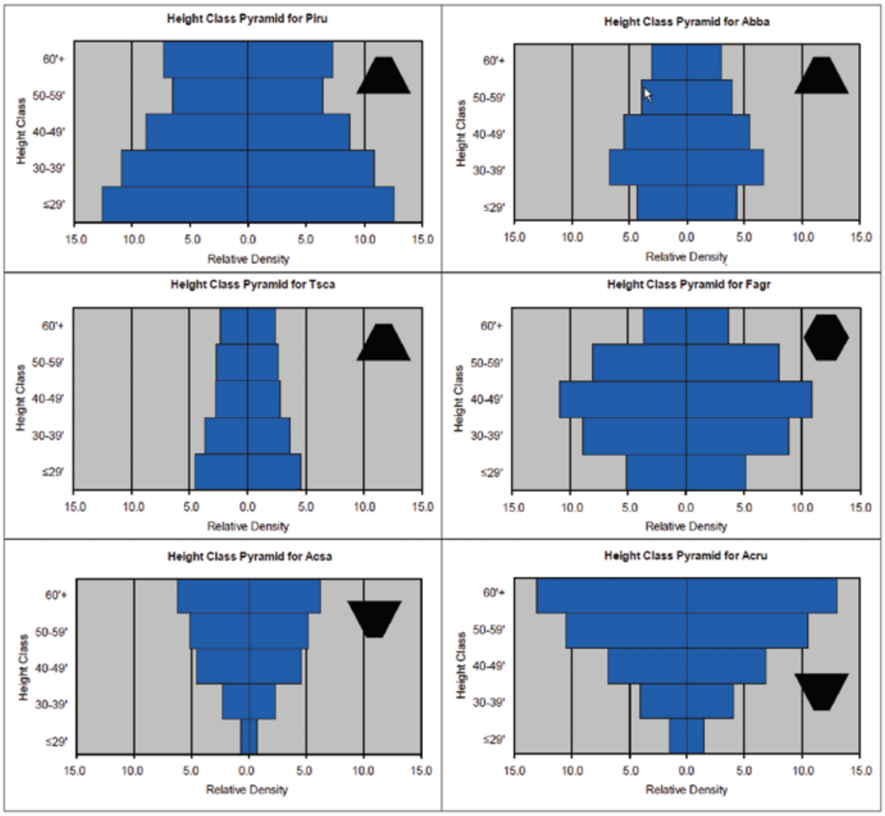
Appendix A5.—The Southern Appalachian Region.

APPENDIX B.

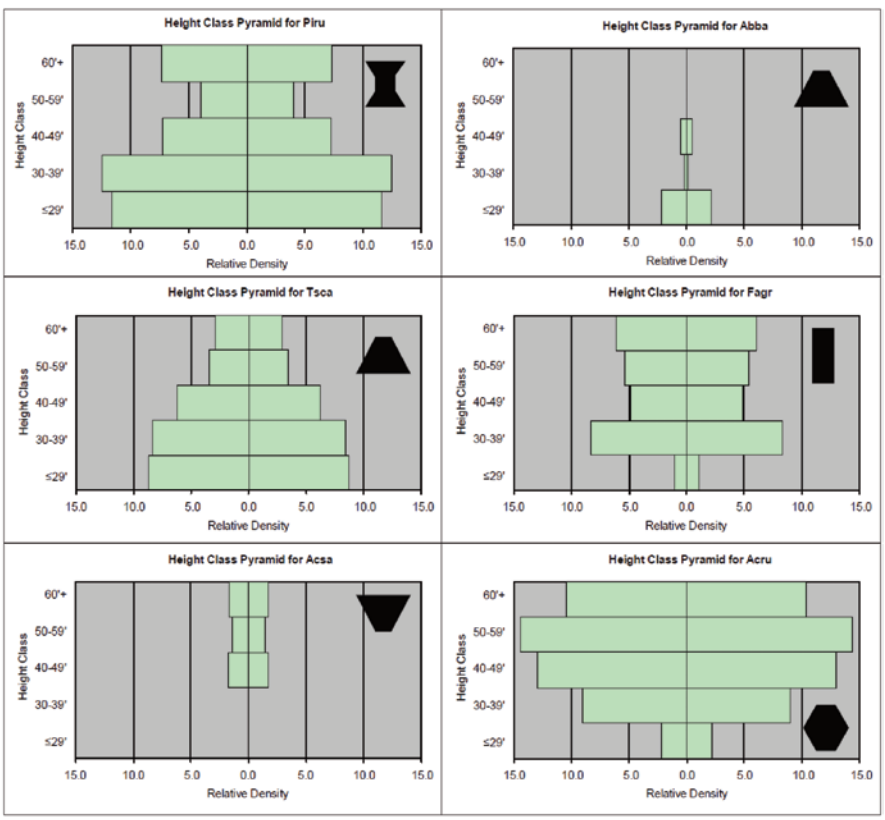
Height-class distributions (population pyramid format) based on relative density for six common species. Population trends are designated by black inset symbols: pyramid = increasing population, hourglass-shaped = decreasing then increasing population, linear = stable or indistinguishable population 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.



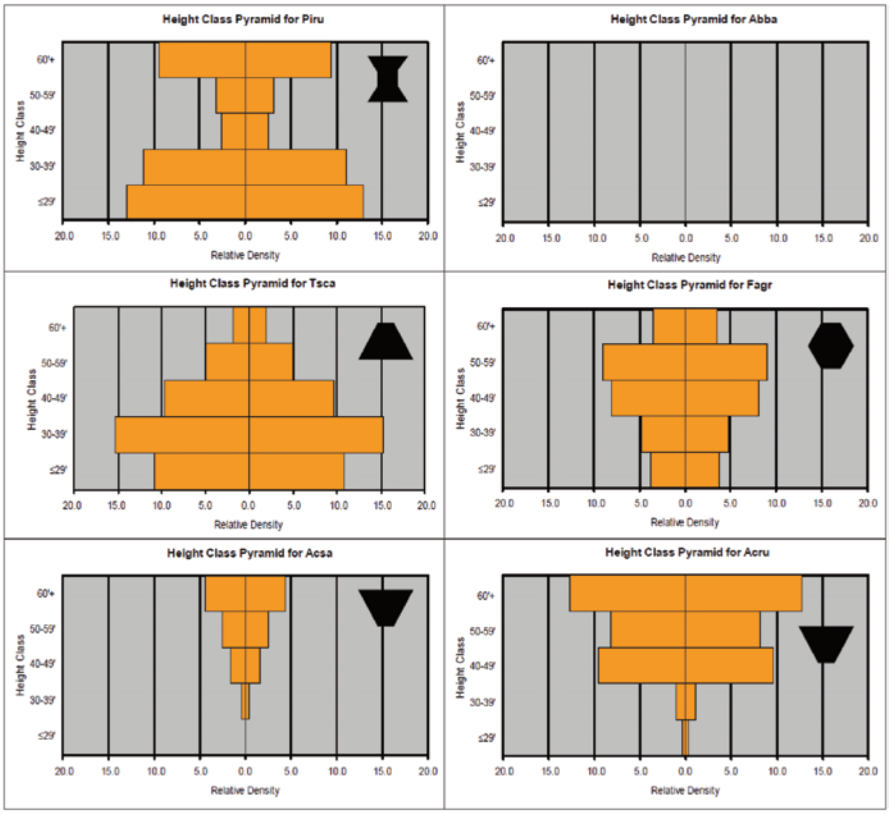
Appendix B1. The New England Region.



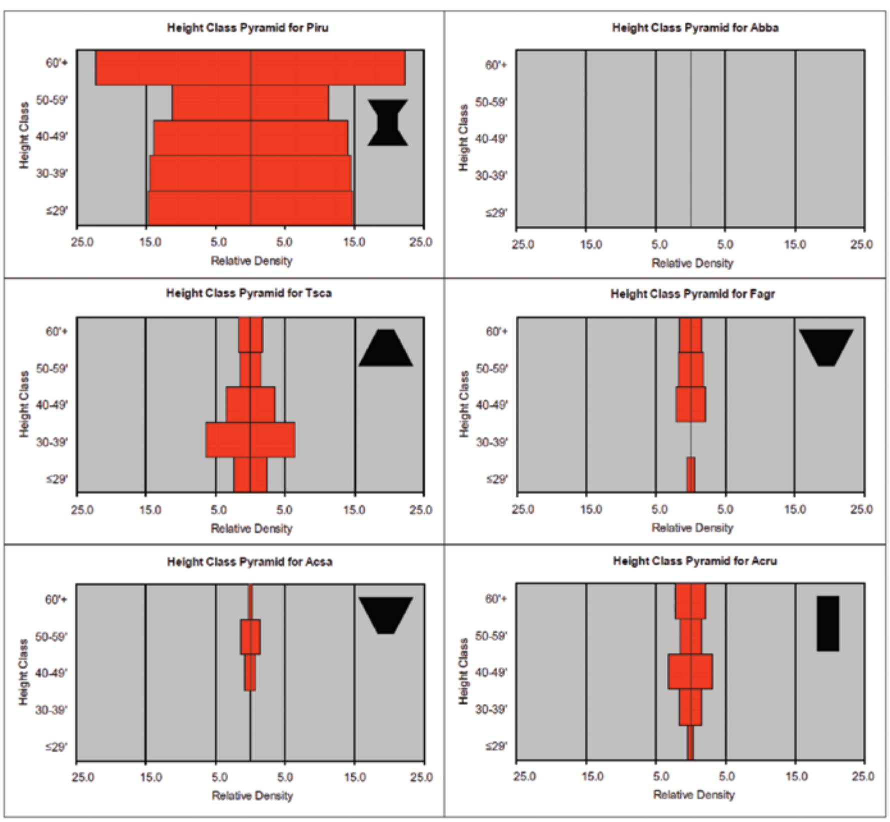
Appendix B2. The Adirondack Region.



Appendix B3. The Northern Appalachian Region.



Appendix B4. The Central Appalachian Region.



Appendix B5. The Southern Appalachian Region.