Tree Species Migration Studies in the White Mountains of New Hampshire

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Abstract
The movement of tree species in either latitude or elevation has attracted increased recent attention due to growing national/international concerns over climate change. However, studies on tree species movements began in the early 1970s in the White Mountains of New Hampshire, mostly due to ecological interests in the episodic behavior of upper-elevation tree species on some of the most scenic mountains. Observations taken while making elevational transects appeared to indicate that regeneration of some species was advancing or retreating in relation to the main stand of mature trees. This process was formalized into a graphical model that would predict rates of movement which was then tested on the Bartlett Experimental Forest located in the White Mountain National Forest. This paper describes the several types of migrational models that were developed as well as long-term remeasured plot evidence against significant recent changes in the species distributions.

Cover Photo
INTRODUCTION

Change in the distribution of tree species has been a subject of considerable interest in New England. One line of research focused on prehistoric species distributions as evidenced through pollen analysis (e.g., Gajewski 1987, Spear et al. 1994) in relation to early trends in climatic regimes. For example, at Mirror Lake in New Hampshire, near the Hubbard Brook Experimental Forest, pollen diagrams have traced the overwhelming changes from spruce-birch-pine dominance 10,000 to 12,000 years ago through pine-oak during the period from 6,000 to 10,000 years ago to beech-hemlock-birch from 6 thousand years ago to the present (Spear et al. 1994).

More recently, in response to concerns over climate change, computer models have projected major changes in species distributions based primarily on projected changes in temperature/precipitation regimes from available global circulation models coupled with covariates related to soils, elevation, and landscape variables (e.g., Iverson and Prasad 1998, Iverson et al. 2011). Related analyses (Woodall et al. 2009) of the latitudinal peaks in tree biomass versus seedling abundance have provided broad-scale snapshots of species migrational tendencies in eastern United States.

In the 1970s, prior to the research dominated by climate-change hypotheses, research in the White Mountains of New Hampshire attempted to describe the observable elevational characteristics of tree species and, as followup, to examine the evidence for tree species migration, especially at the upper limits of their elevational ranges. The purpose of this paper is to describe the elevational transects, the field-based models derived from this work, and documented changes in species distributions provided by long-term remeasurements.

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ELEVATION TRANSECTS

In the early 1970s, transects were run up the sides of Mt. Washington (elevation 6,290 feet) and Mt. Whiteface (elevation 4,020 feet) with the purpose of describing the species and size/age development of the vegetation in relation to elevation (Leak and Graber 1974a). The disturbance histories varied: Mt. Washington had been logged up to about 3,000 feet elevation in the 1800s primarily for softwood. Mt. Whiteface had never been logged.

On Mt. Washington, diameters were measured on all stems taller than 4.5 feet on plots located at every 33-foot rise in elevation. The largest and smallest stems by species were aged by increment cores, sectioning, or counting terminal bud scars.

On Mt. Whiteface, basal areas were measured by species with a 10-factor prism at every 50-foot rise in elevation and the largest and smallest stems in the prism count, or 3.3- by 33-foot subplot, were measured for diameter and age. These transects provided an elevational sequence showing species occurrence, abundance, and sizes between around 2,000 to 3,900 feet (Mt. Whiteface) or 4,500 feet (Mt. Washington) above sea level (Fig. 1). In general, softwoods were more abundant at elevations of 2,625 to 2,950 feet and above, while hardwoods (except paper birch) were most abundant below that level. Most of the high-elevation paper birch was mountain paper birch (*Betula papyrifera* var. *cordifolia*).

During the intensive field work required for these transects, R.E. Graber, research ecologist, noted that many species showed elevational trends in size distributions: in some cases, small (apparently young) trees occurred far upslope or downslope of the body of mature trees; in other areas, large and small trees were together. Graphical analysis of maximum and minimum age in relation to elevation showed, in some cases, the trends illustrated in Figures 2, 3, and 4 where species such as yellow birch (*Betula alleghaniensis*) and paper birch appeared to have an upward-moving elevational front (young trees out in front of older trees) while other species, such as beech (*Fagus grandifolia*), showed a stationary front. Based on these preliminary observations, a graphical model of tree species movements was developed as well as a description of several types of migrational fronts.

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**Figure 1.**—Elevational ranges of woody species on Mt. Whiteface and Mt. Washington, based on occurrence of stems over 1 year old. Transects began around 2,000 and 2,100 feet above sea level and ended around 3,900 and 4,500 feet, respectively (Leak and Graber 1974a).
Figure 2.—Maximum and minimum age for beech over elevation on Mt. Whiteface, showing approximate shape of migrational fronts (Leak and Gruber 1974a).

Figure 3.—Maximum and minimum age for yellow birch over elevation on Mt. Whiteface, showing approximate shape of migrational fronts (Leak and Gruber 1974a).

Figure 4.—Maximum and minimum age for paper birch over elevation on Mt. Whiteface, showing approximate shape of migrational fronts. In this case, the curves are drawn as envelope curves, ignoring some of the irregularities in plotted points (Leak and Gruber 1974a).
MIGRATIONAL MODELS

Assuming that tree species move at a fairly constant rate (a simplification), the relationship of age over distance or elevation would appear like Figure 5 (Leak and Graber 1974 b). The rate of movement would simply be the inverse of the slope of the relationship of maximum age plotted/regressed over distance. Figure 5 shows this relationship even if the trend is discontinuous due to missing data. A stationary front is represented by trees of maximum age and minimum age occurring at the same location. A retreating front shows a reverse slope.

Obviously, this approach is viable where the movement is gradual and continuous, without discontinuous breaks as might occur with dispersal by birds or human transportation. It is most applicable to shade-tolerant species, which gradually invade the understory, but also should apply to less tolerant species at high elevations where natural wind disturbance is frequently severe. Heavy disturbances from land-use changes or heavy harvesting, for example, would disrupt the understory and midstory development and age relationships. Figure 5 also illustrates age-distance relationships where there is no movement (stationary) or a retreating front. This model is similar to the approach applied by Woodall et al. (2009) at a broader regional scale based on the latitudinal distribution of biomass versus seedling counts; however, the White Mountain approach provides an estimated time-scale.

To test the validity of this model and to further examine the preliminary graphics from Mts. Washington and Whiteface, another study was conducted in the 1990s on Upper Haystack Mountain (2,995 feet elevation) on the Bartlett Experimental Forest in central New Hampshire (Solomon and Leak 1994). Fixed plots along the contour coupled with prism plots were taken at every 100 feet horizontal distance up to an elevation of 2,420 feet, and then every 50 feet to an elevation of 2,700 feet. The site was classified at each point to aid in the interpretation of species occurrences (Leak 1982). Elevations were then developed from contour maps. Ages were taken on four species: beech, sugar maple (Acer saccharum), red spruce (Picea rubens), and eastern hemlock (Tsuga canadensis).

Age/diameter at breast height (d.b.h.) regressions were developed to predict tree ages throughout the range in tree size; R² values ranged from 0.40 (red spruce) to 0.95 (sugar maple).

Although variability was high, several consistent migrational patterns emerged (Fig. 6). Red spruce and beech showed stationary fronts, i.e., no indication of migrational change in elevation. Red spruce showed a double, stationary front due to the species absence on the fine till soils better suited to deciduous species (Leak 1982). Sugar maple showed a retreating/collapsing front at its upper elevational limit (about 2,400 feet); there were small seedlings, but no trees of intermediate age apparently due to competition from an aggressive beech understory. Hemlock showed an advancing front; the inverse of the slope of a linear regression of age over distance provided an estimated migration rate of about 2 feet per year (horizontal distance)—very slow but measurable.

Based on the Haystack study (Solomon and Leak 1994), a series of hypothetical advancing-front scenarios were developed ranging from constantly advancing fronts, accelerating or decelerating, to incipient, catastrophic, and stationary fronts (Fig. 7). As yet, all of these possibilities have not been field-detected. “Incipient” means the apparent beginning of an advancing front not yet fully developed. “Catastrophic” (or collapsing) means the disappearance of entire age classes.

LONG-TERM MIGRATION RECORDS

Although the models developed for the White Mountain region reveal migrational tendencies, confirmation of species’ changes in elevation comes only from long-term remeasurements. Fortunately, such long-term confirmation is available from the cruise plots on the Bartlett Experimental Forest. A network of about 450-500 plots, mostly quarter-acre in size, were established in 1931-32 covering a range in elevation from about 700 feet above sea level to over 2,900 feet near the top of Upper Haystack Mountain. Complete remeasurements in 1931-32, 1991-92, and 2002-03 of all trees in the 2-inch class (1.5 to 2.5 inches d.b.h.) and larger, and some partial remeasurements in intervening years, provided a detailed account of successional trends and changes in species abundance by elevation classes. In examining species’ movements,
it is important to recognize that species’ occurrences are limited by site conditions (Demers et al. 1998) (see also Fig. 6). Hemlock is the ideal indicator species since it is climatically limited, found at mid- to lower elevations in the White Mountains, but also adapted to the shallow-bedrock sites found at higher elevations. Additionally, hemlock is a very tolerant and aggressive species on suitable sites. More demanding species such as sugar maple and ash are very uncommon on such sites, especially on low-nutrient bedrock types such as granite.

Analyses of these cruise plot records up through 1984 (partial remeasurement) (Leak 1987) and 1991-92 (Leak and Smith 1996) showed little indication that hemlock was invading stands above about 2,000 feet elevation. A detailed analysis of changes in seedling/sapling understory trees (1.5 to 4.5 in. d.b.h.) based on the 2002-03 remeasurement (Table 1) again showed little evidence that hemlock was invading the upper elevations dominated by red spruce and miscellaneous hardwoods (Leak 2009). An overstory analysis gave similar findings (Leak and Yamasaki 2010) showing that the percent composition of hemlock at mid-elevations roughly doubled but remained near zero above about 2,100 feet except for a few large trees (17 inches d.b.h. and larger). The upper-elevation numbers are variable due to the heavy natural wind disturbances that occur on these shallow-bedrock sites where hardwoods (especially yellow birch and beech) are aggressive open-canopy invaders. The Haystack transect (Fig. 6) indicated that hemlock was moving at about 2 feet in horizontal distance per year. Over 70 years (the cruise-plot record),

<table>
<thead>
<tr>
<th>Elevation (ft)</th>
<th>Year</th>
<th>Red Spruce (%)</th>
<th>Hemlock (%)</th>
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<tr>
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<td>1931-32</td>
<td>9</td>
<td>22</td>
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<tr>
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<td>1931-32</td>
<td>10</td>
<td>25</td>
</tr>
<tr>
<td>1600-1700</td>
<td>1931-32</td>
<td>8</td>
<td>13</td>
</tr>
<tr>
<td>1996</td>
<td>1931-32</td>
<td>8</td>
<td>16</td>
</tr>
<tr>
<td>1700-1800</td>
<td>1931-32</td>
<td>22</td>
<td>10</td>
</tr>
<tr>
<td>2000</td>
<td>1931-32</td>
<td>11</td>
<td>8</td>
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<td>1800-1900</td>
<td>1931-32</td>
<td>9</td>
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<tr>
<td>1996</td>
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</tr>
<tr>
<td>1900-2000</td>
<td>1931-32</td>
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<td>7</td>
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<tr>
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<tr>
<td>1987</td>
<td>1931-32</td>
<td>32</td>
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Table 1.—Percent seedlings/saplings (1.5 to 4.5 inches d.b.h.) of red spruce and hemlock by year and elevation on the Bartlett Experimental Forest (Leak 2009).
Figure 6.—Predicted maximum and minimum ages (stems more than 3.28 feet tall) over horizontal distance for the major species on Haystack Mountain (Solomon and Leak 1994).

As a supplement to the White Mountain studies, species changes were analyzed on more than 500 U.S. Forest Service Inventory and Analysis (FIA) plots throughout Maine during the period from 1950-60 to the early 1980s, an average period of 24 years (Solomon and Leak 1994). The basic approach was to compare the latitudes, longitudes, and elevations initially occupied by major

this would amount to about 140 feet horizontal distance. At 25-50 percent slope, this horizontal movement would amount to about 35-70 feet elevation, not a large change but perhaps somewhat more than shown by the cruise-plot record. However, Fig. 6 represents long-term past movement along a single transect, possibly influenced by early harvesting activity.
species with those newly occupied at the end of the 24-year period. Results indicated that white pine and balsam fir had moved slightly (but significantly) lower in both elevation (50 and 23 feet, respectively) and latitude (2.1 and 0.85 miles, respectively). Very likely, these changes were due to land-use impacts (primarily cessation of agriculture), which are very difficult to assess and often very confusing in developing regional evaluations.

**SUMMARY AND CONCLUSIONS**

Transects of tree species and ages on Mts. Whiteface, Washington, and Haystack in the White Mountains of New Hampshire were utilized in developing a series of geometrical models showing migrational patterns of tree species in either elevation or distance. These studies were followed by examination of changes in species
occurrences on U.S. Forest Service Forest Inventory plots in Maine and longterm, remeasured cruise plots, over a range of elevations, on the Bartlett Experimental Forest in New Hampshire.

Despite national/international concerns over the purported impacts of climate change on forest conditions, this series of studies in New England’s White Mountains and adjacent Maine showed no consistent patterns of climate-related species’ movements in either elevation or latitude. The primary agent of change in species composition of the northern hardwood-hemlock and spruce-fir types in this region continues to be natural succession.

LITERATURE CITED


The movement of tree species in either latitude or elevation has attracted increased recent attention due to growing national/international concerns over climate change. However, studies on tree species movements began in the early 1970s in the White Mountains of New Hampshire, mostly due to ecological interests in the episodic behavior of upper-elevation tree species on some of the most scenic mountains. Observations taken while making elevational transects appeared to indicate that regeneration of some species was advancing or retreating in relation to the main stand of mature trees. This process was formalized into a graphical model that would predict rates of movement which was then tested on the Bartlett Experimental Forest located in the White Mountain National Forest. This paper describes the several types of migrational models that were developed as well as long-term remeasured plot evidence against significant recent changes in the species distributions.

KEY WORDS: tree species migration, tree species elevation ranges, New England, forest climate-change impacts, mountain ecology, tree migration models