United States
Department of
Agriculture

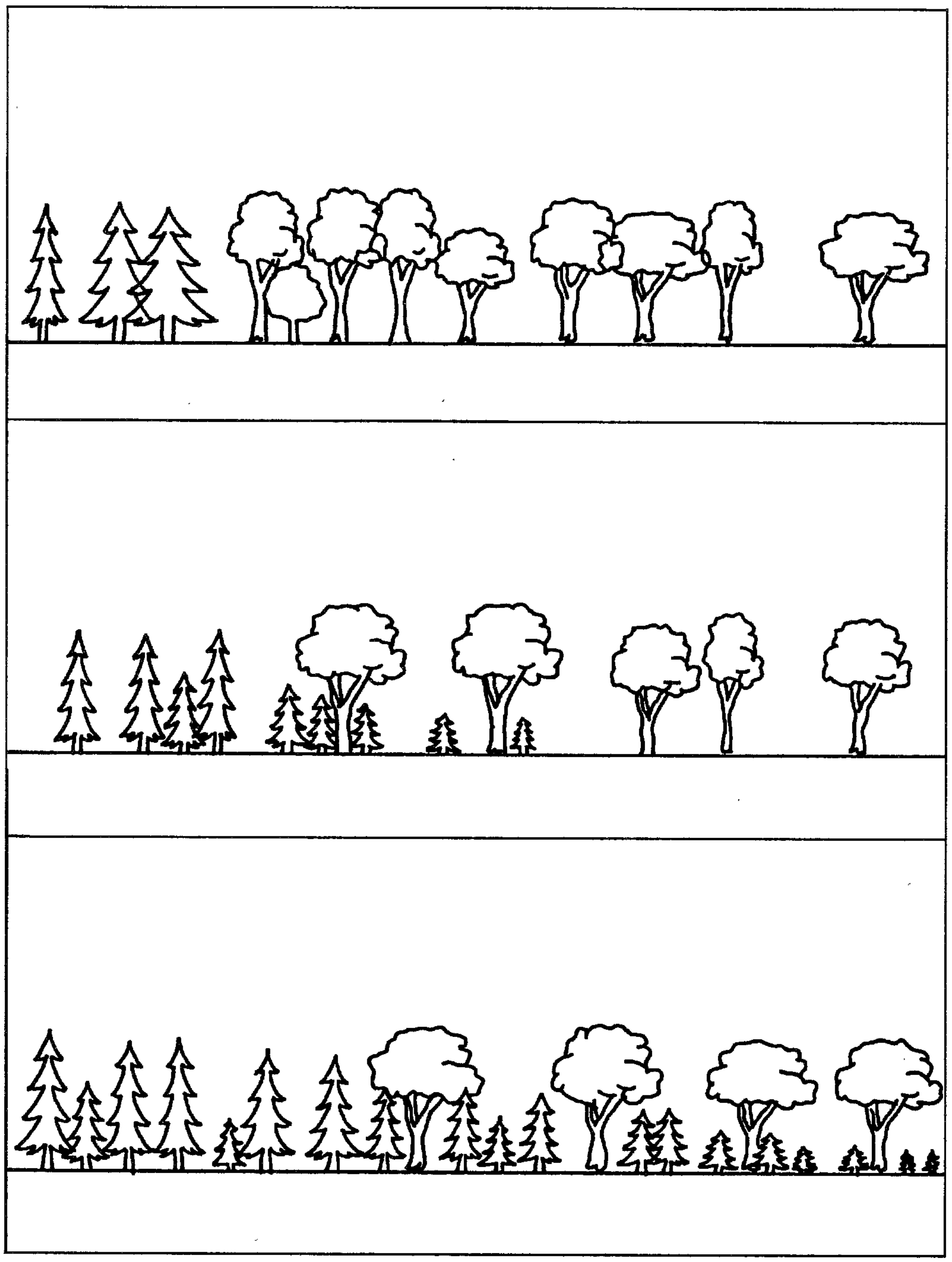
Forest Service

**Northeastern Forest
Experiment Station**

Research Paper NE-688

Migration of Tree Species in New England Based on Elevational and Regional Analyses

Dale S. Solomon
William B. Leak



Abstract

Concerns over possible increases in global temperature have renewed interest in the detection, measurement, and analysis of tree-species migration. Previous work has consisted mostly of computer simulations of changes in species ranges. In this study, two complementary approaches were used to examine movements of tree species in New England, where there is a documented increase (at Hanover, New Hampshire) in mean annual and summer temperatures of about 2°C since 1835. We used advancing-front theory to examine age trends over distance and elevation in undisturbed stands on Haystack Mountain in New Hampshire. Then we examined changes in species occurrence over a 24-year period on USDA Forest Service survey plots throughout Maine. On Haystack Mountain, well-defined stationary fronts (no movement) were identified for red spruce (*Picea rubens* Sarg.) and beech (*Fagus grandifolia* Ehrh.); these occurred at the borders of distinct changes in site conditions, which serve as temporary obstacles to species' movements. A catastrophic front was depicted for sugar maple (*Acer saccharum* Marsh.): no established understory stems less than about 100 years old were evident at elevations above 720 m on a site complex composed of shallow bedrock interspersed with deeper till. A constant, very slowly moving advancing front was exhibited by hemlock (*Tsuga canadensis* (L.) Carr.). In Maine, white pine (*Pinus strobus* L.), and balsam fir (*Abies balsamea* (L.) (Mill.) decreased significantly in average latitude and elevation over the 24-year period; average species' elevations decreased by only 16 and 7 m, respectively, while latitudes decreased (southerly) by about 0.1 and 0.04 degrees (11.3 to 4.5 km). The other significant change was an increase (westerly) in longitude of sugar maple by about 0.1 degree (6.9 km). Succession--not climatic shifts--following land use changes or cutting probably was responsible for these trends for sugar maple. Forest managers should be aware that natural succession as influenced by disturbance, land use, and site currently is the dominant influence affecting species changes in New England forests. At present, potential ranges of the major species in terms of elevation and regional position appear stable and in alignment with known site requirements.

The Authors

DALE S.SOLOMON is Project Leader of a work unit engaged in research on methods for measurement, analysis, and modeling of forest growth and structure at the Northeastern Forest Experiment Station in Durham, New Hampshire. He received a B.S. degree in forestry from Pennsylvania State University and joined the U.S. Department of Agriculture in 1962 after receiving an M.S. degree in mensuration and statistics from Yale School of Forestry, and a Ph.D. degree in forest growth modeling from the University of Maine. He is currently conducting research on forest ecosystem modeling for forest types in the Northeastern United States.

WILLIAM B. LEAK, research forester with the Northeastern Forest Experiment Station at Durham, received B.S. and M.F. degrees from the State University of New York at Syracuse. He joined the Northeastern Station in 1956 and is conducting research on site evaluation, silviculture, and ecology of northern hardwoods.

Manuscript received for publication 9 November 1993

USDA FOREST SERVICE
5 RADNOR CORP CTR STE 200
P.O.BOX 6775
RADNOR, PA 19087-8775

July 1994

Introduction

Concerns over global climate change have led to renewed interest in the detection and analysis of tree-species migration. Most previous work and most inferences on the projected effects of climate change have been concerned with historical movements based on the pollen record and computer models of climatic change coupled with hypothesized species responses (Brubaker 1986; Davis and Zabinski 1989; Gajewski 1987; Peters 1990; Pastor and Post 1988; Solomon and West 1987). Average increases in temperature of 1.5° to 4.5°C in Eastern North America have been predicted, resulting in simulated tree-species range shifts of 500 to 1,000 km within periods of 200 years (Overpeck et al. 1991) or even as short as 50 to 100 years (Peters 1990). There is one documented increase of 1.7° and 2.2°C in mean annual and mean summer temperature, respectively, since 1835 in Hanover, New Hampshire. This change was hypothesized as being responsible for the elimination of midslope red spruce (*Picea rubens* Sarg.) in northern New England and an upward displacement of the coniferous/deciduous elevational boundary by about 400 m (Hamburg and Cogbill 1988).

However, since there have been no attempts to directly measure species migration in New England, we conducted a study of tree-species movement based on two approaches: advancing-front theory (Leak and Graber 1974; Solomon et al. 1990) in stands on Haystack Mountain, New Hampshire, and remeasurement analysis of USDA Forest Service inventory plots throughout Maine. The objectives of this study were to search for incipient migration of species and to determine the methodology, including the effects of site and the influence of managed versus unmanaged forest conditions.

Under the first approach, age trends were measured in old, uncut stands along a transect up Haystack Mountain in New Hampshire. The objective was to search for relationships of maximum and minimum tree age over elevation or distance that would reflect species movement, an approach referred to as advancing-front theory. The second approach was to analyze changes in species occurrence over an average period of 24 years on Forest Service survey plot records taken throughout Maine, an area of 89 percent forestland that has been mostly managed or cutover in the past. If there has been a rise in mean New England temperatures of 2°C, and if the previous computerized range changes are accurate, a remeasurement period of 24 years should detect incipient movement, especially since the management disturbance could hasten migrational trends by reducing competition for space and light. The first approach provides a means for examining the details of species migration, including the influence of site, without complications from cutting and past land-use influences. The second approach deals with overall regional implications.

Advancing-Front Theory

It has been suggested that species movement will be reflected by an advancing front, that is, where seedlings and young trees are positioned in a sequential pattern away from a stand of mature trees (Leak and Graber 1974; Solomon et al. 1990). The concept of "front" applies to the main population of a species, ignoring isolated individuals. The best places to search for these fronts are in essentially undisturbed stands of tolerant species near the climatic limits of the type, or, better, on mountain slopes where the cover type or any of its component species is limited in elevation by climatic factors. If regular movement of a species is taking place at a constant rate, maximum age of the species plotted over distance from the mature stand (or elevation) should form a straight descending trend line or front (Fig. 1A). The rate of movement would equal 1/slope of age regressed over distance. Likewise, increasing or decreasing rates of movement would be evidenced by concave- upward (Fig. 1B) or concave-downward (Fig. 1C) trends; the rate of movement would equal the inverse of the tangent at any point on these curves. Retreating fronts would be similarly defined (Figs. 1D-F) using the minimum age of the species. Incipient fronts (Fig. 1G), the very early stages of species movement, would be indicated by an age/distance trend line that spans a short period. Where environmental change triggers a massive disappearance (or appearance) of regenerating stems, a catastrophic type of front (Fig.1H) seems likely. Figure 1H represents a sudden areawide cessation of regeneration. Continued repetition of this process would produce a sequential step-like pattern that could be used for predictive purposes.

Where no movement is taking place, a stationary front would occur (Fig. 1I) where maximum and minimum ages occur and end at the same point on the landscape. The relationships in Figure 1 seem fairly logical, but there are many questions about the acquisition and interpretation of data, including sampling methods, variability, site relationships, and factors influencing species longevity.

Methods

Haystack Mountain

Haystack Mountain borders the Bartlett Experimental Forest in the White Mountain National Forest, New Hampshire. A series of plots was taken on the south-facing slope of the mountain along the marked boundary of the Experimental Forest. Beginning at an elevation of 543 m, plot locations were established every 30.5 m in horizontal distance, moving upslope to an elevation of 738 m, and then every 15.2 m, moving upslope to an elevation of 823 m--the base of the last steep incline to the mountaintop at 913 m. Substantial stand disturbance was evident above this point. At each plot location, all stems between the size of 1 m tall to 12.7 cm d.b.h. were recorded on a 23- by 1.5-m strip along the contour. At each end of the strip, a prism tally was made of all larger stems using a 4.59 m^2/ha (20 ft^2/acre) prism. The presence or absence of seedlings smaller than 1 m tall was recorded by species.

Seventy-five stems of the following four species were aged: beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer*

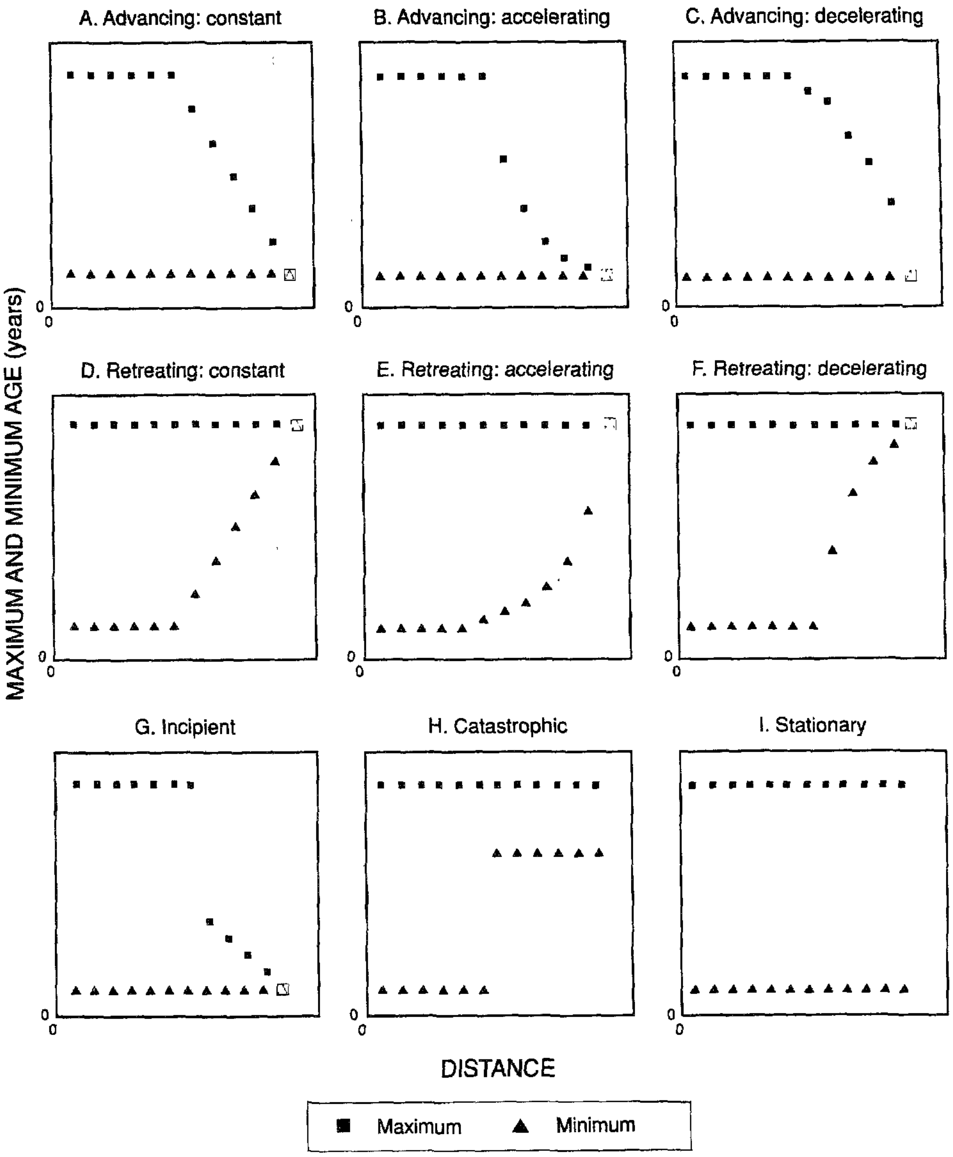


Figure 1.--Schematic examples of types of fronts: Advancing (A-C), Retreating (D-F), Incipient (G), Catastrophic (H), and Stationary (I).

saccharum Marsh.), red spruce (*Picea rubens* Sarg.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). These were the four most abundant shade-tolerant species in the cover types along the transect, which included lower elevation hemlock-spruce, mid-elevation northern hardwoods, and higher elevation spruce-hardwood and spruce-fir. All stands were mature and either uncut or lightly cut in the past. At each plot location, the site or habitat (Leak 1982) was recorded. The predominant conditions were: (1) gravely outwash combined with loose rock supporting coniferous stands; (2) well-drained pan soils supporting coniferous stands; (3) fine till soils supporting northern hardwoods; (4) an association of fine till supporting northern hardwoods with shallow bedrock supporting coniferous stands; and (5) shallow bedrock with conifers.

Elevations of the plot locations were established from detailed contour maps of the Experimental Forest. Numbers of understory stems (≥1 m tall and ≤ 12.7 cm d.b.h.) and basal areas of overstory stems were summarized by plot location for the four major tolerant species. Statistics on balsam fir (*Abies balsamea* L.) were included for descriptive purposes, though this species was not sufficiently abundant for an analysis of age distribution. Maximum age of overstory and minimum age of understory (or smallest overstory stem) was determined by age/d.b.h. regressions developed for each species (Table 1). The regression for red spruce was age/log d.b.h. The regressions for the other species were age/d.b.h.+(d.b.h.)^2. The regression fit was good in the small size classes; most of the variability was in the large sizes and old trees.

Table 1.--Sample numbers and regression statistics for age/d.b.h. and age/log d.b.h. (red spruce) equations

Species	No. of samples	Adjusted R square	SD about regression
Red spruce	19	.401	48
Sugar maple	19	.953	13
Beech	23	.787	32
Hemlock	14	.846	54

Maine Survey Plots

Records were available from more than 500 plots that were first measured in the 1950's and 1960's and finally remeasured in the early 1980's with one intermediate remeasurement, an average total period of 24 years. Each plot consisted of a 0.08-ha (0.2-acre) circular plot where trees larger than 25 cm d.b.h. were recorded, and an enclosed 0.04-ha plot for trees between 10 and 25 cm d.b.h. Plots were included in the analysis if they contained trees at any time during the measurement period and if the plot was not eliminated by land-use change. Latitude, longitude, and elevation were available for each plot. To assist in both the visual and quantitative analysis, the state was sectioned into locations, defined as 1- by 1- minute rectangles of land area. Initial numbers of locations per major species ranged from 239 for balsam fir to 31 for red oak (*Quercus rubra* L.); plot numbers ranged from 483 to 36 (Table 2). The basic analytical approach was to compare the latitudes, longitudes, and elevations of plots and locations initially occupied by live trees of each major species with those newly occupied by the species (live trees or cut stumps) over the measurement period. Group t-tests were used to determine significant differences.

Results

Haystack Mountain

Species Distribution

Overstory basal areas of beech and sugar maple were 10 to 20 m^2/ha throughout most of the elevation range of the study up to 800 or 820 m (Fig. 2). Basal area of sugar maple is slightly lower than average on the dry pan and gravel/loose rock sites below 600 m, but neither of these deciduous species is excluded by lower elevation site conditions. However, red spruce is abundant only on the dry pan and gravel sites below 600 m and on the bedrock/till and bedrock sites above 720 m. Hemlock is found only on dry pan and gravel at about 590 m and below. Understory stems (Fig. 3) follow a pattern similar to overstory basal areas. The noticeable exception is the lack of sugar maple understory above 720 m.

Examination of Figures 2 and 3 indicate that there are several breaks in species' populations where we might look for moving fronts: beech and sugar maple at about 800 m elevation, hemlock and spruce at 600 m, spruce at 720 m, and the lack of sugar maple understory above 720 m--a condition that might suggest a retreating front. Both spruce and fir were evident in the disturbed stands on shallow bedrock above 823 m, but beech and sugar maple were not. Site apparently is an influential factor that currently limits the occurrence of a species, thus serving as a temporary barrier to species movement. However, it has been shown that the same soil will support different species in different climatic zones (Leak 1982). So, as the climate changes, we would anticipate that species will be able to cross previous site boundaries due to changes in their competitive position.

Age Distribution

The concept of vegetative stability is suggested by graphs of predicted maximum and minimum ages over horizontal distance for the four important tolerant species (Fig. 4). Typical stationary fronts, where maximum- and minimum-age trees occur and end at the same position, are evident for red spruce at about 500 and 975 m distances, and for beech at about 1,250 m distance. (In developing the graph for beech, several maximum-age trees just outside the prism plots were incorporated into the data.) Apparently, climatic change has not been sufficient to enable these species to cross site boundaries and invade other communities. The concept of "front" applies to the main population of a species, since we nearly find scattered, isolated trees of any species on most sites at most elevations. By contrast, hemlock exhibits a declining trend of maximum age over distance; note that this front does not yet cross the boundary into another site condition. Linear regression fits the points with an adjusted R

Table 2.--Summary of initial numbers of Maine plots, 1- by 1-minute locations by major species, and appearance and disappearance of locations during a 24-year average period

Item	Red spruce	Hemlock	Balsam fir	White pine	Sugar maple	Beech	Red oak
	Number						
Initial plots[a]	442	159	483	154	174	163	36
Initial locations	234	115	239	117	126	119	31
Appearance	10 (4.3)[b]	14 (12.2)	23 (9.6)	20 (16.4)	21 (16.7)	21 (17.6)	14 (45.2)
Disappearance	9 (3.8)	4 (3.5)	7 (2.9)	14 (12.1)	7 (5.6)	9 (7.6)	1 (3.2)

[a]Total number of plots within locations.
[b]Percent in parenthesis.

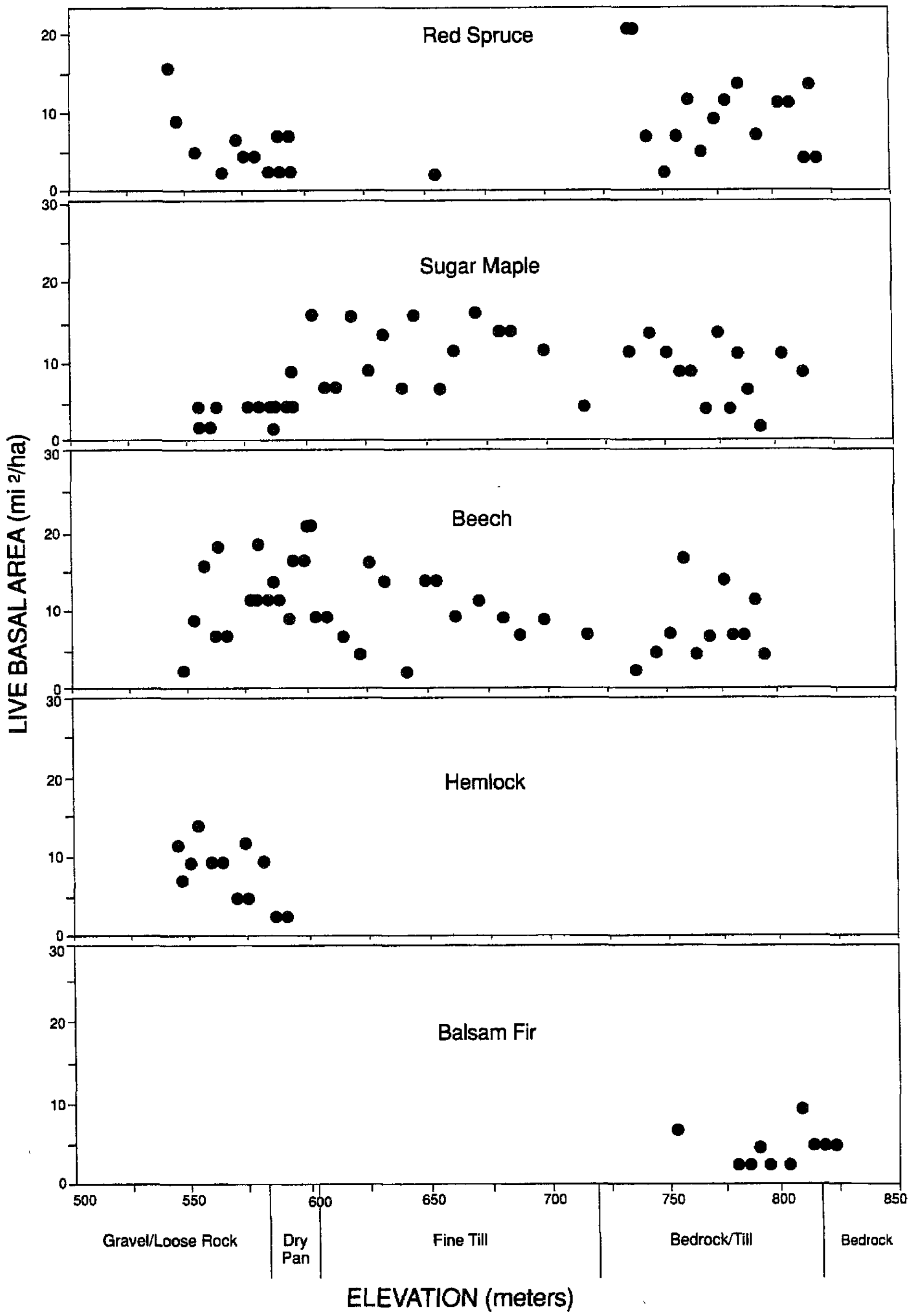


Figure 2.--Live basal area of overstory trees larger than 10 cm d.b.h. by elevation and site for the major species on Haystack Mountain in New Hampshire.

square of 0.62, significant at the 0.05 level, so the trend is indicative of a constant advancing front. However, the graph indicates that a concave-upward regression might provide a better fit if we had more points; this would reflect an accelerating advancing front. An incipient front is another possible interpretation. The inverse of the linear regression coefficient provides an estimated migration rate of 0.6 m per year--very slow compared to the rates of over 100 m per year suggested by Davis and Zabinski (1989) for species movement during the early postglacial period. Does the hemlock trend simply reflect a change in longevity over distance or elevation? Probably not. The site has not changed, and only moderate changes in elevation have occurred.

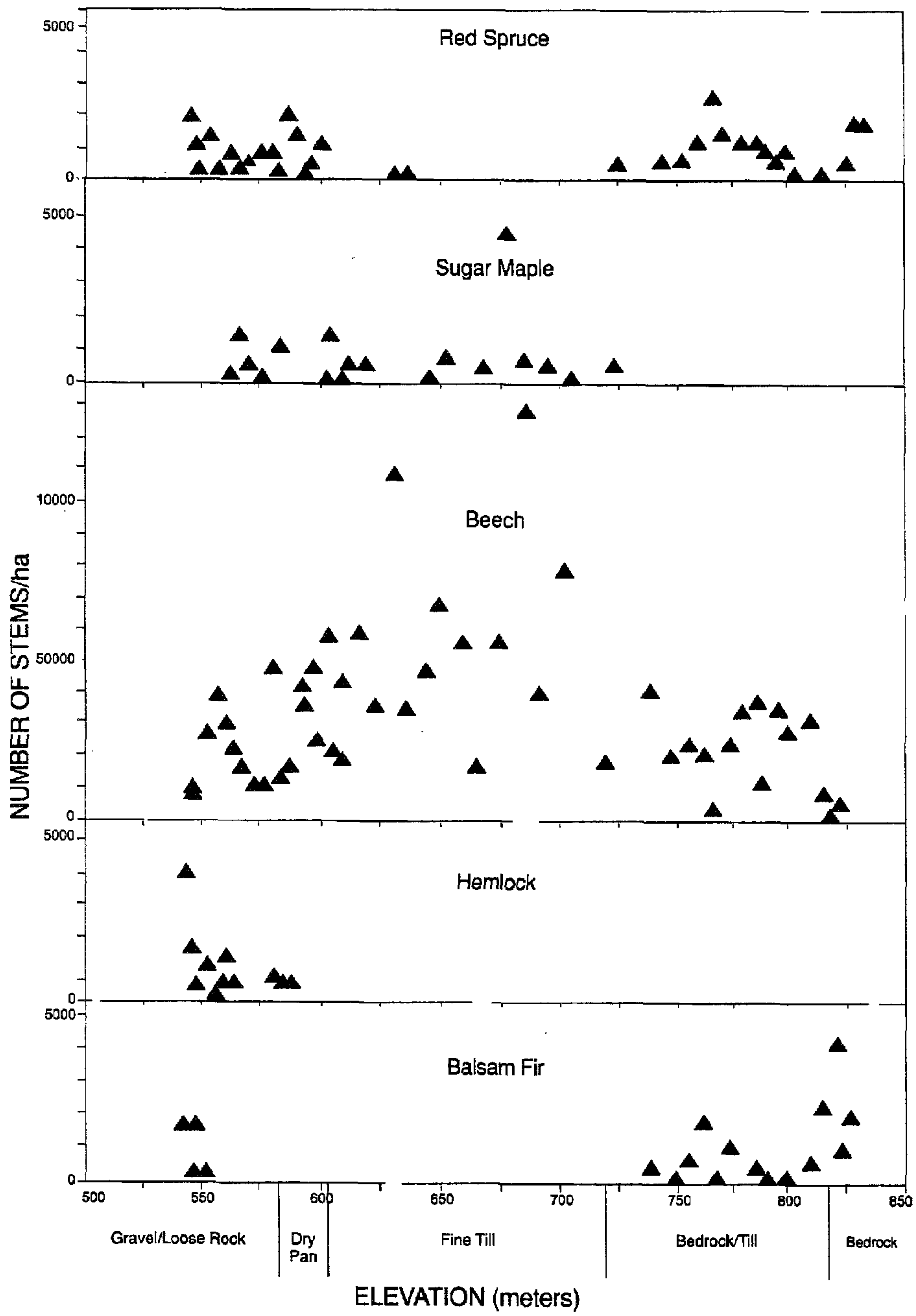


Figure 3.--Number of stems more than 1 m tall and less than 10 cm d.b.h. by elevation and site for the major species on Haystack Mountain in New Hampshire.

Possible changes in longevity might be illustrated in Figure 4 by the slightly lowered curves for beech and sugar maple at about 900 to 950 m distance, near the change from till to bedrock/till. With a larger age sample, variables such as site and elevation should be incorporated into the age/d.b.h. regressions to better isolate changes in longevity. Does the hemlock front simply reflect cutting history? Probably not. Hemlock is the least valuable of all the species, and the downward trend occurs farthest from the road (an old logging railroad bed). We conclude that the hemlock front represents a very slowly moving, somewhat irregular migrational change. It is interesting to note that overstory basal area of hemlock and understory density both decline within the advancing front (Figs. 2-3), a characteristic of fronts noted previously (Solomon et al. 1990).

Maximum and minimum ages of sugar maple beyond 1,000 m distance (Fig. 4) illustrate a typical catastrophic front; a

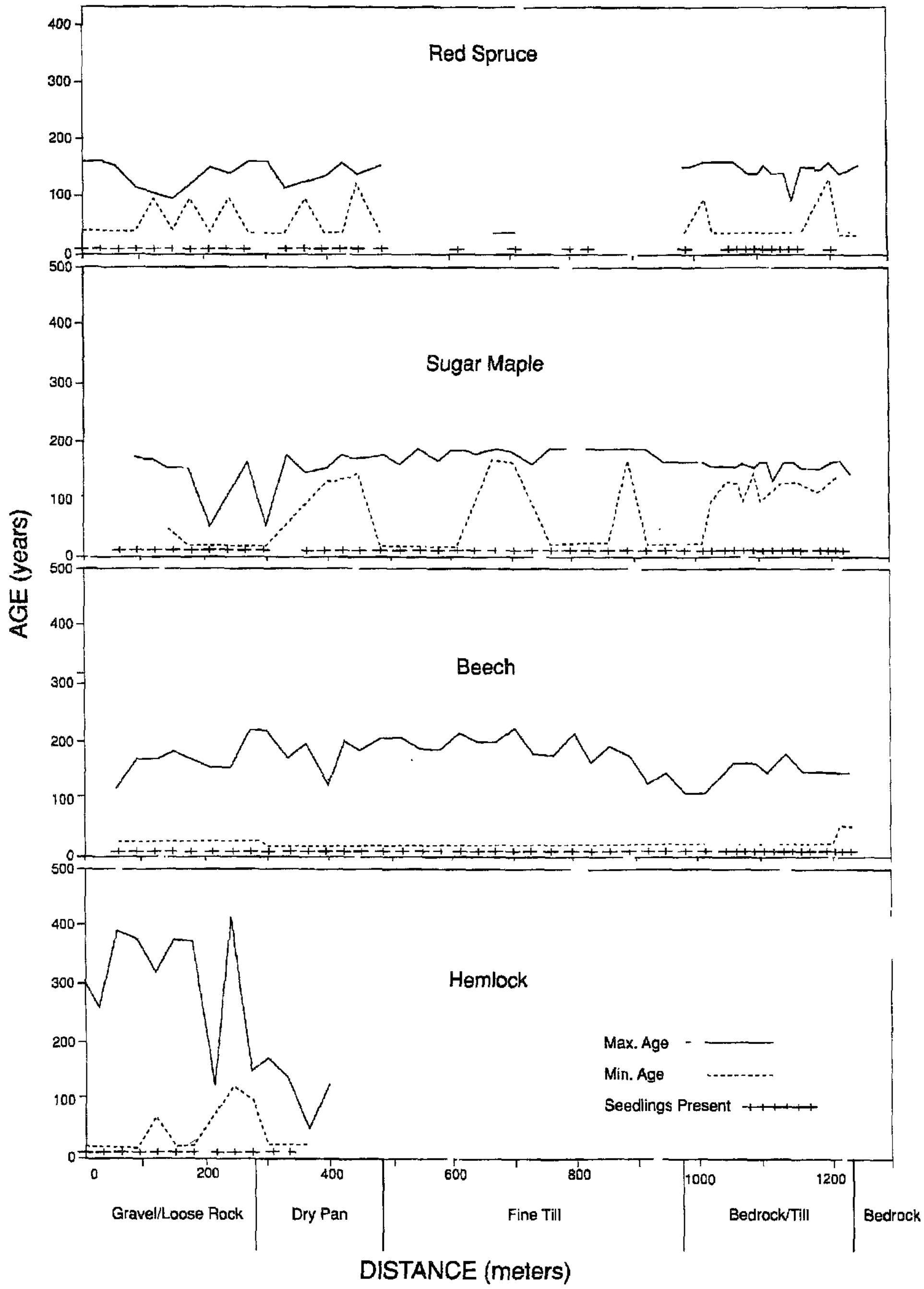


Figure 4.--Predicted maximum and minimum ages (stems more than 1 m tall) over horizontal distance for the major species on Haystack Mountain.

retreating front would have exhibited a declining trend between minimum age and distance. Regeneration establishment ceased about 100 years ago on bedrock/till, though young seedlings still are observed. There is no indication of a similar collapse at other locations or sites at the same time or at a later date. However, it is interesting to note that sugar maple understories are minimal compared to beech even on the best site (fine till) (Fig. 3) while overstories are comparable (Fig. 2), implying that some reduction in sugar maple regenerative potential may be occurring throughout the study area. No explanation can be offered for the presence of a sugar maple catastrophic front; climatic warming does not seem a logical explanation.

Maine

The percentage of new locations occupied by each major species over the 24-year period ranged from 4 to 45 while the percentage of lost locations ranged from 3 to 12 (Table 2). These initial percentages indicated that movement of species was substantial. The next step was to determine whether there were directional or elevational trends. Tests in elevation, latitude, and longitude between the initially occupied and newly occupied plots showed that white pine (*Pinus strobus* L.) and balsam fir were moving slightly lower in both elevation and latitude (Table 3, Fig. 5). Average elevations of the two species declined by only 16 and 7 m, respectively, while average latitudes changed by 0.1 and 0.04 degrees, about 11.3 and 4.5 km. The other significant change was an increase in the average longitude of sugar maple by 0.1 degree (6.9 km); the species also increased slightly though insignificantly in elevation. Hemlock, which showed a tendency toward movement on Haystack Mountain, remained stable in elevational and regional position; it is doubtful whether the small amount of movement indicated by the Haystack transect would be detected by the regional analysis in Maine. Red oak, which exhibited a high percentage of new locations, showed a slight but insignificant tendency toward a southerly and westerly movement. There is no indication of a pronounced upward or northerly trend in species ranges as might be expected if incipient global warming were occurring; in fact, the opposite seems to be the case.

Discussion

The elevation and regional analyses reported in this paper provide a fairly consistent picture of vegetative change. The transect on Haystack Mountain provided clear examples of stationary fronts for beech and red spruce coinciding with site changes that appeared to provide a temporary obstacle to species movement. Sugar maple exhibited a one-step catastrophic front at higher elevations where established understory trees less than about 100 years old were missing; this appears to be a specific site-related phenomenon that cannot be explained at present. Hemlock had a well-defined but slowly moving advancing front. The plot survey in Maine substantiated to some degree the results on Haystack Mountain by reinforcing the concept of stability in elevation and position of most species. The primary exception was the apparent southerly movement in the range of white pine and balsam fir as reflected by a decrease in average latitude of 0.1 and 0.04 degrees. This movement is contrary to what might be expected under a scenario of global warming. We interpret this trend as a natural successional change on lands disturbed by cutting and/or agriculture. This points to one drawback in the use of regional survey plots to analyze species movements: it will be difficult to separate out slight or incipient change due to climatic trends or environmental impact from natural succession following earlier disturbance. Apparently, the latter factor is the dominant current underlying cause of species movement in Maine and probably most other New England States. Currently, there is no evidence from our study that if a climatic change is occurring, it has not materially affected the occurrence or competitive position of tree species in New England. Forest managers should be concerned primarily with species changes resulting from normal successional trends following previous disturbance from agriculture, clearing, and cutting. However, they should expect greater changes in the long term.

Advancing-front theory rests on the assumption that tree-species age structure over distance (or elevation) will reflect migrational trends: advancing fronts should be evidenced by a decreasing trend in maximum age over distance; retreating fronts will be reflected by an increasing trend in minimum age over distance; and stationary fronts exhibit no trend. The reasonable success that we achieved with this approach resulted from several factors:

Table 3.--Average elevation, latitude, and longitude of Maine plots occupied by major species at three measurement periods spanning a 24-year average period from the 1950's and 60's to the 1980's

Measurement period	Red spruce	Hemlock	Balsam fit	White pine	Sugar maple	Beech	Red oak
				Elevation (m)			
1	242(7)[a]	136(8)	238(7)	150(9)	265(10)	243(11)	121(16)
2	240(8)	135(8)	241(7)	142(9)	273(10)	250(11)	117(16)
3	237(7)	136(7)	231(7)**	134(8)**	272(10)	245(11)	119(14)
				Latitude (degrees)			
1	45.66(.04)	44.98(.06)	45.69(.04)	44.82(.07)	45.64(.07)	45.41(.06)	44.15(.10)
2	45.68(.04)	44.96(.06)	45.71(.04)	44.73(.07)	45.62(.07)	45.42(.07)	44.12(.09)
3	45.64(.04)	44.95(.06)	45.65(.04)**	44.72(.06)*	45.58(.06)	45.40(.06)	44.10(.07)
				Longitude (degrees)			
1	69.05(.04)	69.18(.08)	69.08(.04)	69.50(.08)	69.30(.07)	69.25(.07)	70.00(.14)
2	69.01(.04)	69.20(.08)	69.09(.04)	69.53(.08)	69.36(.07)	69.27(.07)	70.01(.14)
3	69.02(.04)	69.23(.07)	69.07(.04)	69.44(.07)	69.39(.06)**	69.26(.07)	70.05(.12)

[a]Standard error in parenthesis; **Significant at 0.01 level; *Significant at 0.05 level.

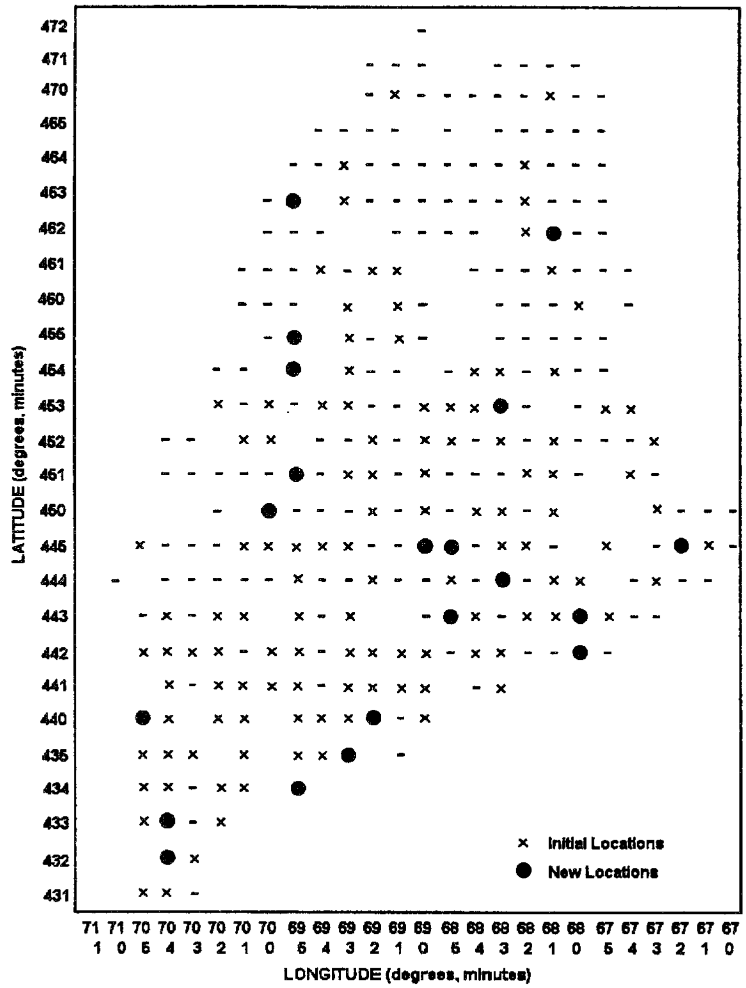


Figure 5.--Initial locations in Maine with living white pine, new locations after an average 24-year period, and locations without white pine at either point in time.

(1) The stands were fairly mature and only lightly disturbed.

(2) Several distinct cover types were present, and the types were clearly demarcated due to elevational and site-related restrictions on species occurrence.

(3) The study concentrated on tolerant species (beech, sugar maple, red spruce, and hemlock), which can regenerate in shade under an existing forest cover.

(4) Sampling was intensive: plot locations every 30.5 to 15.2 m in horizontal distance up the slope, with two prism samples of the overstory (which intensively samples the larger trees) and a strip sample (1.5 by 23 m) of the understory at each plot location.

Ideally, ages would be determined on each plot. In this study, age/d.b.h. regressions were used to estimate approximate maximum and minimum ages per species.

A second important phase in migrational studies of this type would be to relate rates of movement to climatic variables or other environmental factors. For well-developed, rapidly moving fronts, we have suggested that rates of movement in different portions or segments of the front could be correlated to historical weather variables or to surrogates such as diameter growth. This would provide the basis for modeling species movements in response to any given or chosen set of climatic variables (Solomon et al. 1990). Similarly, climatic variables could be correlated to species movements on remeasured plots such as the Maine survey plots used in this study. These approaches would provide the basis for relating climate to actual changes in species elevations and locations rather than to hypothesized changes based on computer simulations.

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Solomon, Dale S.; Leak, William B. 1994. **Migration of tree species in New England based on elevational and regional analyses.** Res. Pap. NE-688. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 9 p.

With field measurements of migration patterns, we used two complementary approaches to examine tree-species movement after a documented increase in temperatures. The advancing-front theory was used to examine age trends over distance and elevation for both a mountain site in New Hampshire and a regional comparison across the State of Maine. Well-defined stationary fronts were identified for red spruce (*Picea rubens* Sarg.) and beech (*Fagus grandifolia* Ehrh.), while a catastrophic front was depicted for sugar maple (*Acer saccharum* Marsh.) and a constant slow-moving advancing front was exhibited by hemlock *Tsuga canadensis* (L.) Carr.). The regional analysis, in Maine, indicated that white pine (*Pinus strobus* L.) and balsam fir (*Abies balsamea* (L.) (Mill.) decreased significantly in average latitude and elevation over a 24-year period. The potential ranges of the major species in terms of elevation and regional position appear stable.

Keywords: modeling; climate change

Headquarters of the Northeastern Forest Experiment Station is in Radnor, Pennsylvania. Field laboratories are maintained at:

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Burlington, Vermont, in cooperation with the University of Vermont

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