Relationships Between Environmental Factors and Hemlock Distribution at Mt. Ascutney, Vermont

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Abstract

In order to quantify relationships between environmental factors and the distribution of eastern hemlock (*Tsuga canadensis* (L.) Carr.) and other tree species, sites were established every 100 m along four contour lines, lying at 455 m (1500'), 610 m (2000'), 760 m (2500') and 915 m (3000') on Mt. Ascutney, a monadnock in the Connecticut River valley of eastern Vermont that rises to 960 m (3150'). At each site, basal areas of all trees were determined with a 2.5 BAF metric prism. Dominance, or relative basal area per hectare, of each species was then calculated. At each site, slope, aspect and topographic position were recorded. Fuzzy set ordination was then used to find relationships between these environmental factors and hemlock distribution. Overall, hemlock was the most dominant species at 455 m, the lowest elevation (it was not found at the two higher ones). Hemlock was an important codominant at 610 m. At 455 m, hemlock was a significant component at all aspects, but was most dominant on northwest aspects. At 610 m, it was most important on west aspects. It was also most dominant at intermediate topographic positions (e.g. slopes), with little difference between elevations. Although hemlock is often considered to be important in cool, dark, wet stream bottoms, the results of this study indicate that hemlock is also important at more well-drained upland sites.

Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is an important species in the northeastern forest. The hemlock woolly adelgid (*Adelges tsugae* Annand), a tiny sucking insect thought to be introduced from Japan (McClure 1992), has caused significant mortality of hemlock in New England since its introduction in the mid-1980s (McClure 1991, Watson 1992, Bonneau and Civco 1996, Royle and Lathrop 1997). The adelgid is currently not found in most of northern New England, but is expected to spread across the entire range of hemlock (McClure 1989, 1990).

The effects of hemlock mortality are well-studied in southern New England (Orwig and Foster 1998, Jenkins et al. 1999). However, while hemlock remains an important part of the northern New England forest, the associated species change. For example, black birch (*Betula lenta* L.), which is one of the most important successional species after adelgid-induced mortality in southern New England (Orwig and Foster 1998), is not present in most of northern New England. Thus, the pattern of succession after hemlock mortality in northern New England may differ from that seen so far in southern New England. Therefore, the object of this study was first to find where hemlock is distributed at an upland site in the upper Connecticut River valley of Vermont and New Hampshire. Based on the current locations and tree species associations found at sites where hemlock is now found, an attempt was then made to predict which species will take over after hemlock mortality occurs.

Methods

Data were collected from Mt. Ascutney (43°27' N, 72°27' W), a monadnock in the Connecticut River valley of eastern Vermont, that rises to an elevation of 960 m (3150'). Sites were established every 100 m along four contour lines, lying at 455 m (1500'), 610 m (2000'), 760 m (2500') and 915 m (3000'), so as to circumnavigate the entire mountain. At each site, basal areas per hectare of trees were determined with a 2.5 BAF metric prism (Avery and Burkhart 1983). Slope and aspect were also recorded. Dominance of each species at each site was calculated as its basal area per hectare divided by site total basal area per hectare and ranged from 0 to 1. Aspect values were calculated as (cos(q-30°)+1)/2 (Roberts 1986), where q is the aspect, so that plots on northeast aspects would have values near 1, while plots with southwest aspects would have values near zero. Slope was expressed as the "percent" slope = tan (slope (°)). Topographic position was recorded subjectively and coded from 1 to 3, with a 1 indicating a ridge top and a 3 indicating a stream bottom. Both total basal area per hectare and relative basal area (dominance) of each species at each elevation were calculated. Mean basal areas of each species at each elevation were also determined. A total of 383 sites were included from all four elevations; of this number, 154 sites were at 455 m and 130 were at 610 m.

The distribution of sites with hemlock at the lower two elevations (hemlock was not found above 610 m) was also examined in detail. Circular plots showing site aspect and dominance were generated. Mean angles of hemlock-dominance-weighted aspects and angular dispersions were calculated (Zar 1984). The Moore nonparametric modification of the Rayleigh test for significant direction using aspect angles weighted by hemlock dominance was also applied to both elevations (Zar 1984). Those sites with hemlock present were assigned to one of four aspect classes: NE (>0-90°), SE (>90-180°), SW (>180-270°) and NW (>270-360°). At each aspect class and elevation, other tree species with a mean dominance greater than 0.10 were noted. Each aspect class was then further divided into four classes based on hemlock dominance (<0-0.25, <0.25-0.50, <0.50-0.75, and >0.75-1). The two associated species with the largest dominances were then noted (three species were listed if the second and third largest were similar).

Fuzzy set ordination (FSO), as described in Boyce (1998), was performed to examine relationships between tree species and site factors. FSO is a technique introduced by Roberts (1986), who has shown it to be a general technique

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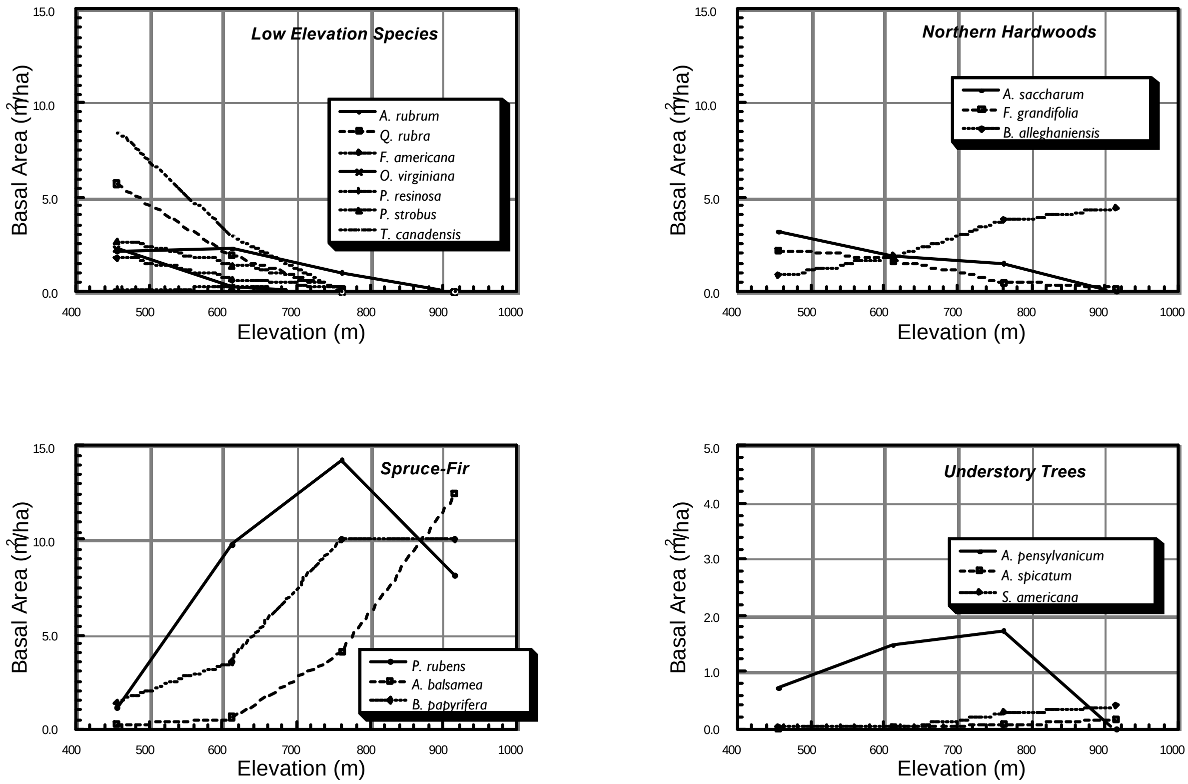

Figure 1.—Mean basal area per hectare of each species at each actual elevation.

that includes direct gradient analysis (Whittaker 1967), Bray-Curtis ordination (Bray and Curtis 1957) and environmental scalars ordination (Loucks 1962). An investigator using fuzzy set ordination must hypothesize a relationship between the environment and the vegetation before performing the ordination. Sites are assigned values that can range from 0 to 1 that denote their membership in a set. For example, the values of site in a fuzzy set of "high elevations" would range from 0 (the lowest site) to 1 (the highest site). One very useful operator in vegetation analysis is the anticommutative difference (Roberts 1986), which can be understood as "while not." This can be used, for example, to construct a fuzzy set that includes the membership of sites that are similar in composition to high elevation sites while not similar to low elevation sites. This is referred to as "apparent elevation" and shows the elevation of a site based on its composition. Thus, a spruce-fir stand would have a higher apparent elevation than an oak-pine stand found at the same elevation. Details of the ordination procedure are given in Boyce (1998). After FSO was performed, species dominance was plotted against apparent elevation to determine which species were associated with high and low apparent elevations. Mean site attributes (topographic position, slope and aspect values) of each species, weighted by dominance, were determined for each elevation.

Results

In terms of mean basal area, forests at 455 m were dominated by hemlock and red oak (*Quercus rubra* L.) (Fig. 1). A number of other hardwood and conifer species were also found in small amounts. By 610 m, however, red spruce (*Picea rubens* Sarg.) had become the dominant species, with white birch (*Betula papyrifera* Marsh.) and hemlock as important codominants. At 760 m, red spruce and white birch were the most dominant species, while balsam fir (*Abies balsamea* (L.) Mill.) had become an important component. Red spruce basal area peaked at 760 m and the basal area of white birch leveled off, but the dominance of balsam fir increased so that it had become the dominant species at 915 m, followed by white birch and red spruce. At no elevation was the "Northern Hardwood" forest type, consisting of sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton), ever dominant. Among understory trees, striped maple (*A. pensylvanicum* L.) achieved its greatest dominance at 760 m, while mountain maple (*A. spicatum* Lam.) and mountain-ash (*Sorbus americana* Marsh.) were most dominant at 915 m.

Plots with low apparent elevations were dominated by red oak and hemlock (Fig. 2), and were found on sites with south-facing aspects and steep slopes. Sites with the

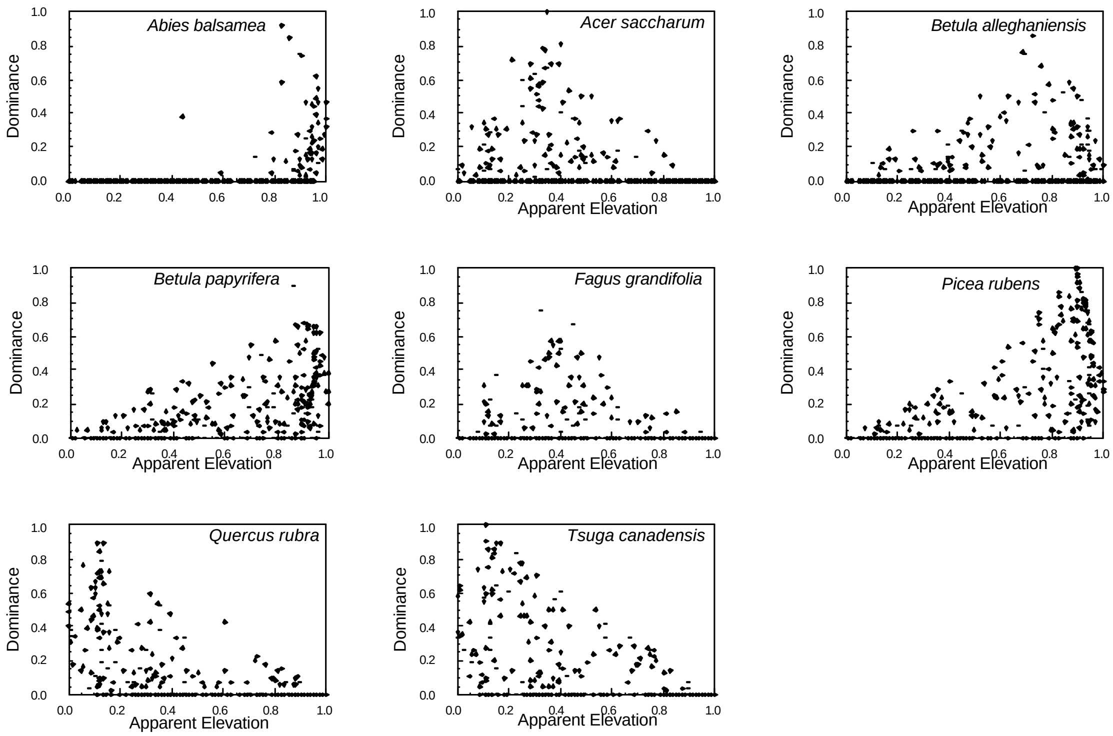

Figure 2.—Plots of dominance (relative basal area) vs. apparent elevations for important species on Mt. Ascutney.

highest apparent elevations were dominated by balsam fir, red spruce and white birch (Fig. 2). Hemlock was generally found on midslopes at both 455 and 610 m, rather than on ridgetops or stream bottoms; there was little variation in topographic position with elevation (Fig. 3). Hemlock sites had one of the higher mean percent slopes of those species found at both elevations, although there was a good degree of variation (Fig. 4). Hemlock mean aspect values were approximately 0.6, indicating a preponderance of sites that faced a bit north of true east and west, but the variation was quite large, indicating that hemlock was widely distributed at many different aspects (Fig. 5).

Analysis of actual aspect weighted by dominance showed a mean northwest aspect at both elevations (Fig. 6). At 455 m, mean aspect was 340°, with an angular deviation of 70°, while at 610 m, mean aspect was 307° and angular deviation was 57°. Despite high angular deviations, both directions were statistically significant (Fig. 6). At 455 m, the most important associated species was red oak at all aspects except the northeast, where sugar maple and beech were important (Table 1). White pine and beech were also important on the southwest and southeast aspects, respectively. As hemlock increased in dominance, however, red spruce became increasingly important, except on southwest aspects, where red oak and white pine were the most important associates. Yellow and white birch were important associates on northeast and northwest aspects as hemlock increased in dominance. At 610 m, red spruce was the most important associate (Table 1). Yellow and white birch were also important on the northern aspects, while white pine was also important on the southern aspects. At this elevation, there was little difference in associates among dominance classes.

Both red oak and hemlock reached their maximum dominance at or below the lowest apparent elevation examined in this study (Fig. 7). Both species are capable of completely dominating a stand at low apparent elevations. Although northern hardwoods are not at present a very important component of the forests on Mt. Ascutney, Figure 7 shows that they are capable of becoming the dominant species at lower-middle apparent elevations. Yellow birch actually reached its peak of dominance at higher apparent elevations than the other two “Northern Hardwood” species. Red spruce was found at all apparent elevations, but it reached its greatest dominance at or above the highest apparent elevations, where it could completely dominate a site. Balsam fir could also completely dominate high apparent elevations but was not found at lower apparent elevations. White birch achieved its maximum dominance at the highest apparent elevations, but it never completely dominated a stand like the two conifer species did. Among understory trees, only striped maple was able to reach high levels of maximum dominance, which occurred at middle apparent elevations. Both mountain maple and mountain-ash attained low levels of maximum dominance at high apparent elevations. Among other tree species, only white

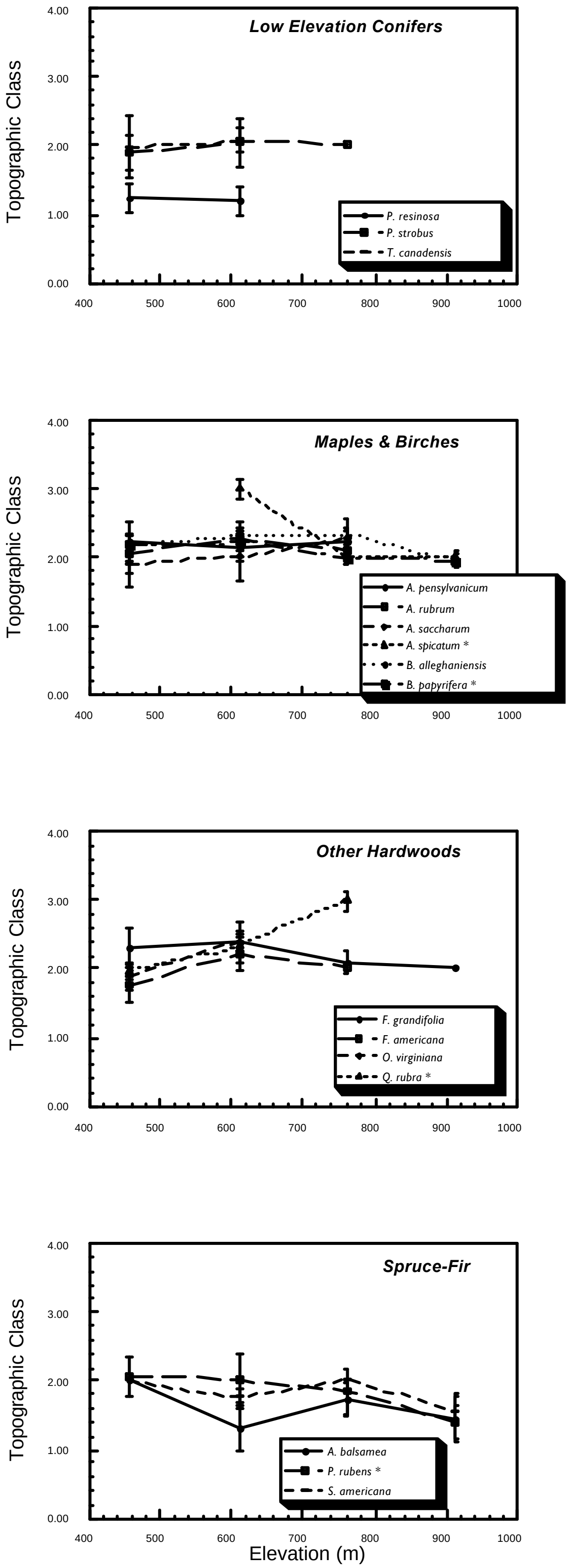

Figure 3.—Mean topographic position (1=ridgetop, 2=intermediate position (slope), 3=stream bottom) of each species at each elevation, weighted by dominance of the species at each site, vs. actual elevation. Species with statistically significant linear increases or decreases with elevation (P<0.05, F-test) are indicated with a star. Error bars are standard deviations.

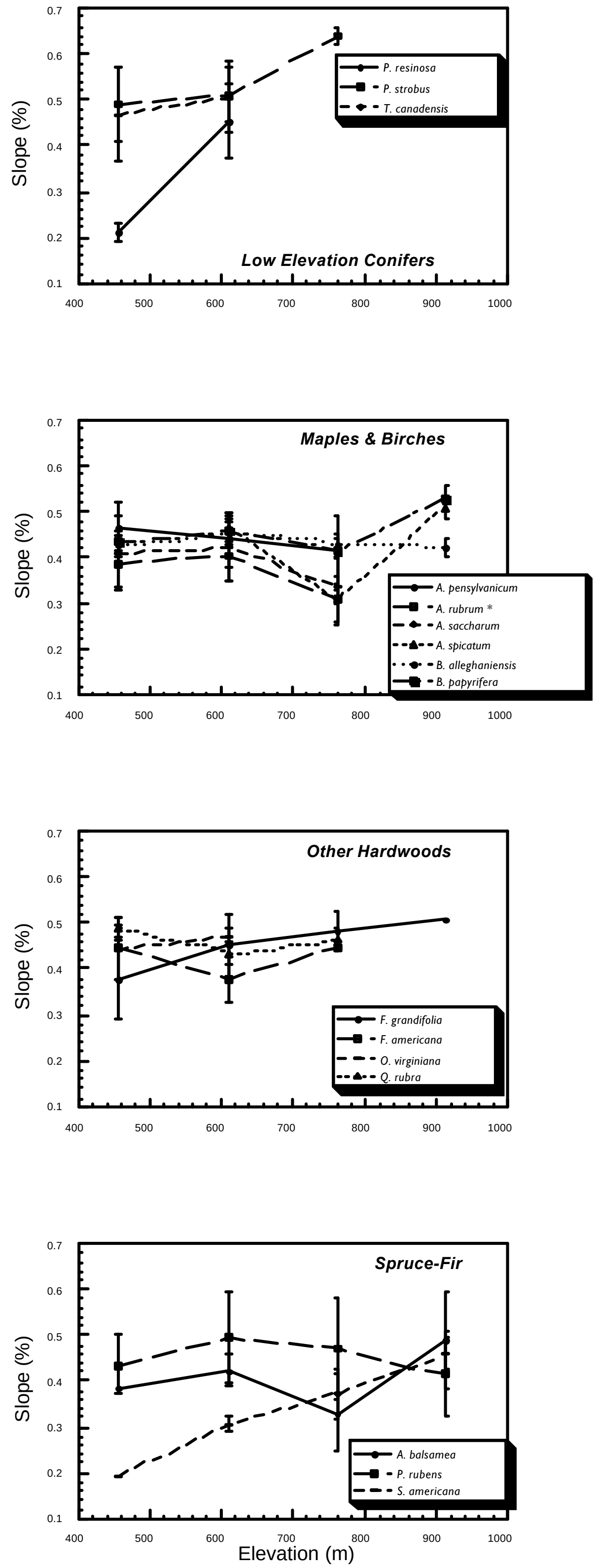

Figure 4.—Mean slope of each species, weighted by dominance of the species at each site, vs. actual elevation. Species with statistically significant linear increases or decreases with elevation (P<0.05, F-test) are indicated with a star. Error bars are standard deviations.

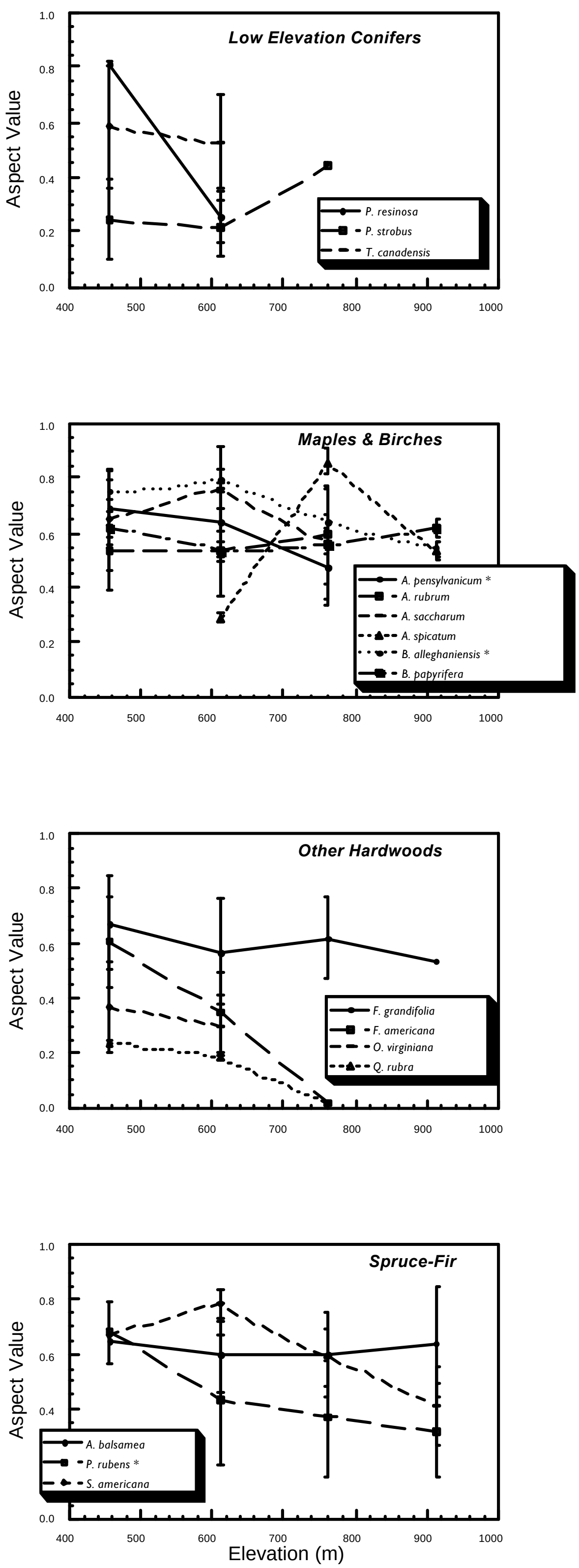

Figure 5.—Mean aspect value of each species, weighted by dominance of the species at each site, vs. actual elevation. Note than an aspect of 30° has an aspect value of 1, while an aspect of 210° has an aspect value of 0. Species with statistically significant linear increases or decreases with elevation (P<0.05, F-test) are indicated with a star. Error bars are standard deviations.

pine (*Pinus strobus* L.) showed the potential to almost completely dominate a stand. Red maple (*Acer rubrum* L.) was widely distributed across apparent elevations but appeared incapable of attaining more than codominant status. Hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) is usually an uncommon understory or subcanopy tree (Burns and Honkala 1990), but there were stands at lower apparent elevations on Mt. Ascutney where it appeared capable of making up more than 50% of relative basal area.

Discussion

Hemlock is currently an extremely important species on Mt. Ascutney, with the highest basal area at 455 m and an important codominant at 510 m. Boyce (1998) asserted that it has the potential to dominate many sites at 455 m and in fact does; however, analysis of the upper bounds of dominance indicates that it probably reaches its most importance at elevations below those sampled in this study. Hemlock is widely distributed on the lower reaches of this mountain. While there is a significant trend toward greater hemlock dominance at northwest aspects, especially at 610 m, the species is clearly widely distributed. Figure 6 shows that hemlock is less prevalent on the southeast aspects at 610 m. This may be due in part to the hurricane of 1938, which strongly affected the southeast-facing slopes of Mt. Ascutney (ATA 1992); indeed, the southeastern side of Mt. Ascutney has noticeably fewer conifers that other aspects (R. Boyce, personal observation). This effect may be enhanced at higher elevations because of increasing wind speeds.

At the upland sites sampled here, hemlock is found mainly on slopes. This species is typically found to occupy stream bottoms (e.g. Burns and Honkala 1990). Why is this not the case at the upland sites sampled here? There appears to be a parallel response to elevation of both hemlock and red spruce. Boyce (1998) found that red spruce was restricted to stream bottoms at the lower elevations on Mt. Ascutney. However, it moved to slopes and ridges at higher elevations, which may be due to the increasing moisture that is available at all topographic positions at higher elevations (Boyce 1998). Hemlock appears to exhibit a similar trend, albeit at lower elevations than spruce.

A wide variety of species associate with hemlock at both elevations. At 455, red oak is the most dominant hemlock associate (Table 2). On sites with northeast aspects, however, sugar maple and beech are the most important. However, in stands at this elevation dominated by hemlock (more than 75% of the basal area), red spruce is the most important associate. At 610 m, red spruce is by far the most important associate overall and at most of the different levels of hemlock dominance as well.

So what does this imply for these upland hemlock stands when they are attacked by hemlock woolly adelgid? Studies in southern New England have shown that the adelgid causes a rapid shift from a coniferous to a deciduous forest, with the most common colonizers being red maple, oaks (*Quercus* spp.) and black birch (Orwig and Foster 1998).

Table 1.—Dominance of hemlock and associated species by aspect class at 455 m and 610 m, along with total number of sites with hemlock. Each aspect class is also divided into four hemlock dominance classes; the two most important asociated species are listed for each dominance class, along with the number of sites for each dominance class (e.g. n^{25} is the number of sites in the 0-.25 class).

Aspect	N	Species	Mean dominance	n^{25}	0-.25	n^{50}	.25-.50	n^{75}	.50-.75	n^{100}	.75-1.0
455 m											
NW	23	Hemlock Red oak	0.50 0.13	7	Red oak Sugar maple	4	Yellow birch Red oak	8	White birch Red oak	4	Red spruce
NE	35	Hemlock Sugar maple Beech	0.38 0.12 0.10	15	Sugar maple Beech	9	Red spruce White birch	6	Sugar maple White birch	5	Yellow birch Red spruce
SE	13	Hemlock Red oak Beech	0.42 0.19 0.11	4	Red oak Hophornbeam Beech	4	Red oak White pine	3	Beech Red oak	2	Red spruce Striped maple
SW	16	Hemlock Red oak White pine	0.33 0.30 0.11	6	Red oak White pine	6	Red oak White pine	4	Red oak White pine	—	
610 m											
NW	15	Hemlock Red spruce White birch	0.30 0.31 0.12	8	Red spruce White birch	4	Red spruce White pine White birch	3	Red spruce Striped maple	—	
NE	10	Hemlock Red spruce White birch Yellow birch	0.24 0.33 0.12 0.11	7	Red spruce Yellow birch White birch	2	Red spruce White birch	1	Yellow birch Sugar maple Beech	—	
SE	1	Hemlock Red spruce White pine	0.26 0.35 0.17	—		1	Red spruce White pine	—		—	
SW	15	Hemlock Red spruce White birch	0.24 0.31 0.15	9	Red spruce White birch	6	Red spruce White pine	—		—	

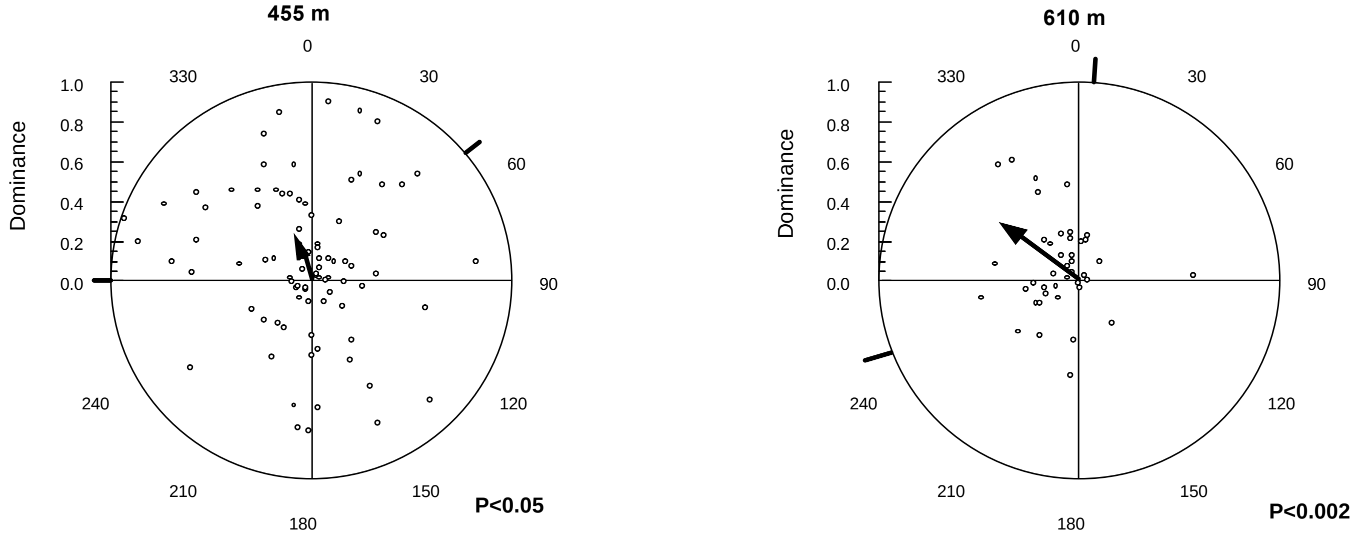

Figure 6.—Aspect and dominance of sites with hemlock present at 455 and 610 m. Mean vector length and directions (Zar 1984), weighted by hemlock dominance, are shown for each elevation by an arrow with its base at the origin. Angular dispersions are denoted by marks on the periphery of the circle. The mean vector length, direction and angular dispersion for 455 m are 0.26, 340° and 70°, respectively. The mean vector length, direction and angular dispersion for 610 m are 0.51, 307° and 57°, respectively. The Moore nonparametric modification of the Rayleigh test for significant direction, using aspect angles weighted by hemlock dominance, rejected the null hypothesis of no significant directionality at both elevations (455 m: R'=1.19, P<0.05; 610 m: R'=1.62, P<0.002).

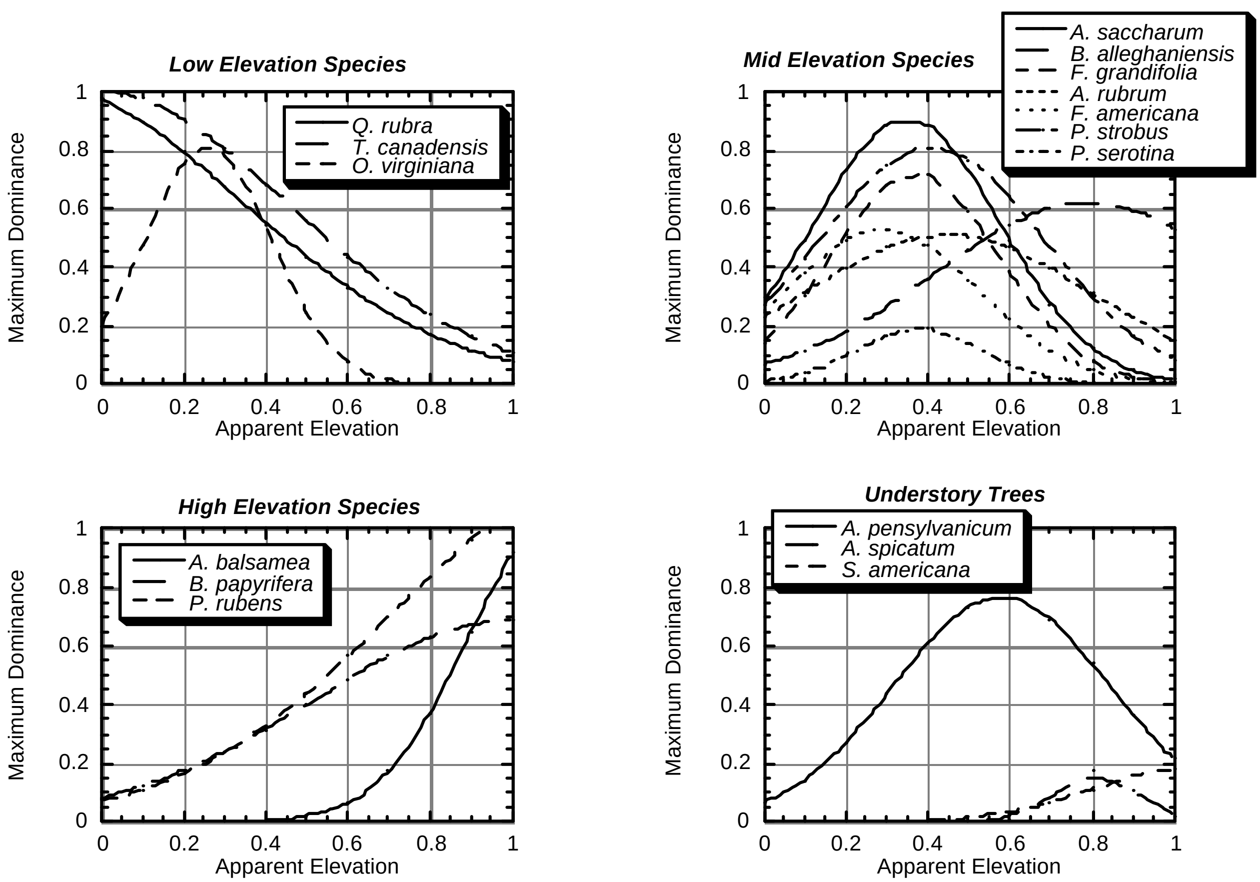

Figure 7.—Upper bounds of dominance of each species vs. apparent elevation. Upper bounds were derived from the data in Fig. 2, using the procedure described in Boyce (1998).

Thus, those hemlock sites with red oak, maples, and birches as associates are likely to be replaced by those species. However, red spruce is an important component in hemlock-dominant stands at 455 m and most stands at 610 m. Red spruce is generally considered a late-successional species that responds slowly to disturbance. However, the "gradual" gaps (sensu Krasny and Whitmore 1992) caused by hemlock decline may allow red spruce to take over what are currently hemlock-dominated stands. If the decline is more rapid, however, yellow or white birch-dominated stands may be more likely. Also, red spruce is in decline in New England (Peart et al. 1992), though not noticeably at Mt. Ascutney (R. Boyce, personal observation). Perkins et al. (1988) noted that yellow and white birches rapidly colonized areas impacted by spruce decline in northern New England; since these species are often important in stands with hemlock, they may also colonize stands with adelgid-induced hemlock mortality.

Because of Mt. Ascutney's proximity to the Connecticut River, the lower elevations lie in Westveld's (1956) "Transition Hardwoods" region, which is shown by the importance of species such as red oak and hophornbeam (Fig. 4). The typical "Northern Hardwoods" forest (sugar maple, beech and yellow birch), which dominates nearby sites in the White and Green Mountains between 610 and 760 m (Bormann et al. 1970, Siccama 1974), is not as important at this site. This mountain is already highly disturbed; within the last 100 years, Mt. Ascutney has experienced logging, fires, granite quarrying and a hurricane (ATA 1992). Disturbance is a likely explanation for the relative importance of white birch at low elevations, as well as the importance of striped maple, which generally requires disturbance to reach the tree stratum (Fig. 7). Thus there are already an abundance of pioneer species present. While the hemlock woolly adelgid is expected to drastically decrease hemlock abundance, the forest is likely to recover quickly. There is likely to be an initial conversion to hardwood stands, particularly birch. While stands currently dominated by oaks may remain that way, stands that are colonized by birch may eventually convert to red spruce, especially at 610 m, provided spruce is not itself in decline.

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