

Fuzzy set ordination along an elevation gradient on a mountain in Vermont, USA

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Abstract. Fuzzy set ordination was used to examine relationships between tree species and site factors on Mt. Ascutney, Vermont, USA. Prism plots were established at four elevations (455, 610, 760 and 915 m) along contour lines that encircled the mountain. In addition to elevation, which was the most important factor affecting tree species composition, slope, aspect and exposure to solar radiation all affected composition; however, these latter three factors were important only at 455 m. Topographic position was important at higher elevations as well. The responses of tree species to any of these factors were highly individualistic. Plots of the upper bounds of relative basal area of each species against the apparent elevation of sites where that species was found were useful in predicting how important an individual species could become over the course of forest succession. For example, northern hardwoods, which comprise the most common forest type of this region, are not very common on this mountain. This approach shows, however, that they are currently at levels well below their potential maximum; this is probably due to past disturbance.

Keywords: Fuzzy set theory; New England; Northern hardwoods; Spruce-fir.

Nomenclature: Spurr & Barnes (1980).

Introduction

Elevation has a profound effect on tree species composition in northern New England. In general, forests dominated by northern hardwoods at low elevations give way to predominantly coniferous forests dominated by *Picea rubens* and *Abies balsamea* at high elevations (Bormann et al. 1970; Siccama 1974). The mean elevation of the ecotone is 730-760 m in northern New England, with a decrease of approximately 100 m per degree of latitude (Cogbill & White 1991). However, the elevational range spanned by individual species is not only affected by latitude. Even in the limited geographical region of the central White Mountains of New Hampshire, the elevation of the deciduous/coniferous ecotone

varies by 60 m (Foster & Reiners 1983). Other factors such as aspect and slope are well known to affect species distributions along elevational gradients (e.g. Whittaker 1956; Barbour 1988; Peet 1988; Busing et al. 1993).

Ordination can be used to find associations between site factors and species distributions (Pielou 1984). Fuzzy set ordination was introduced by Roberts (1986) as a heuristic alternative to traditional ordination techniques. Unlike these latter techniques, 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 sites in a fuzzy set of 'high elevations' would range from 0 (the lowest site) to 1 (the highest site). Conversely, the values of sites in a low-elevation fuzzy set would range from 0 (the highest site) to 1 (the lowest site). The sets are considered to be fuzzy because each site or element in the set can have partial membership; in classical set theory, elements are either completely in or completely out of a given set. The operations of classical set theory, such as union and intersection, can also be performed on fuzzy sets. 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 actually at high elevation.

Roberts (1986) has shown that fuzzy set ordination is a general technique that includes specific types of ordination that ecologists are more familiar with, such as direct gradient analysis (Whittaker 1967), Bray-Curtis ordination (Bray & Curtis 1957), and environmental scalars ordination (Loucks 1962). Species responses to environmental factors are not restricted to any particular function; they can be, for example, nonlinear or discontinuous. Also, each axis of the ordination is chosen beforehand, so the basis of interpretation is predetermined. Thus, the ecologist can use fuzzy set ordination to explicitly test hypotheses.

The object of this study is to use fuzzy set ordination to determine the effect of environmental factors on tree species composition along an elevational gradient on a mountain in Vermont in the northeastern USA.

Methods

Data were collected from Mt. Ascutney (43°27' N, 72°27' W), a monadnock in the Connecticut River valley of eastern Vermont, which 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 of trees were determined with a 2.5 BAF metric prism (Avery & Burkhart 1983). Slope and aspect were also recorded. 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 and relative basal area (dominance) of each species were calculated. A total of 383 sites were included.

Membership in the set of high elevation plots was determined as $\mu_A(x) = [e(x) - e_{\min}] / [e_{\max} - e_{\min}]$, where $e(x)$ is the elevation of plot x , and e_{\max} and e_{\min} are the maximum and minimum plot elevations (Roberts 1986). Membership in the set of low elevation plots was computed as $\mu_B(x) = 1 - \mu_A(x)$. Similarity between every pair of sample plots was calculated using Stander's index (Sullivan 1975; Johnson & Millie 1982; Brower et al. 1990; Zhang 1994; Zhang & Oxley 1994); Stander's index is related to Simpson's index of dominance (Brower et al. 1990) and is computed as:

$$S_{ab} = \frac{\sum_{i=1}^n x_{ai} x_{bi}}{\sqrt{\sum_{i=1}^n x_{ai}^2 \sum_{i=1}^n x_{bi}^2}} \quad (1)$$

where S_{ab} is the similarity of plot a to plot b and x_{ai} is the dominance of species i in plot a . The use of Stander's index minimizes the 'curlover' effect (R.L. Boyce unpubl.), a distortion introduced by fuzzy set ordination that is analogous to the arch effect encountered in principal component analysis (Pielou 1984). In fuzzy set ordination, points that should be at the highest apparent elevation are 'pulled in' to slightly lower apparent elevations, and points that should be at the lowest apparent elevations are pulled in to slightly higher elevations (D. Roberts pers. comm.). The set of plots similar to high elevation plots was calculated as:

$$\mu_C(x) = \frac{\sum_{y \neq x} [S_{xy}(\mu_A(y))]}{\sum_{y \neq x} [\mu_A(y)]} \quad (2)$$

The set of plots similar to low elevation plots (set D) was calculated similarly. Set E, the set of plots similar to high elevation plots while not similar to low elevation plots, or the apparent elevation, is the anticommutative

difference (Roberts 1986) of sets C and D and was computed as:

$$\mu_E(x) = \mu_{C \cap D}(x) = \left\{ 1 + [1 - \mu_D(x)]^2 - [1 - \mu_C(x)]^2 \right\} / 2 \quad (3)$$

The values of set E, or the apparent elevations, were then normalized so as to cover the full range from 0 to 1. To assign membership in the set of cool, moist plots, an aspect value was calculated (Roberts 1986), so that plots on northeast slopes would have values near 1, while plots on southwest exposures would have values near 0. Membership in the set of plots with steep slopes was calculated as the percent slope = $\tan(\text{slope})$ (°). The cosine of the beam slope angle at local noon on the summer solstice was used to estimate solar radiation received by each plot, which combines both aspect and slope into one index (D. Roberts pers. comm.). Topographic position of each site was assigned the value 1 if it was on a ridgetop, 3 if in a stream bottom, and 2 at intermediate positions (based on Busing et al. 1993).

Analysis of variance (ANOVA) of apparent elevations, where actual elevation was the independent variable, was performed with a planned linear contrast (Steel & Torrie 1980) to show whether apparent elevation changed with actual elevation in a linear manner (Mize & Schultz 1985). For each elevation, rank correlations (Zar 1984) between site attributes and apparent elevation were performed. An ANOVA of apparent elevation, with topographic position as the independent variable and with a linear contrast, was performed instead of rank correlation, as there were only three topographic position scores. Species dominance was plotted against apparent elevation to determine which species were associated with high and low apparent elevations. Mean site attributes of each species, weighted by dominance, were determined for each elevation. Mean basal area of each species at each elevation was also determined.

Plots of relative basal area, or dominance, of each species vs. apparent elevation showed that the upper bounds on these distributions could be approximated by a normal or Gaussian curve. For each species, the upper bounds of the dominance distribution vs. apparent elevation was estimated, using a procedure derived from Blackburn et al. (1992). Data were divided into eight equal apparent elevation classes. A Gaussian curve was then fit to the maximum value in each apparent elevation class, using the Levenberg-Marquardt nonlinear

Table 1. Analysis of variance of apparent elevation vs. actual elevation. A linear contrast was calculated as well.

| Factor | % total variation explained | <i>P</i> |
|------------------|-----------------------------|----------|
| Actual elevation | 66.7 | < 0.0001 |
| Linear contrast | 18.9 | < 0.0001 |

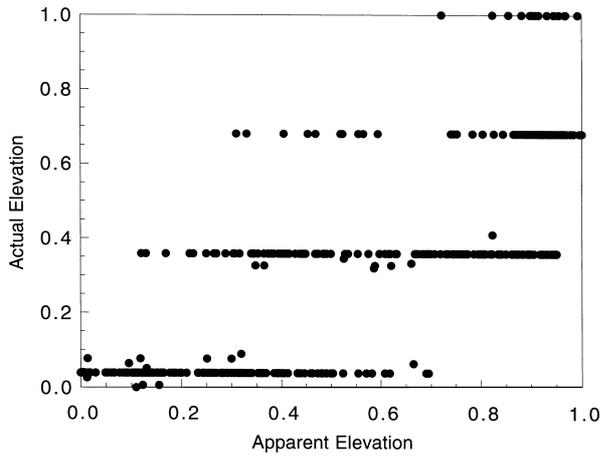


Fig. 1. Actual vs. apparent elevation. For the analysis of variance, sites that were slightly higher or lower than the nominal elevations (455 m, 610 m, 760 m, 915 m) were grouped with the appropriate elevation.

Table 2. Rank correlation of aspect, slope and solar radiation with apparent elevation, by actual elevation. Values of Spearman's r and P -values are given; significant correlations ($P \leq 0.05$) are shown in bold. A positive value of r indicates that the factor increases with increasing apparent elevation, while a negative values shows that it decreases.

| | Aspect | Slope | Solar radiation |
|--------------|--------------------|---------------|-----------------|
| 455 m | | | |
| r | 0.3942 | -0.2129 | -0.2537 |
| P | < 0.0001 | 0.0085 | 0.0017 |
| 610 m | | | |
| r | 0.0481 | 0.1020 | -0.1034 |
| P | 0.5848 | 0.2468 | 0.8748 |
| 760 m | | | |
| r | -0.1333 | -0.0057 | -0.0145 |
| P | 0.2245 | 0.0588 | 0.8947 |
| 915 m | | | |
| r | 0.1571 | 0.2946 | -0.4321 |
| P | 0.5565 | 0.2703 | 0.1059 |

curve-fitting algorithm employed by the data analysis and graphing program KaleidaGraph™ (Anon. 1994).

Results

Actual elevation explained about 2/3 of the variation in apparent elevation (Fig. 1, Table 1), while the planned

linear contrast explained only 19%. Aspect, slope and solar radiation explained variation in the apparent elevations of sites only at 455 m (Table 2). Topographic position was also a significant factor in explaining apparent elevation at 455 m (Table 3), and a linear contrast showed that sites with the lowest apparent elevations were on ridges, while sites with the highest apparent elevations were in stream valleys. At higher elevations

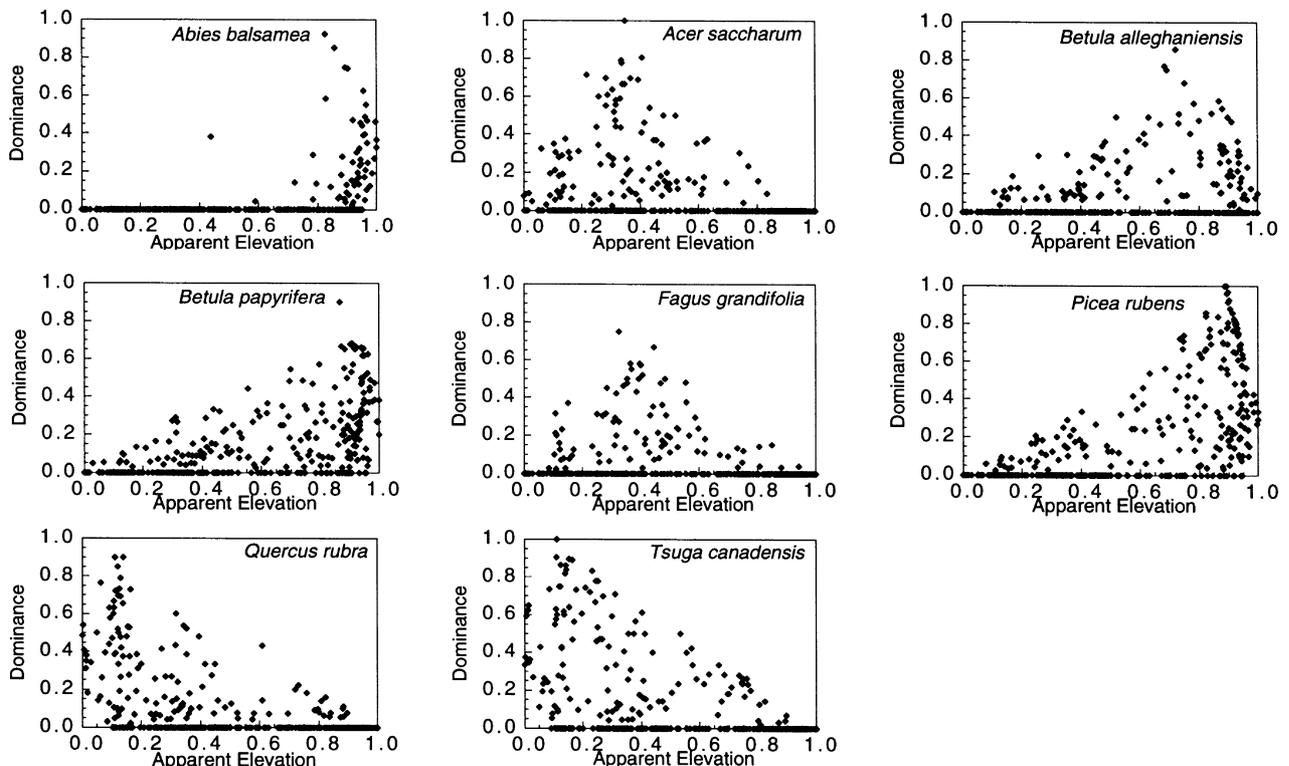


Fig. 2. Plots of dominance (relative basal area) vs. apparent elevations for selected species.

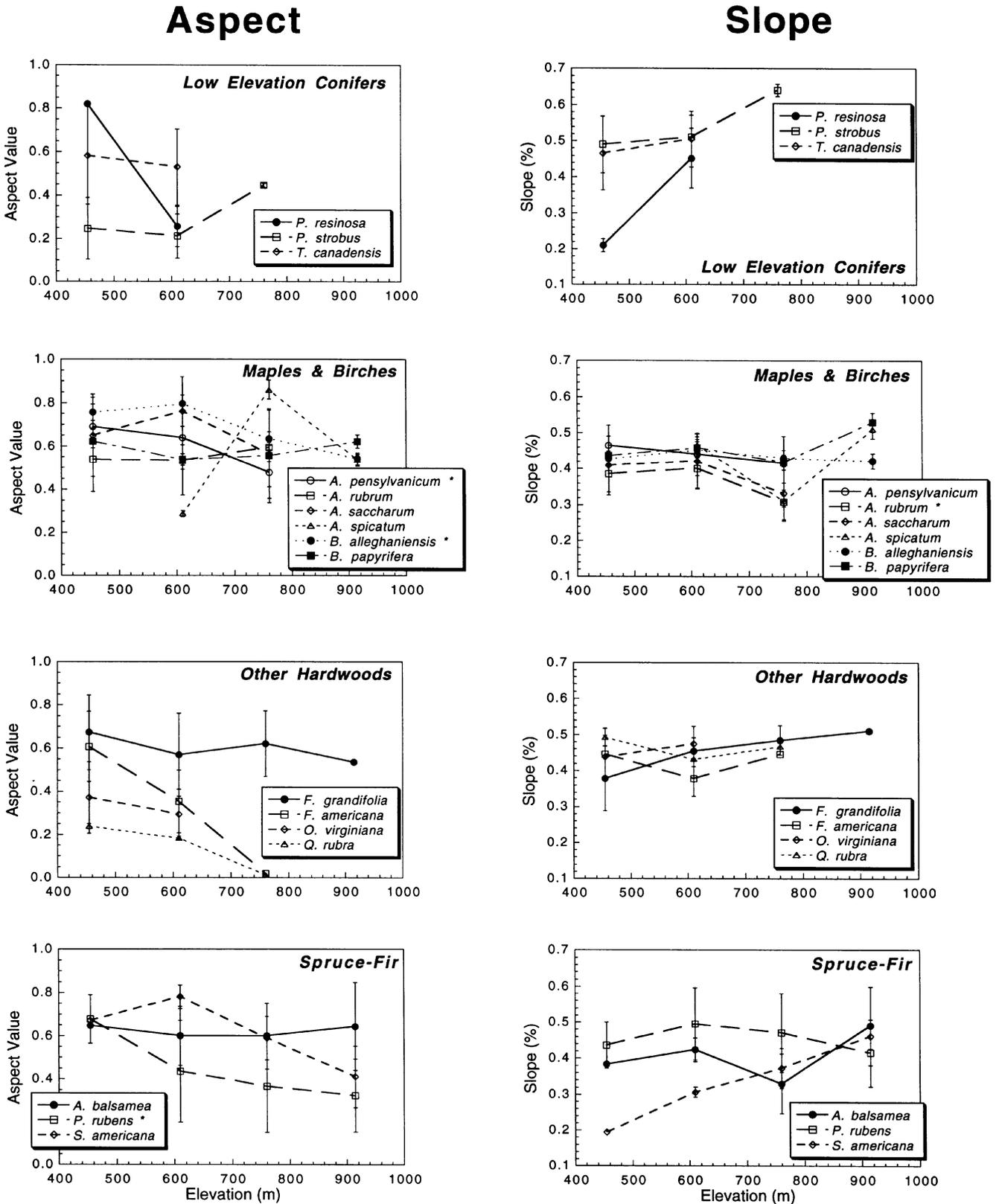


Fig. 3. Mean aspect and slope of each species, weighted by dominance of the species at each site. Species with statistically significant planned linear contrasts ($P < 0.05$, F -test), indicating a significant increase or decrease with elevation, are indicated with a star. Error bars are standard deviations.

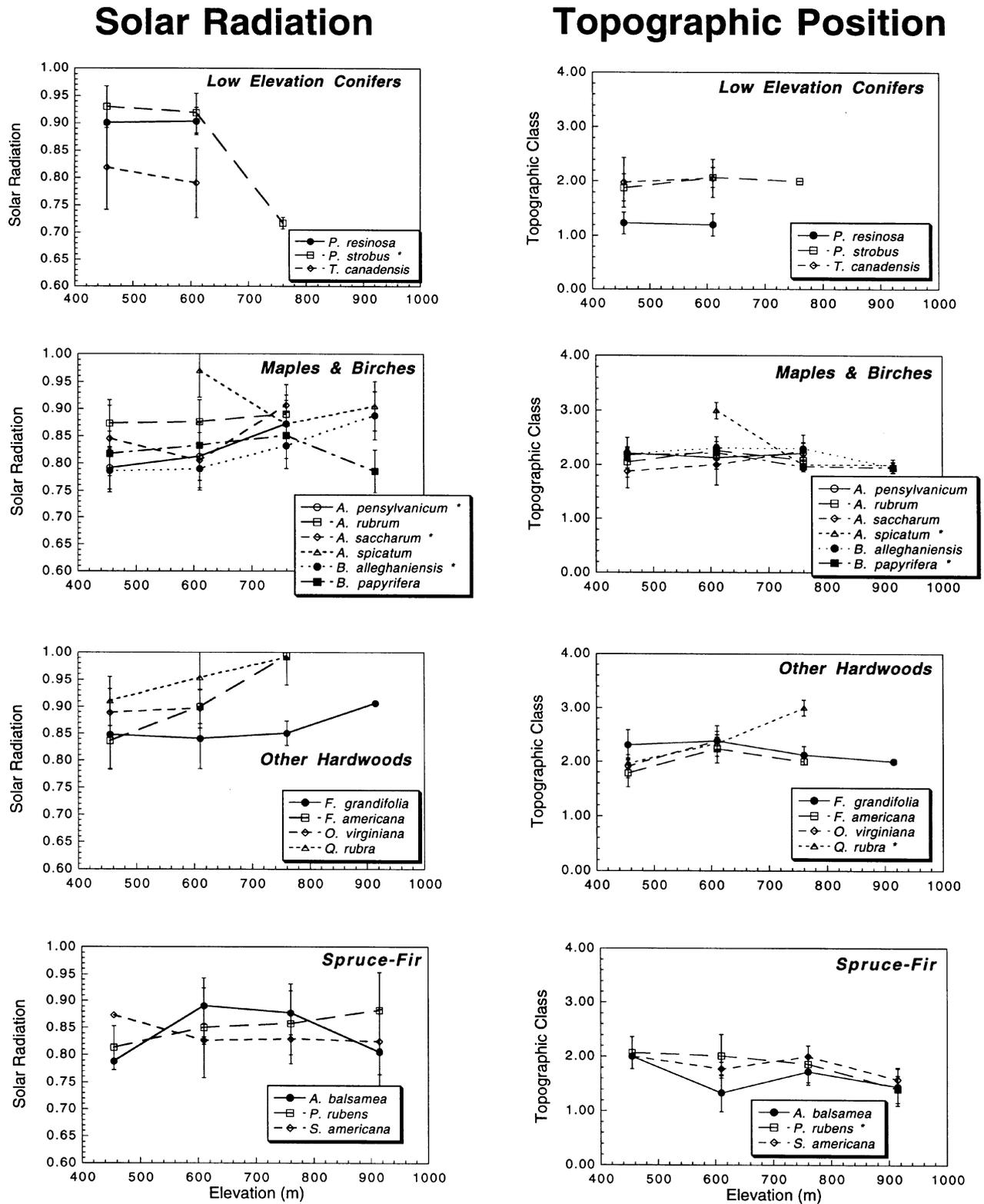


Fig. 4. Mean solar radiation exposure and topographic position (1 = ridgetop, 2 = intermediate position, 3 = stream bottom) of each species at each elevation, weighted by dominance of the species at each site, vs. actual elevation. Species with statistically significant planned linear contrasts ($P < 0.05$, F -test), indicating a significant increase or decrease with elevation, are indicated with a star. Error bars are standard deviations.

Table 3. Analysis of variance of apparent elevation vs. topographic position at each elevation. A linear contrast on actual elevation was also calculated; % = percentage of the total variation explained

| Elevation (m) | Topographical position | | Linear contrast | |
|---------------|------------------------|--------|-----------------|--------|
| | % | P | % | P |
| 455 | 4.8 | 0.0235 | 3.1 | 0.0273 |
| 610 | 1.7 | 0.3453 | 0.68 | 0.3508 |
| 760 | 6.6 | 0.0618 | 6.5 | 0.0197 |
| 915 | 4.8 | 0.4314 | - | - |

this trend reversed, and sites with high apparent elevations were found on ridges. However, only the linear contrast at 760 m was statistically significant (Table 3). Plots with low apparent elevations were dominated by *Quercus rubra* and *Tsuga canadensis* (Fig. 2) and were found on sunny sites with south-facing aspects and steep slopes. Sites with the highest apparent elevations were dominated by *Abies balsamea*, *Picea rubens* and *Betula papyrifera* (Fig. 2).

Certain species, such as *Quercus rubra*, exhibited a strong preference for south-facing exposures at all elevations where they were found (Fig. 3). Others, such as *Picea rubens* and *Betula alleghaniensis*, were found on north-facing slopes at 455 m, but shifted toward south-facing exposures at higher elevations. Some, such as

Betula papyrifera, showed no trends with elevation. *Abies balsamea*, *Acer rubrum* and *Betula papyrifera* all showed statistically significant differences in mean slope between elevations (Fig. 3). Species found at sites with statistically higher levels of solar radiation at increasing elevation included *Acer pensylvanicum*, *A. saccharum*, *Betula alleghaniensis* and *Quercus rubra*, while others showed similar non-significant trends (Fig 4).

Analysis of species distribution among topographic positions showed that *Pinus resinosa* is strongly associated with ridges (Fig. 4). The two *Betula* species were generally found in the higher topographic positions, indicating a preference for sites not on ridges. However, at 760 m and above, *Betula papyrifera* began to appear on the ridges. The low-elevation conifers *Pinus strobus*

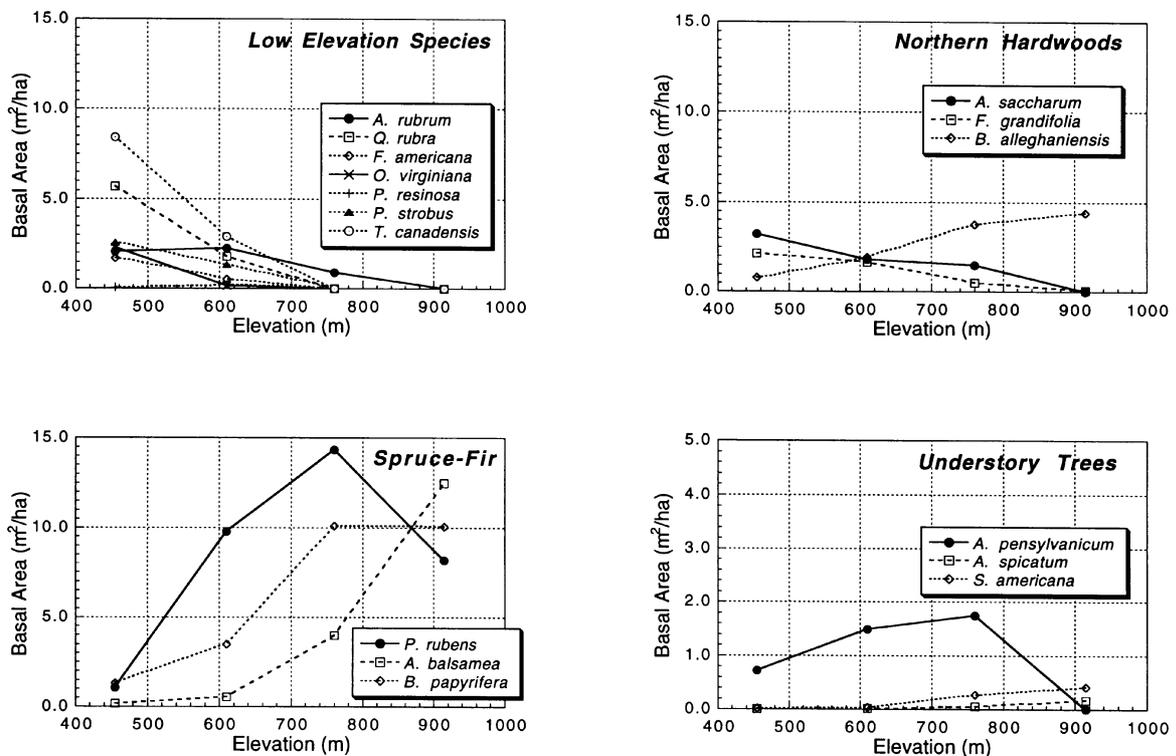


Fig. 5. Mean basal area of each species at each actual elevation.

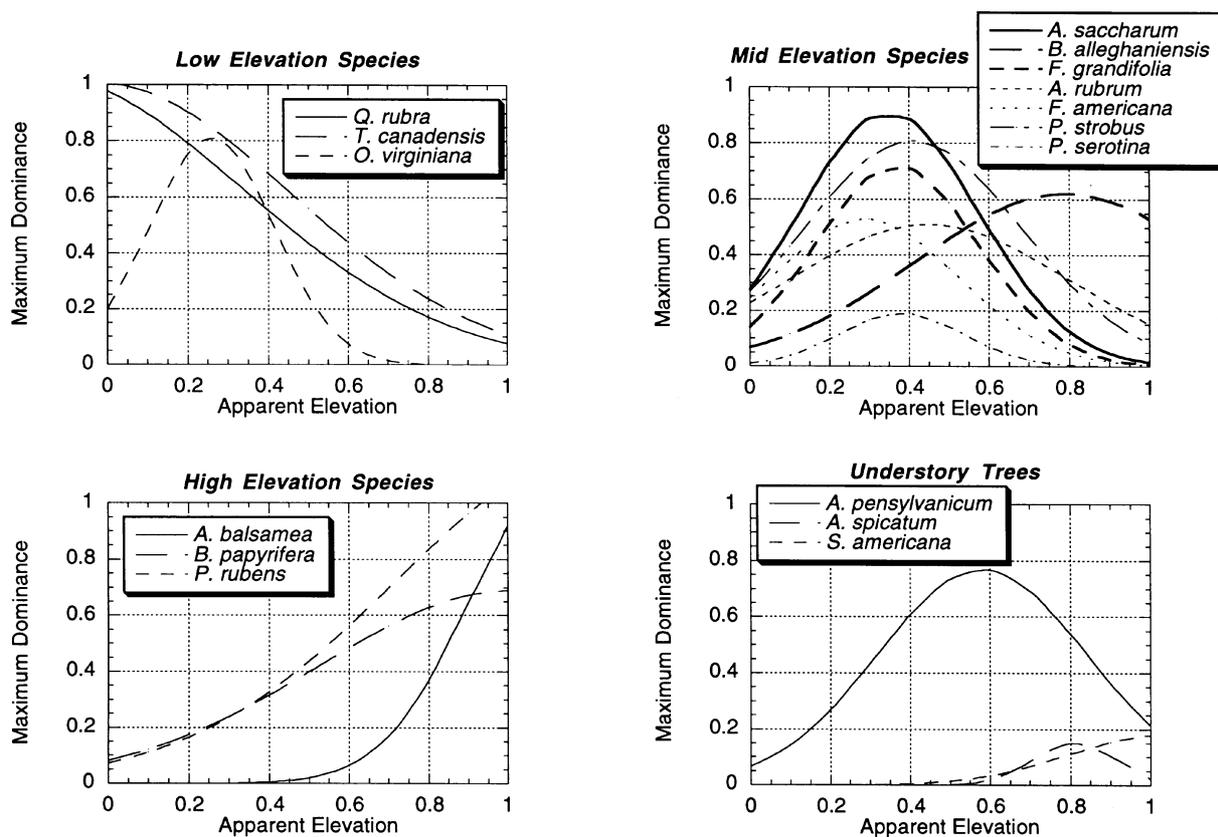


Fig. 6. Upper bounds of dominance of each species vs. apparent elevation.

and *Tsuga canadensis* were generally found in intermediate topographic positions, and there was little variation in topographic position with elevation. *Quercus rubra* and *Ostrya virginiana* were also found in intermediate topographic positions at 455 m but began to move toward stream valleys at higher elevations. Among the maples, *Acer pensylvanicum* was found in more sheltered topographic positions at 455 m than either *A. rubrum* or *A. saccharum*, but these differences disappeared at higher elevations; overall, the maples were found at intermediate positions. *Picea rubens* appeared mainly in more sheltered topographic positions at low elevations, but it moved toward more exposed positions at the higher elevations. By contrast, *Abies balsamea* generally favored ridges at all elevations.

In terms of mean basal area, forests at 455 m were dominated by *Tsuga canadensis* and *Quercus rubra* (Fig. 5). A number of other hardwood and conifer species were also found in small amounts. By 610 m, however, *Picea rubens* had become the dominant species, with *Betula papyrifera* and *T. canadensis* as important co-dominants. At 760 m, *P. rubens* and *B. papyrifera* were the most dominant species, while *Abies balsamea* had

become an important component. *P. rubens* basal area peaked at 760 m and the basal area of *B. papyrifera* leveled off, but the dominance of *A. balsamea* increased so that it had become the dominant species at 915 m, followed by *B. papyrifera* and *P. rubens*. At no elevation was the 'Northern Hardwood' forest type, consisting of *Acer saccharum*, *Fagus grandifolia* and *Betula alleghaniensis*, ever dominant. Among understory trees, *A. pensylvanicum* achieved its greatest dominance at 760 m, while *A. spicatum* and *Sorbus americana* were most dominant at 915 m.

Both *Quercus rubra* and *Tsuga canadensis* reached their maximum dominance at or below the lowest apparent elevation examined in this study (Fig. 6). 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, Fig. 6 shows that they are capable of becoming the dominant species at lower-middle apparent elevations. *Betula alleghaniensis* actually reached its peak of dominance at higher apparent elevations than the other two 'Northern Hardwood' species. *Picea rubens* 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. *Abies balsamea* could also completely dominate high apparent elevations but was not found at lower apparent elevations. *Betula papyrifera* 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 *Acer pensylvanicum* was able to reach high levels of maximum dominance, which occurred at middle apparent elevations. Both *A. spicatum* and *Sorbus americana* attained low levels of maximum dominance at high apparent elevations. Among other tree species, only *Pinus strobus* showed the potential to almost completely dominate a stand. *Acer rubrum* was widely distributed across apparent elevations but appeared incapable of attaining more than codominant status. *Ostrya virginiana* is usually an uncommon understory or subcanopy tree (Burns & 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

Elevation is an important determinant of species composition in northern New England (Bormann et al. 1970; Siccama 1974; Cogbill & White 1991). The results of this study show that other factors do play roles, albeit ones that generally decrease in importance toward higher elevations. The lowest elevation examined in other studies of forest vegetation in northern New England has generally exceeded 455 m; those studies have examined sites with similar slopes and aspects (e.g. Bormann et al. 1970; Siccama 1974). The rapid increase of precipitation and cloudiness with elevation in the northeastern USA (Siccama 1974; Dingman 1981; Reiners et al. 1984) may be responsible for the lack of correlation with aspect, slope and solar radiation at sites above 415 m (Table 2). A similar decrease in the importance of these factors at higher elevations has been observed in the southern Appalachians (Busing et al. 1993). This stands in stark contrast to the importance of these factors at all elevations in the western USA (e.g. Roberts 1986; Peet 1988).

A number of species, including *Abies balsamea*, *Acer rubrum* and *Betula papyrifera*, all showed statistically significant differences in mean slope between elevations (Fig. 3B), but it is unclear if these trends were biologically significant or if they reflected unmeasured factors, such as soil type. A number of species, including *Quercus rubra* and *B. alleghaniensis*,

were found at more southerly aspects, with higher solar radiation loads, at higher elevations. It appears that these species were restricted to the warmer sites at their upper elevational extents, which may indicate that these species were close to their minimum growing season heat sum requirement. Species that did not show this pattern may have been restricted by other factors, such as lack of suitable sites for regeneration or patterns of past land use and history.

The restriction of *Pinus resinosa* to ridges is consistent with previous work in Vermont (Engstrom & Mann 1991). Throughout most of its range this species usually requires fire for regeneration; since fires are quite rare in Vermont, the species is not common there. In Vermont it is usually restricted to steep, rocky ridgetop environments. Fire could, however, also play a role; there were several severe fires in the late 19th century on Mt. Ascutney (Anon. 1992). Trees were not aged, but many *Pinus resinosa* trees are large enough to date from that period (R.L. Boyce pers. obs.). *Betula papyrifera* is more likely to be found on ridges at higher elevations. Wind disturbance is expected to be greater on these exposed areas, which probably creates more sites for successful establishment of this species (Burns & Honkala 1990). However, this trend may be due in part to the lack of stream valley topographic positions at 915 m, which is very near the summit of Mt. Ascutney. The movement of *Quercus rubra* and *Ostrya virginiana* into more topographically sheltered sites at higher elevations was unexpected and may be because these sites are warmer than exposed ridges during the growing season. *Picea rubens* may require the moister conditions of stream valleys to compete well at low elevations. As water becomes more available at higher elevations, *P. rubens* may then be free to move to more exposed topographic positions. *Abies balsamea* appears to favor exposed topographic positions throughout the elevational range covered in this study. Busing et al. (1993) found similar preferences for exposed topographic positions in *P. rubens* and *A. fraseri* in the southern Appalachians.

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 *Quercus rubra* and *Ostrya virginiana* (Fig. 4). The typical 'Northern Hardwoods' forest (*Acer saccharum*, *Fagus grandifolia* and *Betula alleghaniensis*), 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. In part, this may be due to the large amount of disturbance that has occurred on this mountain; within the last 100 years, Mt. Ascutney has experienced logging, fires and a hurricane (Anon. 1992).

Disturbance is a likely explanation for the relative importance of *Betula papyrifera* at low elevations, as well as the importance of *Acer pensylvanicum*, which generally requires disturbance to reach the tree stratum (Fig. 4).

Plots of upper bounds against apparent elevation are useful in determining what the maximum dominance of a species could be at a particular kind of site; Thomson et al. (1996) and Blackburn et al. (1992) have used this technique to address similar questions. It is clear that the lowest and highest apparent elevations have the potential to be dominated by a *Quercus/Tsuga* association and a *Picea/Abies/Betula* association, respectively. In fact, actual basal areas at actual low and high elevations are dominated by these assemblages. However, actual middle elevations are not currently dominated by northern hardwoods, even though they have the potential to be, as shown by the upper bound plots (Fig. 6). A similar approach was used by Fulton (1996) to show where *Quercus rubra* could potentially grow in the southeastern USA, even though it is not currently found at all sites where it could grow. Such an approach will not tell one when during succession species will dominate, because it does not discriminate between early and late successional species. For example, it is unlikely that *Acer pensylvanicum* will be important in the future unless the forests on Mt. Ascutney are greatly disturbed. Also, this approach will only be successful if surveyed stands are multi-aged, as in this study (R.L. Boyce pers. obs.), since the range of possible dominances at a given apparent elevation is determined by the variation in the data themselves. An assemblage of early successional even-aged stands, which contains little or no late successional species, will be of little use in predicting the possible relative basal areas of the late successional species, since the upper bounds of those species at that point in time will be quite low. Thus, this approach will be most successful when sites representing the largest possible number of successional states are included.

Palmer (1994, 1995) has criticized the use of fuzzy set ordination, particularly when environmental factors are chosen after using a multivariate gradient analysis technique, such as detrended canonical correspondence analysis, as was done by Zhang & Oxley (1994). However, the environmental factors used in this study –elevation, slope, aspect, solar radiation and topographic position – were chosen beforehand. Palmer (1995) also argued that as the number of variables increases, the chances of finding a spurious relationship by chance increases, analogous to the false differences found using a comparison-wise test (e.g. *t*-test) instead of an experiment-wise test (e.g. Tukey's or Scheffé's test) after an analysis of variance. However,

this remains to be shown. If in fact this is true, one rather conservative way to correct for finding spurious relationships would be by using a Bonferroni correction, i.e. dividing the acceptable critical *p*-value (usually 0.05) by the number of variables examined (Day & Quinn 1989). As there are five variables in this case, the acceptable *p*-value for statistical significance would be 0.01. Examination of Tables 1-3 shows that the conclusions of this study after using a Bonferroni correction would be unchanged, except that trends of topographic position with apparent elevation would be a bit weaker.

In conclusion, fuzzy set ordination at a northeastern USA site showed that relationships between tree species and the site factors of aspect, slope and solar radiation were strongest at the lowest elevation surveyed, but became much less important at higher elevations. There are indications that topographic position remains important at all elevations, however. Upper bound plots indicate that the low abundance of northern hardwood species is probably temporary; in the absence of large-scale disturbance, these species are predicted to dominate mid-elevation forests.

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