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Gradient analysis of old spruce–fir forests of the Great Smoky Mountains circa 1935

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The response of old-growth spruce–fir vegetation to environmental gradients was investigated using 1930s plot data from the Great Smoky Mountains. Gradients related to forest composition and position of the ecotone with the deciduous forest were identified using canonical correspondence analysis (CCA) and their role in vegetation response to climate change was considered. The data were subsequently stratified into three elevation classes and ordinated separately using CCA to identify gradients at various elevations. The effect of elevation on tree stratum composition and structure was profound. Secondary gradients influencing the tree stratum included slope aspect, potential solar radiation, and topographic position. *Abies fraseri* basal area and density were high above 1800 m elevation. Comparable basal area levels of *Picea rubens* were attained at elevations ranging from 1400 to 1900 m. Total stand basal area and density increased with elevation. The importance of topographic position increased with elevation, while that of slope aspect and potential solar radiation decreased. Presumably, the increasing incidence of cloud cover with elevation diminished the effect of slope aspect and potential solar radiation at higher elevations. The transition from deciduous forest occurred in the 1300–1600 m elevation range. A substantial proportion (24%) of plots had mixed composition (30–70% spruce–fir by basal area), suggesting that the ecotone is not abrupt in old-growth forest. Environmental variables other than elevation did not have a strong effect on ecotone position. Attempts to infer long-term ecotone dynamics along the elevation gradient based on species size-class data were inconclusive.

Key words: *Abies fraseri*, gradient analysis, Great Smoky Mountains, old-growth forest, *Picea rubens*, spruce–fir forest.

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Les auteurs ont étudié la réaction de la végétation surannée de sapin et d'épinette aux gradients environnmentaux, en utilisant les données de parcelles d'observation installées au cours des années 30, dans les montagnes Great Smoky. Ils ont identifié les gradients reliés à la composition de la forêt et à la position de l'écotone avec la forêt décidue, en utilisant l'analyse de correspondances canoniques (CCA), et ils ont examiné leurs rôles dans la réaction de la végétation aux changements climatiques. Les résultats ont été subséquement regroupés par strates selon trois classes d'élévation et mis en séquences séparées à l'aide de la CCA pour identifier les gradients à différentes élévations. Les effets de l'altitude sur la composition et la structure de la strate arborescente est très importante. Les gradients secondaires qui influencent la state arborescente incluent la pente, la radiation solaire potentielle, et la position topographique. Au dessus de l'élévation de 1800 m, la surface basale et la densité de l'*Abies fraseri* sont élevées. Pour obtenir des surfaces basales comparables chez le *Picea rubens*, il faut aller aux élévations de 1400–1900 m. La surface basale totale et la densité augmentent avec l'élévation. L'importance de la position topographique augmente avec l'élévation, alors que la pente et la radiation solaire potentielle diminuent. On présume que l'augmentation de l'ennuagement avec l'altitude diminue les effets de la pente et de la radiation solaire potentielle aux plus hautes altitudes. La transition à parir de la forêt décidue s'effectue autour de 1300–1600 m. Une forte proportion des parcelles montre (24%) une composition mixte (30–70% pour la surface basale épinette–sapin) ce qui suggère que l'écotone n'est pas abrupte dans la forêt surannée. Les variables environmentales autres que l'élévation n'ont pas d'effet marqué sur la position de l'écotone. Les essais pour tenter de déduire la dynamique à long terme de l'écotone le long du gradient d'altitude en utilisant les données des classes de dimension par espèce ne permettent pas de conclure

Mots clés : *Abies fraseri*, analyse de gradient, monts Great Smoky, forêt surannée, *Picea rubens*, forêt de sapin et épinette.
[Traduit par la rédaction]

Introduction

The largest continuous expanse of old-growth spruce–fir forest in eastern North America is located in the Great Smoky Mountains. Restricted to high-elevation sites with cool, moist conditions, red spruce (*Picea rubens*) and Fraser fir (*Abies fraseri*) dominate approximately 17 900 ha in the Smoky Mountains, 68% of which is old-growth forest (Pyle 1984). The old-growth forest has no history of logging; however, in recent decades Fraser fir has experienced high mortality from the balsam woolly adelgid (*Adelges piceae* Ratz.), a non-native insect pest (Speers 1958; Amman and Speers 1965; Eagar 1984). Fir mortality has been severe enough to substantially impact community composition and ecosystem dynamics (Witter and Ragenovich 1986; Busing et al. 1988; Nicholas et al. 1992). Although southern Appalachian red spruce does not exhibit the widespread decline observed in the northern Appalachians (Siccama et al. 1982; Vogelmann et al. 1985; Peart et al. 1992), the potential for negative responses to air pollution or climate change is a major concern (Johnson et al. 1992). These changes may lead to long-term alterations in spruce–fir forest structure and dynamics (Busing and Clebsch 1987).

Forest plot data from the 1930s, prior to these impacts, provide baseline information on healthy old-growth stands. From these data we can relate stand composition and structure to site conditions such as elevation, slope aspect, potential solar radiation, and topographic position. These variables largely determine site temperature and moisture and therefore affect

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TABLE 1. Distribution and elevation of old-growth spruce–fir forest plots by watershed in the Great Smoky Mountains (GSM)

Watershed	N	Relation to GSM crest	Plot elevation (m) Min.	Plot elevation (m) Max.
Cosby Creek	1	North	1372	1372
Little Pigeon River	18	North	1082	1990
W Prong Little Pigeon River	11	North	1326	1768
Little River	5	North	1426	1573
Forney Creek	1	South	1689	1689
Noland Creek	2	South	1478	2024
Deep Creek	9	South	1234	1768
Oconaluftee River	4	South	1469	1783
Bradley Fork	11	South	1204	1677
Raven Fork	33	South	1280	1852
Straight Fork	11	South	1280	1786
Cataloochee Creek	13	South	1295	1707
Big Creek	14	South	1286	1958

vegetation in the Smoky Mountains (Whittaker 1956). In turn, we can predict composition and structure from site variables affecting these stand characteristics. An understanding of vegetation–site relationships may also prove useful in predicting forest response to climate change (Gosz 1992). In this case, the position of the ecotone between montane spruce–fir forests and deciduous forests is highly pertinent. The ecotone is a critical ecosystem boundary, as it is representative of the continental transition from temperate to boreal forest in Canada. Determining what site variables affect the position of the montane ecotone is essential to the understanding and prediction of its dynamics. It is generally held that the elevation of montane ecotones is lower on steep north-facing slopes, which tend to have low solar radiation and cool temperatures. In the high elevations of the Great Smoky Mountains, however, the high incidence of cloud cover may be a mitigating factor and slope aspect effects may be weak. Resolving whether or not slope aspect, potential solar radiation, and other site variables are strongly related to ecotone elevation is critical to the analysis of ecotone dynamics on complex mountain topography.

In the following analyses, based on old-growth spruce–fir plot data from the late 1930s, we address the following questions: (*i*) how do stand composition and structure vary across sites; (*ii*) which site variables affect stand composition and elevation of the lower ecotone; (*iii*) how rapid is vegetation change across the ecotone; (*iv*) what is the size-class structure of old-growth tree populations; and (*v*) is there any evidence from the size-class analyses that populations are migrating along the elevation gradient? Information from this large expanse of montane spruce–fir forest lacking human disturbance provides basic information on compositional response to environmental gradients. It also serves as a basis for predicting and monitoring change in this remnant of primeval spruce–fir forest.

Methods

In a 4-year field study initiated in 1935, F.H. Miller surveyed the vegetation of Great Smoky Mountains National Park (35°35′N, 83°28′W) with approximately one thousand three hundred and seventy-five 0.08-ha plots. It appears that the original sampling design was to place survey plots at specified points on a grid over the park landscape. This approach was modified to facilitate access to sites on the rugged terrain. The result was a system of plots spread evenly over the park, representing the rich diversity of plant assemblages and the wide range of site conditions and disturbance histories on the landscape.

Vegetation and site variables were quantified for each plot in the 1930s. The tree stratum was sampled by tallying stems of each species in four diameter classes (4–11, 12–23, 24–35, and >36 in. dbh) (1 in = 25.4 mm). Plot elevation, slope aspect, percent slope, soil depth, litter depth, and history of logging or fire were recorded during sampling. Plot location was marked on a topographic map. Potential solar beam irradiation was subsequently estimated from the slope and aspect data (Frank and Lee 1966). Aspect classes were coded from 1 to 8 providing a relative indicator of microclimate from warm and dry to cool and mesic: SW = 1, S = 2, W = 3, SE = 4, NW = 5, E = 6, N = 7, and NE = 8. Topographic maps with plot locations were used to obtain topographic position and shelter data. Topographic position was coded from 1 to 5, with 1 indicating a ravine (or cove) and 5 indicating a ridgetop. Shelter was quantified as the negative distance to the nearest permanent stream shown on USGS 7.5′ quadrangle maps.

From a pool of 1376 plots, all plots with *Picea rubens* or *Abies fraseri* trees >10.16 cm dbh and no specified date of logging or burning were selected for analysis. A total of 133 plots met these criteria (Table 1). Canonical correspondence analysis (CCA), a constrained ordination technique, was performed with CANOCO (ter Braak 1986, 1987) using absolute basal area values. Direct gradient analysis with CCA was appropriate for testing hypotheses concerning the effects of environmental gradients on vegetation (Gauch 1982; ter Braak and Prentice 1988). CCA sample scores along axes 1 and 2 were compared with those from unconstrained ordinations to ensure that the environmental variables in the CCAs sufficiently explained compositional variation (ter Braak 1986; Allen and Peet 1990). Eight environmental variables were included in the CCA: elevation, aspect class, percent slope, topographic position, potential solar beam irradiation, shelter, soil depth, and litter depth. In the few cases where site data were missing, a mean value was substituted in the ordination input for the missing environmental variable. To explore the effects of site variables on tree layer composition at various elevations, CCA was also performed separately for the three elevation classes noted above.

Analysis of stand composition and structure involved the determination of stand attributes in a two-way categorization across two major environmental gradients borne out in the CCA: elevation and aspect. Three elevation classes and two aspect classes were chosen, resulting in six stand categories. Mean basal area and density were calculated for all forest plots (basal area >5 m^2/ha) in each category. Diameter distributions of *Picea* and *Abies* were also summarized for each category.

Environmental conditions at the montane ecotone between spruce–fir and other temperate forest vegetation circa 1935 were analyzed with a data set of all undisturbed forest plots >1280 m elevation in the previously selected watersheds (Table 1). The lower end of this range corresponded to the lowest elevation of a plot with combined relative basal area of *Picea* and *Abies* greater than 50% of the total stand basal area (only four plots containing *Picea* or *Abies* occurred below 1280 m elevation). These were added to the data set, making a total of 184 stands with no apparent history of logging or burning. Combined relative basal area of *Picea* and *Abies* was plotted against elevation and several other variables in an attempt to determine how certain site variables (including slope aspect, potential solar radiation, and topographic position) affect elevation of the ecotone. The relative basal area values of *Picea* and *Abies* were plotted separately against these variables as well to test for individualistic species responses near the ecotone.

Nomenclature follows Radford et al. (1968).

Results

Species basal area and density by site

Total stand basal area and stem density increased with elevation and were consistently greater on south-facing slopes (Table 2). Both peaked above 1800 m elevation. The densities (900–3000 stems/ha) at elevations >1800 m were several times greater than those of the lower elevation sites analyzed here.

TABLE 2. Mean basal area (BA, m^2/ha) and density (D, stems/ha) by elevation and aspect classes

	1250–1450 m				1451–1650 m				1651–2024 m				1801–2024 m	
	SE–W		NW–E		SE–W		NW–E		SE–W		NW–E		All	
	BA	D	BA	D	BA	D	BA	D	BA	D	BA	D	BA	D
Abies fraseri	<0.1	3	0.6	17	2.3	58	2.7	58	15.2	474	11.4	284	40.7	1282
Acer pensylvanicum	<0.1	1	0.1	4	0	0	<0.1	1	<0.1	1	0	0	0	0
Acer rubrum	0.7	3	1.4	4	0.5	1	0.1	1	1.4	15	0	0	0	0
Acer saccharum	0.6	6	1.3	7	0.7	4	0.5	6	0	0	0	0	0	0
Acer spicatum	0	0	0	0	0	0	0	0	0	0	<0.1	2	0	0
Aesculus octandra	0.3	3	3.3	11	0.2	2	0.5	2	0	0	0	0	0	0
Amelanchier laevis	0.2	4	0	0	0.1	3	0.1	3	0.2	8	0.1	4	0	0
Betula lenta	1.6	14	0.1	6	0.3	3	0.3	6	0.3	4	0	0	0	0
Betula lutea	2.9	28	9.4	67	4.6	44	7.5	51	6.1	56	6.6	61	0.3	4
Fagus grandifolia	2.5	64	1.1	26	1.7	37	0.8	16	0.1	4	0.6	28	0	0
Fraxinus americana	0.4	1	0.2	1	0	0	0	0	0	0	0	0	0	0
Halesia carolina	0.9	15	0.1	3	0.2	2	0.2	3	0	0	0	0	0	0
Magnolia fraseri	0.2	2	0	0	0	0	0	0	0	0	0	0	0	0
Picea rubens	15.4	92	6.4	44	26.0	171	21.9	143	22.4	154	18.0	115	14.8	101
Prunus pensylvanica	0.1	4	0.4	17	0.1	3	0.1	3	0	0	0	0	0	0
Prunus serotina	0	0	<0.1	1	0.1	1	<0.1	2	0	0	0	0	0	0
Quercus rubra	0.1	1	0	0	0	0	0	0	0	0	0.2	3	0	0
Sorbus americana	0	0	0	0	0	0	0	0	<0.1	1	0.2	8	0.2	8
Tilia heterophylla	0.9	8	0.4	11	0	0	0	0	0	0	0	0	0	0
Tsuga canadensis	11.0	48	6.1	25	4.3	16	0.9	4	0	0	0	0	0	0
Other	0.5	24	0	0	0	0	<0.1	<1	0	0	0	0	0	0
Total	38.4	321	30.9	242	41.1	350	35.7	301	45.7	717	37.0	503	55.9	1395
No. of plots	23	23	17	17	30	30	33	33	17	17	13	13	6	6

NOTE: All plots in a high elevation class (>1800 m), to the far right in this table, were pooled without regard to aspect.

TABLE 3. Mean density (stems/ha) of *Picea* and *Abies* by diameter class, elevation class, and aspect class

	1250–1450 m		1451–1650 m		1651–2024 m		1801–2024 m
	SE–W	NW–E	SE–W	NW–E	SE–W	NW–E	All
Abies fraseri							
>10–30 cm dbh	3	15	51	47	440	244	1194
>30–60 cm dbh	0	2	8	12	40	43	104
>60–90 cm dbh	0	0	0	0	0	0	0
>90 cm dbh	0	0	0	0	0	0	0
Picea rubens							
>10–30 cm dbh	41	18	85	61	74	50	50
>30–60 cm dbh	29	19	49	56	51	40	29
>60–90 cm dbh	21	8	38	24	29	24	23
>90 cm dbh	3	0	3	4	2	2	0

NOTE: All plots in a high elevation class (>1800 m), to the far right in this table, were pooled without regard to aspect. See Table 2 for sample sizes.

Absolute basal area of the coniferous tree species responded strongly to elevation (Table 2). *Abies* was the dominant, by basal area, at sites above 1800 m elevation, while *Picea* dominated stands across a relatively broad elevation range from 1100 to 1900 m. However, *Betula lutea* dominated the mesic slope class (NW–E–N–NE aspects) in the 1250–1450 m elevation zone.

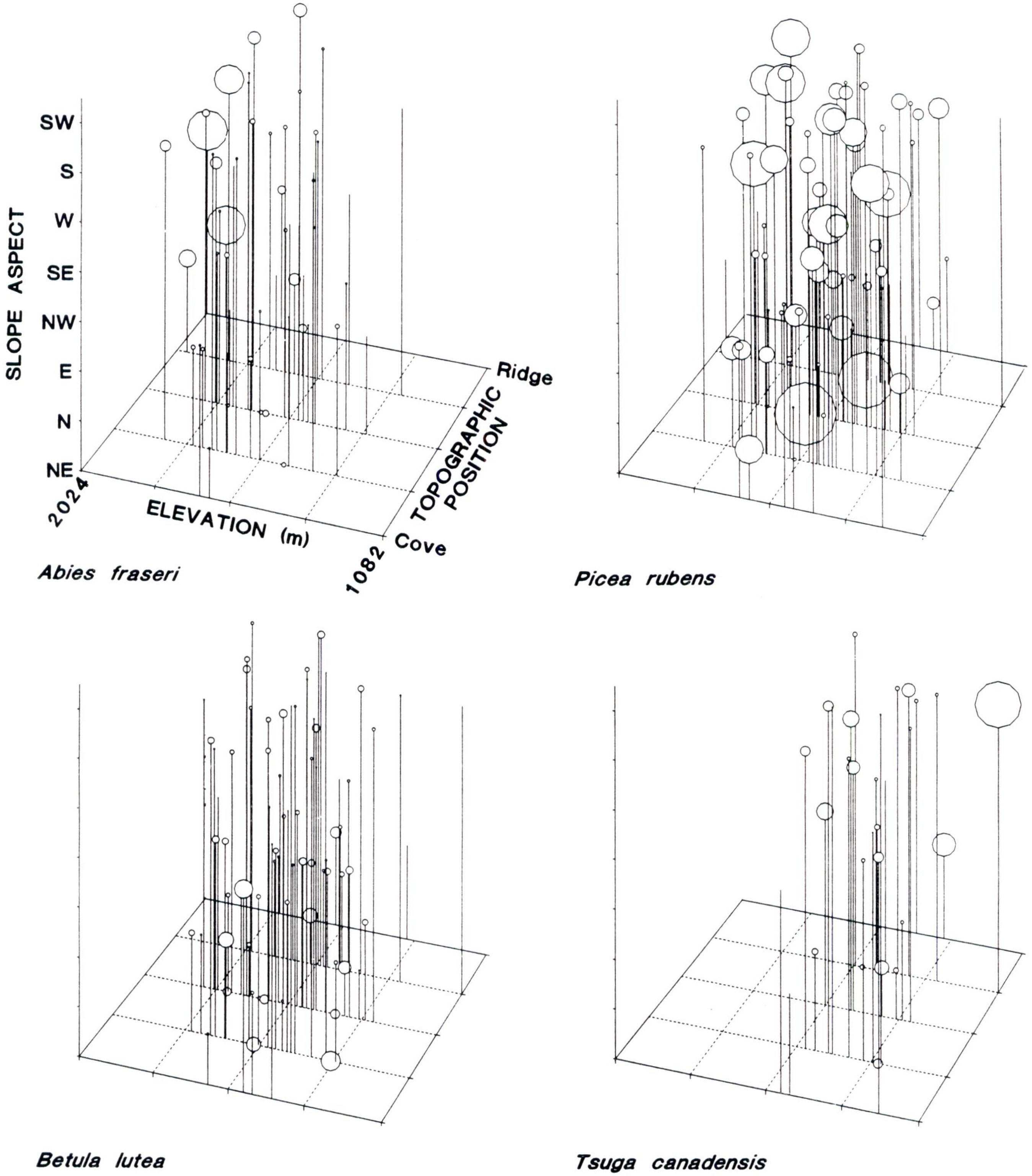
Topographic position effects were evident for some species (Fig. 1). *Betula lutea* tended to attain higher basal area in coves, while *Abies*, *Picea*, and *Tsuga* did not.

Species size-class structure by site

In general, *Abies* and *Picea* exhibited declining densities with increasing stem size (Table 3). The relationship between *Picea* stem density and diameter was approximately linear following logarithmic transformation of density. The mean density of *Abies* in the 10–30 cm class was several times greater than that of *Picea* at elevations above 1651 m. *Abies* stems never exceeded 60 cm dbh and stems over 30 cm were few at elevations <1450 m. In contrast, *Picea* stems exceeded 90 cm dbh, except on sites above 1800 m and on northerly aspects below 1450 m.

Environmental gradients and composition

The most important environmental gradients identified with CCA were elevation, aspect, potential solar radiation, and topographic position (Fig. 2). An inverse relationship existed between the aspect and solar radiation gradients. This was expected because northerly aspects (with low potential solar radiation values) were assigned high aspect values. *Abies* and



Abies fraseri ***Picea rubens***

Betula lutea ***Tsuga canadensis***

FIG. 1. Importance of major tree species along elevation, aspect, and topographic position gradients. Circle size represents absolute species basal area in a sample plot.

Sorbus were at the high end of the elevation gradient. *Aesculus* and *Betula lutea* were at the high end of the aspect gradient, indicating an affinity for north-facing slopes with presumably cool-mesic conditions. By contrast, *Betula lenta* was at the low end of the aspect gradient. The high elevation dominants, *Picea* and *Abies*, tended to be at intermediate positions on the aspect gradient. *Betula lutea* and *Aesculus* were at the low end of the topographic position gradient, indicating an affinity for coves (or ravines) rather than ridges.

When the tree data were stratified into three elevation classes, the relative importance of environmental variables changed (Fig. 3). For example, the influence of topographic

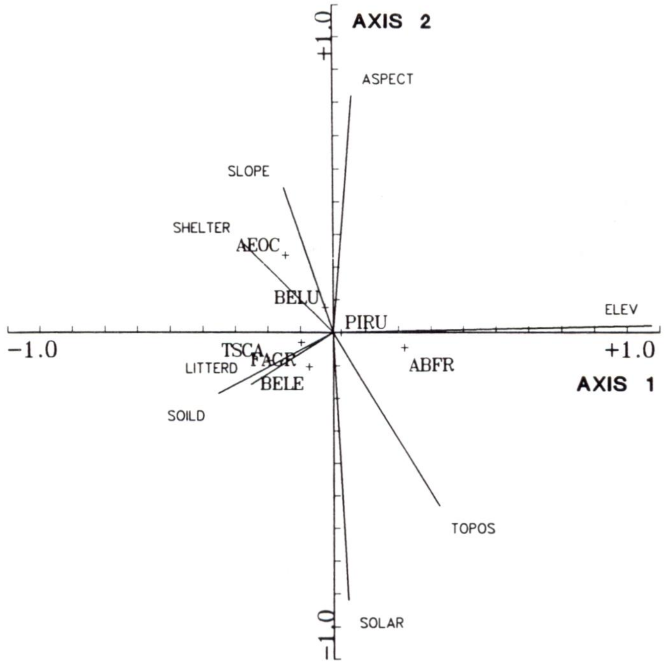


FIG. 2. Tree stratum CCA species scores along the first and second ordination axes with eigenvalues of 0.405 and 0.117, respectively. Environmental gradients are represented as vectors oriented in the direction of maximal change in an environmental variable, with lengths that indicate their importance in relation to differences in species composition. ELEV, increasing elevation; ASPECT, increasingly cool and mesic slope aspects; SLOPE, slope steepness; SHELTER, proximity to a stream; SOILD, increasing soil depth; LITTERD, increasing litter depth; SOLAR, increasing potential solar radiation; TOPOS, increasing topographic exposure, with ridgetops being highly exposed. Four-letter species codes consist of the first two letters of the genus and species names. See Table 2 for full names of species.

position increased with elevation. Variables clearly decreasing in importance with elevation included slope aspect and potential solar radiation.

Tree species responses to environmental variables also differed among CCAs stratified by elevation (Fig. 3). For example, *Abies* was often associated with high topographic positions (ridgetops and convex slopes). It was associated with cove sites, however, in the low elevation class (< 1450 m). An additional contrast was the positive association of *Picea* with steep, concave slopes rather than ridges in the high elevation class CCA.

Site characteristics of the ecotone

The transition from deciduous and *Tsuga*–deciduous forest to *Picea*–*Abies* forest occurred in the 1300–1600 m elevation interval and was strongly associated with elevation. The fact that a substantial proportion (24%) of the samples containing *Picea* or *Abies* were 30–70% spruce–fir by basal area suggested that the ecotone was not abrupt. In comparison, predominantly deciduous forests (< 30% spruce–fir by basal area) comprised 30% of the samples, and predominantly coniferous

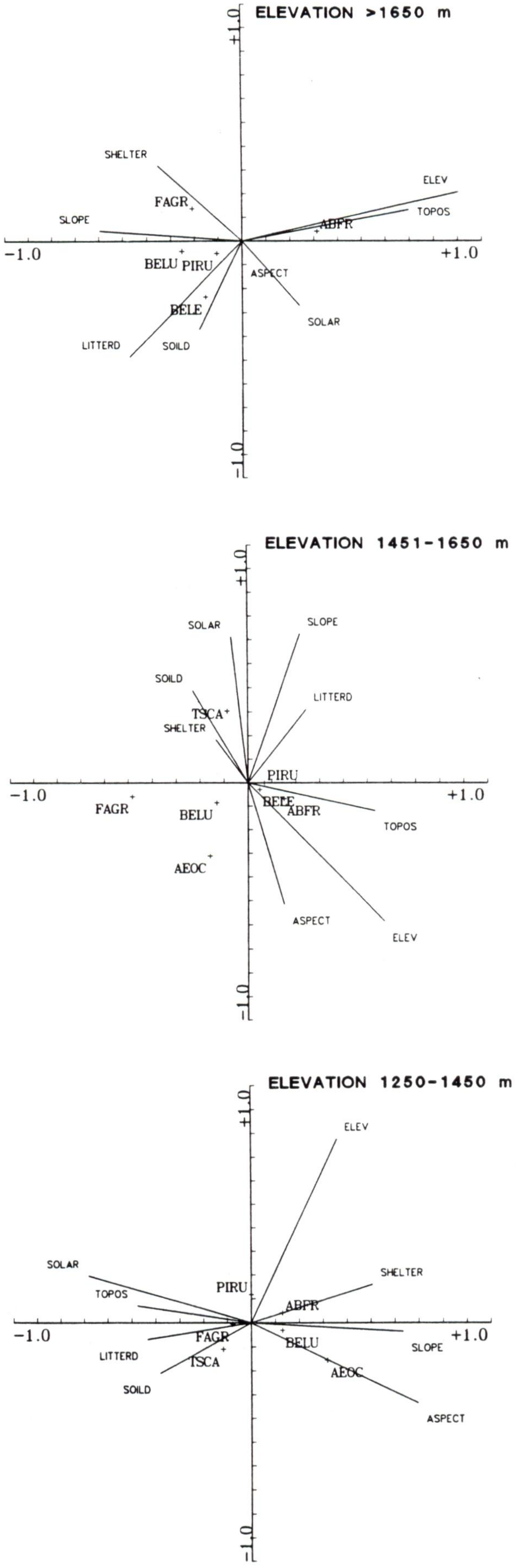


FIG. 3. Tree stratum species scores along the first and second axes of CCAs stratified into three elevation classes. Eigenvalues for each elevation class are as follows: low elevation, axis 1 = 0.354 and axis 2 = 0.302; mid-elevation, axis 1 = 0.222 and axis 2 = 0.105; and high elevation, axis 1 = 0.372 and axis 2 = 0.153. See Fig. 2 for interpretation.

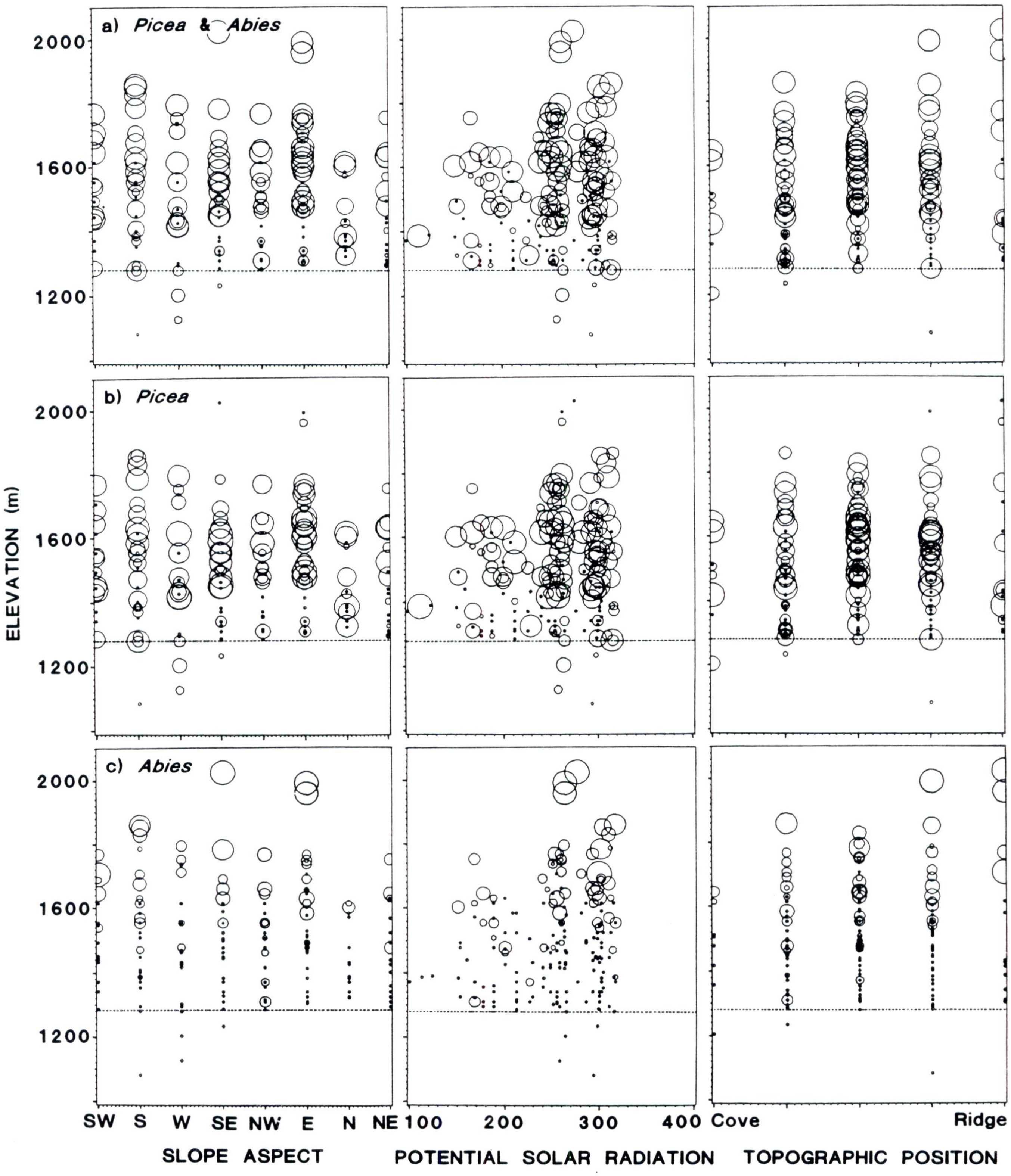


FIG. 4. Relative basal area of high elevation conifers by site variable classes. (A) Combined relative basal area of spruce and fir by elevation and other environmental variables. Circle size indicates relative basal area. Solid dots represent plots lacking both spruce and fir. These are excluded below 1280 m elevation (dashed line). (B) Relative basal area of spruce. Solid dots represent plots lacking spruce. Plots lacking both spruce and fir are excluded below 1280 m elevation. (C) Relative basal area of fir. Solid dots represent plots lacking fir. Plots lacking both spruce and fir are excluded below 1280 m elevation. Potential solar radiation is measured in langleys per year.

forests (>70% spruce–fir by basal area) comprised 46% of the samples.

When considered across all samples, the elevation of the ecotone varied widely (Fig. 4A). Across the study area, spruce–fir dominated plots occurred as low as 1300 m elevation, while forest plots lacking both *Picea* and *Abies* were occasional in the 1300–1500 m elevation range; they were rare above 1600 m elevation, however. Strong effects of other site variables on ecotone elevation were not apparent. The ecotone was not markedly lower on sites with low potential solar radiation or on sites with northerly slope aspects (Fig. 4A). If anything, it tended to be lower on southerly aspects and sites with high potential radiation, but this tendency was weak. Topographic position appeared to have some effect on the elevation of the transition zone as well. The lowest elevation spruce – fir plots occurred on concave slopes and in coves under 1300 m elevation, while spruce – fir dominance was infrequent on ridges below 1400 m elevation. Nonetheless, any effects of these variables on elevation of the ecotone were weak and, because of the limited data set (< 100 plots at > 0.5-km intervals in the 1300 – 1600 m transition zone), strong inferences concerning these effects could not be made.

When considered alone, *Picea* relative basal area responses to several environmental variables at the lower end of its elevation range were much the same as those of the combined spruce – fir basal area responses presented above (Fig. 4B). This was largely a result of the fact that *Picea* was the lower elevation dominant of the spruce – fir zone. The responses of *Abies* relative basal area at the lower end of its elevation range differed markedly from those of *Picea*. Unlike *Picea*, *Abies* was uncommon below 1300 m elevation. Above 1550 m elevation *Abies* tended to increase in importance with elevation across all sites regardless of potential solar radiation and slope aspect (Fig. 4C). At lower elevations (1300 – 1500 m) it was most important on concave slopes with northwest-facing aspects and low potential solar radiation.

Discussion

The analyses of species basal area by site variables support the individualistic concept of association among these species. Although *Picea* usually occurs in *Abies*-dominated stands, the converse is not always true. *Picea* is also associated with *Tsuga*, and *Betula lutea* at lower elevations where *Abies* is unimportant.

Composition of the tree stratum is clearly related to several of the site variables considered. Of these variables, elevation is the most important. Although site temperature and moisture are not directly considered directly in this study, low temperatures and high moisture associated with increasing elevation (Shanks 1954; Stephens 1969) favor *Picea* and *Abies*. Above 1400 m *Picea* frequently dominates stands. At the highest elevations (> 1800 m) *Abies* often dominates. The abundance of *Abies* on unsheltered ridge crests with shallow soils suggests that wind disturbance plays a role in the success of this species. The prolific regeneration of *Abies* promotes rapid colonization following windfall, resulting in dense stands. High densities of *Abies* at the highest elevation sites reflect these processes (Becking and Olson 1978). The absence of large (> 90 cm dbh) individuals of *Picea* from the highest elevation samples and the tendency for *Picea* to occur on sheltered sites at high elevations lend further support to the role of wind disturbance in tree layer composition. Minimum temperatures at the highest elevations of the Great Smoky Mountains are not below the tolerance of *Picea rubens* (Lalumiere and Thibault 1988, cited in White and Cogbill 1992). Apparently, the impact of wind and ice storms on high summits and ridges has been severe enough to favor the comparatively prolific regeneration and growth of *Abies* over that of *Picea* on such sites. It is concluded that temperature, moisture, and disturbance regimes associated with elevation are prime factors in determining the composition of these primeval forests.

Slope aspect also affects microclimate, particularly when realized solar radiation is high. Indeed, slope aspect is an important determinant of tree stratum composition except at the highest elevations. *Picea* is slightly more important on warm-xeric aspects, while *Abies* does not show a strong response to aspect. Several mesophytic deciduous species, including *Betula lutea* and *Aesculus octandra*, are more important on cool-mesic aspects and sheltered, cove sites. In contrast, *Betula lenta* is more important on warm-xeric aspects. The relatively weak response of *Picea* and *Abies* to slope aspect may be related to the low incidence of solar radiation in the high elevations. These forests may be covered by clouds as much as 30 – 40% of the growing season, and cloud cover frequency increases with elevation, reaching maximal levels above 1400 m (Mohnen 1992). Thus, the effects of slope aspect on microclimate may be less marked than at low elevation sites where cloud cover is comparatively infrequent.

Potential solar radiation is a function of slope aspect and steepness. At 36°N latitude, minimum values occur on steep, north-facing slopes. Comparatively cool-moist conditions are expected on such slopes. If a strong aspect effect exists, *Picea* and *Abies* would be expected reach their lowest elevations on such sites. However, *Abies* and *Picea* do not show a strong response to potential solar radiation. Responses of deciduous species are very similar to the aspect effects discussed above in that species favored on cool-mesic aspects are associated with low potential solar radiation. As with slope aspect effects, potential solar radiation effects appear to diminish at high elevations, presumably because of the higher incidence of cloud cover.

Topographic position may play a role in the importance of the high elevation dominants, *Abies*, *Picea*, and *Betula lutea*. *Abies* is often associated with ridgetops. This is particularly true at the highest elevation sites and, as discussed above, the comparatively high disturbance frequency on such sites is one reason for the prevalence of *Abies*. At the highest elevation sites *Picea* tends to occur in sheltered coves rather than on ridges. At the lower end of its elevation range, however, *Picea* often occurs with *Tsuga* on ridges. *Betula lutea* often dominates cove sites at comparable elevations and *Picea* is less important in the coves than on ridges at these lower elevation sites. Golden (1981) also notes that *Picea* is more prominent on upper slopes and ridges at the lower end of its elevation range.

These observations indicate that topographic position may be a key factor in determining ecotone position of the montane spruce – fir forest. Yet, further examination of our data (Fig. 4) suggests that the tendency of *Picea* to attain minimal elevation on ridge sites is weak at best. For *Abies* there does appear to be a topographic position effect at the lower end of its elevation range, but in this case it attains minimal elevations on lower slopes and in coves, not ridges. From these data it is concluded that (*i*) topography, slope aspect, and potential solar radiation do not play a strong role in determining the lower elevation limits of the spruce – fir zone and (*ii*) factors determining the lower limits of *Picea* differ from those determining the lower limits of *Abies*. The latter conclusion supports an individualistic approach to monitoring forest migration along the elevation gradient.

Inferences on migration of the ecotone over time can be made by comparing the size-class structures of *Picea* and *Abies* populations across elevation classes. At the lower end of the transition zone, a population retreating upslope might be expected to have large residual trees and low regeneration, while a population advancing downslope would have the opposite structure (Leak and Graber 1974). The 1935 data indicate a lack of very large *Picea* individuals on northerly slopes in the lower transition zone (< 1450 m). According to Leak and Graber's (1974) reasoning, *Picea* appears to be advancing downslope rather than retreating upslope. However, In the case of *Picea*, the evidence for any trend is weak. The evidence for *Abies* is somewhat stronger. Large residual individuals are not abundant below 1450 m and they are absent on southerly slopes near the lower end of its elevation range. *Abies* also appears to be advancing downslope rather than retreating upslope. By contrast, Leak and Graber (1974) found evidence to suggest that *Picea* and *Abies* were retreating upslope ca. 1970 in northern Appalachian forests. Although the 1930s data base on *Picea* and *Abies* is limited, the continuous expanses of primeval forest across the ecotone in the southern Appalachians are ideal for the study of forest migration. The 1930s data provide a basis for monitoring. Further population studies with larger concentrations of samples within the transition zone may help resolve current and future ecotone dynamics in the southern Appalachians.

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