

Jay M. Ver Hoef, Botany Department,
Iowa State University, Ames, Iowa 50011

Bonita J. Neiland, Department of Agriculture and Land Resources,
University of Alaska, Fairbanks, Alaska 99701

and

David C. Glenn-Lewin, Botany Department,
Iowa State University, Ames, Iowa 50011

Vegetation Gradient Analysis of Two Sites in Southeast Alaska

Abstract

Two study sites in Southeast Alaska, one on the mainland and one on Etolin Island, were compared for tree, shrub, and herb vegetation cover in summer, 1983. For the tree stratum, detrended correspondence analysis (DCA) indicated that soil moisture drainage and study site were the first two factors related to composition differences among samples. DCA indicated that, for the shrub stratum, study site and soil moisture drainage were the first two factors. For the herb layer, the first three factors from DCA were interpreted as soil moisture drainage, elevation, and study site respectively. Direct gradient analysis of species distributions revealed clear patterns for many species with respect to soil drainage and elevation gradients. Even though DCA did not identify elevation as a factor for the tree and shrub strata, individual species within these strata did show responses to elevation. Many species abundances were also clearly differentiated between study sites.

Introduction

The coastal forests that extend from southeastern Alaska to northern California are part of the coniferous forests of Pacific Northwest North America (Waring and Franklin 1979). Cool, maritime climates with winter rains predominate in the region. The climate, topography, and vegetation of Southeast Alaska limit the frequency and extent of natural fires, and extensive areas have been free from large-scale disturbances for great periods of time (Harris and Farr 1974). The most common natural disturbances, windfall (Ruth and Harris 1979) and slope failure (Swanston 1969), occur on a local scale.

Vegetation studies in Southeast Alaska and the nearby coastal conifer forests of British Columbia, Canada, have consisted of broad classifications and descriptions of major environmental gradients. Heusser (1960) and Neiland (1971) reviewed earlier literature. Alaback (1980), Godman (1952), Palmer (1942), Viereck and Dyrness (1980), and Worley (1974, 1975, 1977) provided various classification schemes for Southeast Alaska vegetation. Forest understory associations were described by Neiland (1971), Schoen *et al.* (1981), Rose (1982) and Ver Hoef (1985) for Southeast Alaska, and Eck (1983) for Prince William Sound.

Topography, which has a strong influence on drainage, has been identified as a major factor

correlated with vegetation variation in Southeast Alaska (Lawrence 1958, Neiland 1971, Zach 1950). Orloci (1964), in British Columbia, identified moisture, elevation, and humus quality as the main environmental correlates with vegetation variation.

Although the geographic patterns of forest types are now well understood, their quantitative variation is not. One approach to this is to compare intensively studied sites. This paper reports the quantitative differences in the vegetation of two contrasting environments in Southeast Alaska. The objectives of this study were to: 1) compare quantitatively the forest vegetation on an island, which has a more maritime climate, with that of a nearby site on the mainland, which has a more continental climate, 2) identify environmental gradients underlying vegetation variation within tree, shrub, and herb strata among all stands, and 3) summarize distribution patterns of selected herb, shrub, and tree species along these major environmental gradients.

Study Area

Two study sites were sampled in summer 1983. The Quiet Harbor site is located on the western side of Etolin Island, Southeast Alaska (56°10'N, 132°40'W), approximately 40km southwest of the town of Wrangell (Figure 1). The Aaron Creek study site is located on the mainland of Southeast

Alaska (56°25'N, 131°80'W), approximately 27 km east of the town of Wrangell (Figure 1).

Southeast Alaska has a cool maritime climate (Table 1) with high rainfall. The town of Wrangell

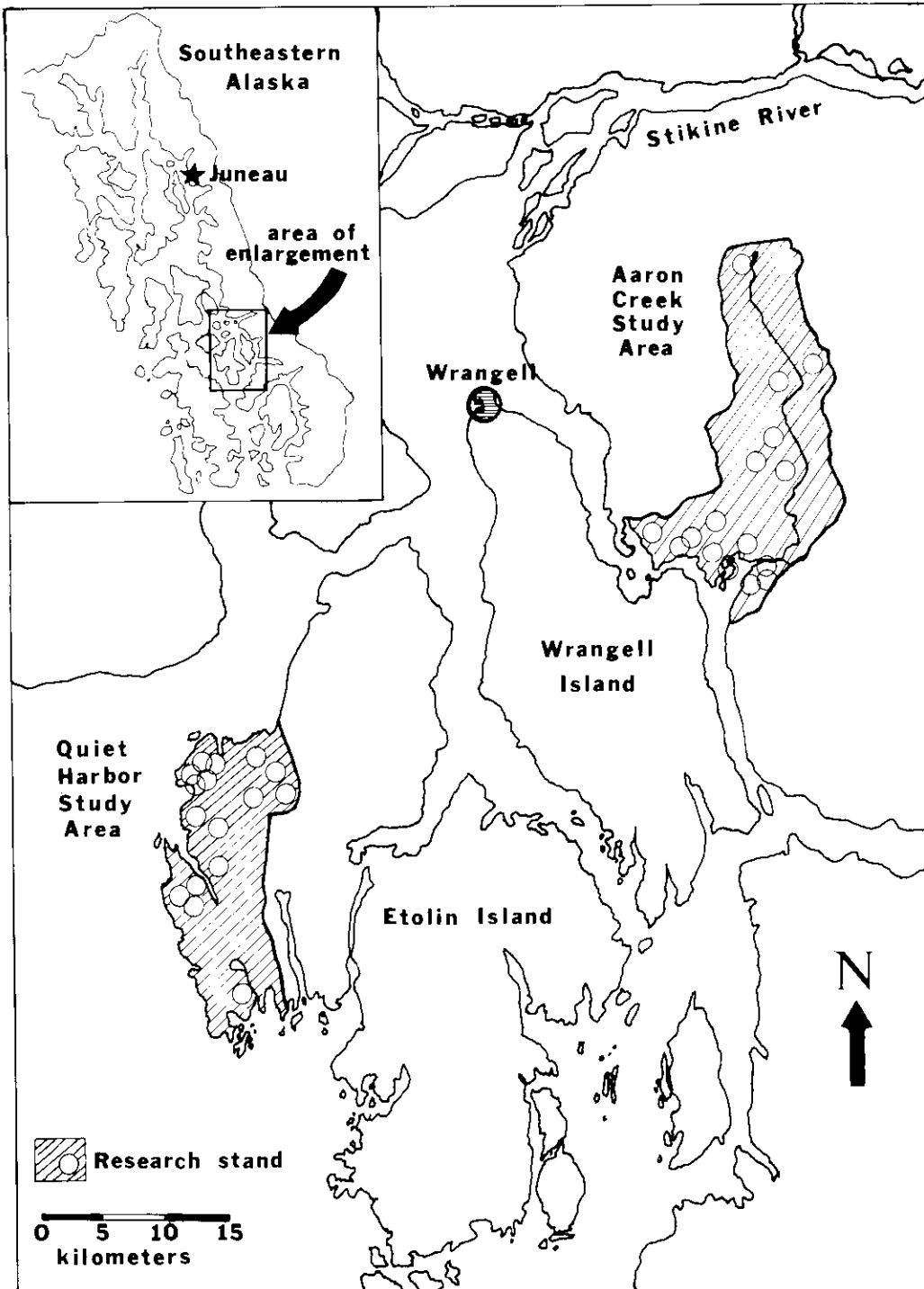


Figure 1. Map of study sites and stand locations near Wrangell, Alaska.

TABLE 1. Temperature ($^{\circ}\text{C}$) characteristics for the Wrangell (mainland) group and Lincoln Rock group from multivariate analysis of weather stations of coastal Alaska. (source: Farr and Hard 1984). Summer: June, July, August. Winter: Dec., Jan., Feb.

	Wrangell group	Lincoln Rock Group
<i>Daily means</i>		
Maximum Summer Temp.	16.9	15.2
Minimum Summer Temp.	8.3	9.8
Mean Summer Daily Fluctuation	8.6	5.4
Maximum Winter Temp.	-0.1	3.9
Minimum Winter Temp.	-5.8	-0.3
Mean Winter Daily Fluctuation	5.7	4.2
<i>Seasonal means</i>		
Summer	12.7	12.6
Winter	-2.9	1.8
Mean Yearly Fluctuation	15.6	10.8

had the nearest weather station to the Aaron Creek study site. From 1953 to 1967, climatic data were collected at Lincoln Rock, approximately 3 km offshore from the Quiet Harbor study site. Both daily and seasonal temperature fluctuations were greater at the Wrangell station, nearest the mainland site of Aaron Creek, than at the Lincoln Rock station, nearest the island site of Quiet Harbor. Daily and seasonal highs are higher, and lows are lower, on the mainland (Table 1). Both sites had almost identical precipitation patterns, averaging approximately 200 cm per year (Farr and Hard 1984).

The Aaron Creek site soil parent material is composed primarily of crystalline metamorphic rocks, whereas the Etolin Island site is primarily underlain by Mesozoic sediments and volcanic rocks (Buddington and Chapin 1929). However, most mineral soils were formed from deep ablation till deposited by receding glaciers. Because of this overburden, bedrock has had little to do with soil development (Harris *et al.* 1974).

Soils in Southeast Alaska are predominantly spodosols, being relatively young, shallow, and poorly developed (Heilman and Cass 1974). Topography, slope angle and elevation combine to alter water drainage, temperature, and erosion, and have had a significant effect on the development of the soils (USDA Forest Service 1982). Moisture saturation and cool temperatures result in low rates of organic decomposition and slow soil development. This in turn allows significant accumulations of organic matter in the soil and

on the surface. Water drainage is often impeded by the organic matter, and the most productive soils in the study areas were those that were well-drained. Both study sites contained the same soil types and were mapped under the same classification system by the USDA Forest Service, although the relative amounts of soil types probably varied between sites.

Vegetation within the two study sites included old-growth forests in a mosaic with bogs, and less extensive alpine, beach and meadow communities. Old-growth forests are defined as those greater than 300 years of age and with uneven canopy coverage due to old tree mortality. Old-growth forests within the study area ranged from open stands with approximately 35 percent cover of predominantly Alaska cedar, *Chamaecyparis nootkatensis* and western hemlock, *Tsuga heterophylla*, on poor sites, to stands with about 80 percent cover of primarily western hemlock and Sitka spruce, *Picea sitchensis*, on more productive sites. (Nomenclature follows Viereck and Little 1972, for trees and shrubs, and Hultén 1968, for herbaceous species. Voucher specimens are filed at the Wrangell Ranger District of the USDA Tongass National Forest, and at the herbarium of the University of Alaska, Fairbanks.) The study sites extended from 0 to 600 m in elevation, slopes faced in all directions, and ranged from flat to extremely steep.

Methods

Aaron Creek and Quiet Harbor were sampled from the middle of June until the middle of August, 1983. Most plants were near or had reached full size. A stand is defined as an area of relatively homogeneous coverage by the dominant tree species.

Stands were selected for sampling using a combination of topographic maps and aerial photos prepared by USDA Forest Service personnel according to soil drainage types. Only forest stands below subalpine soils were included. From these maps, three environmental gradients were recognized prior to fieldwork: 1) soil drainage, 2) elevation, and 3) aspect. Each environmental gradient was stratified into four classes in order to get even sampling among these gradients. The soil classes were based on USDA Forest Service (1982) mapping units: F1 were deep (> 50 cm), well-drained soils; F2 were shallow (< 50 cm),

well-drained soils; F4 were deep, poorly-drained soils; F5 were deep, very poorly-drained soils. Elevation classes were 0-60 m; 61-150 m; 151-300 m; and 300+ m above sea level. Aspect classes were: 1-90 compass degrees; 91-180 degrees; 181-270 degrees; and 271-360 degrees.

A 4 X 4 Latin square experimental design was used as a sampling scheme at each site. This allowed four stands to be sampled from each class of each gradient. A 4 X 4 Latin square was chosen randomly, and the four soil classes were given row cells and the four elevation classes were given column cells. Aspect varied within each Latin square. All stands within each study site that fit into a Latin square cell were identified from aerial photos and topographic maps. From those stands, one stand was chosen at random for each cell in the Latin square, resulting in 32 stands, 16 from each study site. All stands were "old-growth" and, following Neiland (1971), had no disturbance larger than that of a single, large, fallen tree. Stands ranged in size from approximately 1 to 3 hectares.

Data were collected from three vegetation layers. Trees were defined as woody stems greater than 5 cm diameter at breast height (dbh). Shrub layer species, including juvenile trees, were defined as woody stems less than 5 cm dbh, but greater than 40 cm tall. Herbaceous layer species included woody stems less than 40 cm tall and all herbaceous stems.

Three 20 m long, replicate random transects were run across the slope (i.e. parallel to the contour) in each stand. Absolute tree and shrub canopy cover was measured by line intercept (Canfield 1941). Ten 20 X 50 cm quadrats per transect were placed every 2 m and herbaceous cover was estimated using the following cover classes: 0-1%, 2-5%, 6-20%, 21-40%, 41-60%, 81-100%. The adequacy of 30 herb plots per stand was determined by running mean (Kershaw and Looney 1985), and was subjectively assessed as being adequate for the more abundant species but inadequate for the less abundant ones. This was accepted as a compromise that would still allow sufficient numbers of stands to be sampled over the course of the summer.

The midpoints of the cover classes for herbs, and species totals of line intercepts were used to determine mean cover values of all species per stand. Mean species cover values for all vegeta-

tion strata were subjected to detrended correspondence analysis (DCA) using the DECORANA program (Hill 1979). DCA was used because it has been judged to have superior ordination performance (Hill and Gauch 1980, Gauch 1982, Pielou 1984, Kershaw and Looney 1985).

For direct gradient analysis, average cover values for the most common species from each vegetation layer are presented in discrete classes along the soil and elevation gradients as well as by study site. Since ecological data are often statistically "noisy" (Gauch 1982), the array of means of discrete classes along gradients is a convenient way to summarize species distributions (Curtis and McIntosh 1951, Gauch 1982). No confidence intervals are presented. Stands were weighted equally for calculating mean values even though stand size may have varied. Also, sampling was uniform for the gradient classes in order to get enough stands from each class for DCA correlations, even though there may have been proportionally more stands in one class than another. In other words, the mean abundances are relative values for a particular combination of environmental factors. A correlation factor would require a weighting of the mean in the proportion to the total aerial extent of all stands within the gradient classes and such data are unavailable. In addition, the stand values themselves are estimates and subject to sampling error. The values displayed, then, are not true means for the categories. However, the values presented should reasonably reflect trends along the major gradients.

Results and Discussion

Ordination of Vegetation Samples

DCA stand scores for combinations of axes for each vegetation layer are plotted in Figure 2. Each stand is represented by a combination of letters for study site or elevation and/or a numeral for soil class. (Since DCA stand scores are weighted averages of species scores, it is possible for stand scores for axis one to cover a smaller range than axis two, even though DCA species scores had a wider range for axis one than axis two. This is the case in Figures 2a and 2b.)

The first DCA axis for trees (Figure 2a) represents a soil drainage gradient, with the well-drained stands loading in the left portion and the

poorly-drained stands loading in the right portion of the figure, with only a few exceptions. The mean DCA score on axis one is 28 for F1 stands, 72 for F2 stands, 93 for F4 stands, and 160 for F5 stands. The eigenvalue for the first axis is 0.455. The second DCA axis places the Aaron Creek stands toward the bottom of the figure and the Quiet Harbor stands toward the top (Figure 2a). The mean DCA score on axis two for Aaron Creek stands is 78 and for Quiet Harbor stands is 150. The eigenvalue for the second axis is 0.248, summarizing considerably less variation than the first axis. Thus, differences between the two study sites appear to affect tree species composition less than differences between soil drainage classes. Eigenvalues for the third and subsequent axes drop to 0.062 and lower.

For the shrub layer (Figure 2b), the first DCA axis separates Quiet Harbor stands on the right from Aaron Creek stands on the left. On axis one, the average DCA score is 57 for Aaron Creek stands and 140 for Quiet Harbor stands. The eigenvalue for the first axis is 0.311. The second axis represents stand variation along the soil drainage gradient, with well-drained stands toward the bottom and poorly-drained stands toward the top. The mean DCA score on axis two is 86 for F1 stands, 88 for F2 stands, 138 for F4 stands, and 170 for F5 stands. The eigenvalue for the second axis is 0.232. In contrast to the tree species, therefore, shrub composition exhibits greater site differences than soil class differences. Again, eigenvalues for the third and subsequent axes are low.

The first DCA axis for the herb layer (Figure 2c) represents the soil drainage gradient, with well-drained stands on the left and poorly-drained stands on the right. The mean DCA score on the first axis is 93 for F1 stands, 108 for F2 stands, 196 for F4 stands and 258 for F5 stands. The eigenvalue for the first axis is 0.488. The second axis represents herb vegetation response to elevation. Low elevation stands are located in the lower portion and high elevation stands are located in the upper portion of Figure 2c. The mean second axis DCA score is 59 for low elevation stands, 86 for moderately low stands, 96 for high stands and 132 for very high stands. The eigenvalue for the second axis is 0.246. The third axis for herbs (Figure 2d) separates Quiet Harbor stands in the lower portion of the figure, with an average DCA score of 64, from Aaron Creek stands, in the

upper portion, which have an average score of 128. The eigenvalue for the third axis is 0.143. For herbs, site differences do not appear until local environmental factors of soil drainage and elevation differences are accounted for. The remaining eigenvalues are 0.049 and lower.

Each vegetation layer appears to respond differently to environmental factors. Study site separation, soil drainage, and elevation correlate well with vegetation variation at these sites, but their order of importance varies among strata. Within the geographic limits of the analysis, aspect never appeared to be important in stand ordinations.

Study site differences occur over a relatively short geographical range. The sites contain essentially the same species, and the species with the greatest cover were common to both areas. Nevertheless, the quantitative abundances of species will structure communities differently enough to allow separate recognizable patterns for the study sites. This result is most likely due to Etolin's more constant, maritime environment and Aaron Creek's more variable, continental climate (Table 1).

The vegetation responses to soil drainage compare well with findings in nearby areas. Zach (1950), Lawrence (1958), and Neiland (1971) identified drainage patterns as a major gradient in explaining vegetation variation from forest to bog communities in Southeast Alaska. They argued that slope angle (i.e. topography) and proximity to rivers or oceans are the primary influences on drainage patterns. Orloci (1964) identified soil moisture, elevation, and humus quality as the first three ordination axes for the wet hemlock subzone in southern British Columbia. However, his moisture gradient ran from ample moisture to moisture-stressed, with the highest productivity on the ample moisture end of the gradient. There were several species that were common to both this our study and to Orloci's (1964) study; they were found at the well-drained end of our gradient but at the ample moisture end of his gradient. Combined, our results and those of Orloci (1964) can be viewed as a very long moisture gradient of geographic extent, with stands ranging from moisture stressed in British Columbia to excessive moisture in Southeast Alaska.

Tree productivity is directly related to the soil drainage gradient in this study. The highest tree productivity is on F1 soils and the lowest

productivity is on F5 soils (USDA Forest Service 1982). This relationship resembles that noted by Neiland (1970), who performed polar ordinations (Bray and Curtis 1957) of stands throughout Southeast Alaska and found that the primary axis was correlated with minimum to maximum tree productivity, among other factors.

Prior to our results, elevation has not been identified as a factor contributing to forest vegetation variation in Southeast Alaska. This is likely due to the fact that previous investigators combined all strata for a stand, and scores would be largely dominated by tree species, which did not show elevation trends in this study either. Orloci (1964), in British Columbia, and others in mountainous terrain (e.g. Whittaker 1956, 1960; Beals 1969) have also found elevation trends.

Species Distributions on Environmental Gradients

Six tree species occurred in the two study areas. Several of these species show clear patterns along the environmental gradients (Figure 3). Western hemlock and Sitka spruce decrease toward poor soil drainage, while other species increase. Alaska cedar and mountain hemlock, *Tsuga mertensiana*, show increased abundance with elevation, western red cedar, *Thuja plicata*, and lodgepole pine, *Pinus contorta*, decrease, and the others appear independent of elevation. Western hemlock and mountain hemlock species are more abundant at Aaron Creek, western red cedar and lodgepole pine occur only at Quiet Harbor, and the others are probably independent of site.

Most species show a unique distribution when considering these three environmental factors. For instance, Alaska cedar and western red cedar separate more with respect to elevation than to soil drainage. The two hemlocks differ in response to soil drainage and probably to elevation, but they both are more abundant at Aaron Creek than Quiet Harbor. Western hemlock and Sitka spruce, however, exhibit rather similar trends. Western hemlock is very shade tolerant throughout its life, while Sitka spruce is only moderately shade tolerant (Harlow and Harrar 1969). Shading from the forest overstory often inhibits development of juvenile Sitka spruce. However, Sitka spruce grows vigorously in moderate to high light, is often the first successional tree species, and is long-lived. When a gap opens in the overstory, Sitka spruce is able to

overtop its competitors (Harlow and Harrar 1969), thus maintaining its population in old-growth stands.

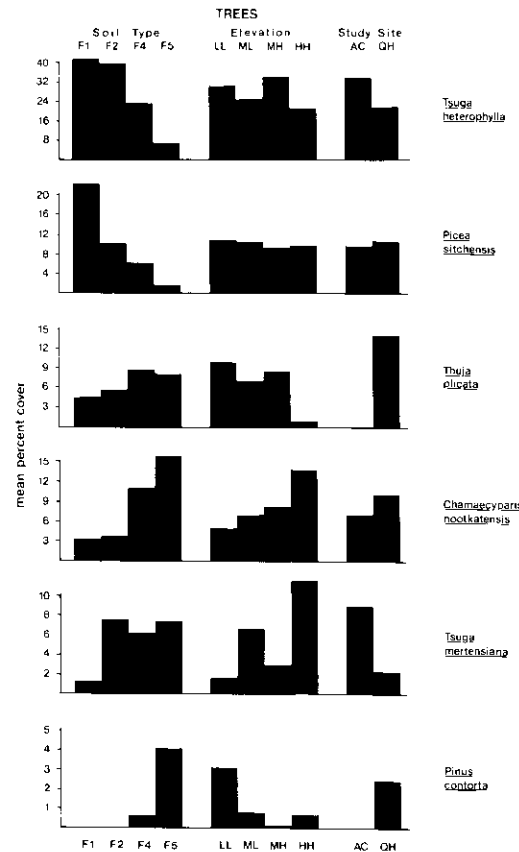


Figure 3. Direct gradient response of six tree layer species to soil type, elevation, and study site. Soils: F1 = deep, well-drained, F2 = shallow, well-drained, F4 = deep, poorly-drained, F5 = deep, very poorly-drained. Elevations: LL = 0-60 m, ML = 61-150 m, MH = 151-300 m, HH = 300+ m. Sites: AC = Aaron Creek, QH = Quiet Harbor.

Shrub species also show a response to the three environmental factors (Figure 4), the composite of which gives most of them a unique distribution. Early blueberry, *Vaccinium ovalifolium*, and Alaska blueberry, *Vaccinium alaskense*, are closely related taxa, but appear to separate based on the soil drainage gradient. As in the tree layer, many shrub species show a response to elevation, even though no elevation axis from stand ordinations was found.

Distributions of western hemlock and mountain hemlock are presented for the shrub layer

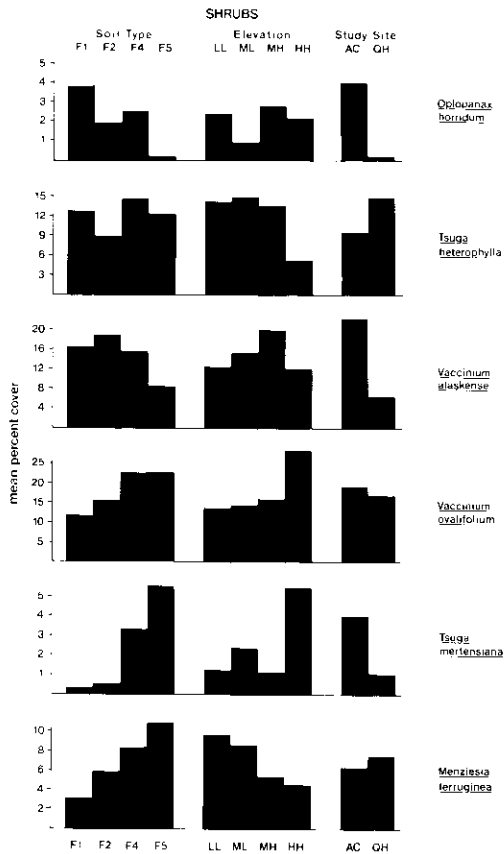


Figure 4. Direct gradient response of six shrub layer species to soil type, elevation, and study site. Symbols are the same as for Fig. 3.

as well as the tree layer. The distribution of juvenile mountain hemlocks closely resembles that of mature mountain hemlocks. However, mature western hemlock and juvenile western hemlock show an inverse relationship between sites and perhaps along the soil drainage gradient. Although the exact factors controlling juvenile establishment and mature tree success are unknown, there have been similar findings in other areas (Walker *et al.* 1972).

There are clear distribution patterns for six common herbaceous species along the environmental gradients (Figure 5). Again, most show a unique distribution. Rose (1982) and Schoen *et al.* (1981) did an agglomerative clustering of understory species in Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) habitat in Southeast Alaska. Their results suggest that five-leaf bramble, *Rubus pedatus*, Canadian dogwood,

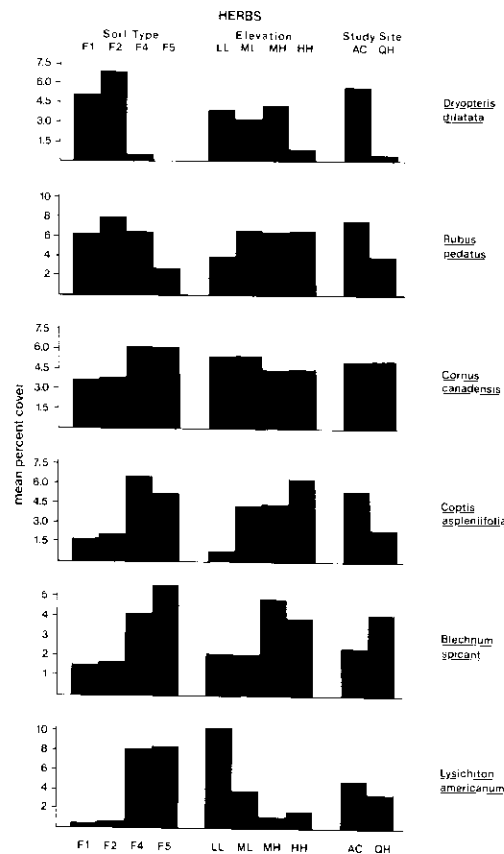


Figure 5. Direct gradient response of six herb layer species to soil type, elevation, and study site. Symbols are the same as for Fig. 3.

Cornus canadensis, and fernleaf goldthread, *Coptis asplenifolia*, are part of an association which grows on productive sites, while Devil's club, *Oplopanax horridum*, and skunk cabbage, *Lysichiton americanum*, are part of an association of poorly-drained areas and less productive sites. Our results indicate that, over the whole range of forest conditions, Canadian dogwood and fernleaf goldthread are not good indicators of well-drained sites (Figure 5), while Devil's club grows most abundantly on the well-drained soils (Figure 4). The most likely explanation for this discrepancy is that Schoen *et al.* (1981) and Rose (1982) sampled only on F1 and F2 soils, which support the only suitable forests as winter deer habitat, since forests on F4 and F5 soils do not have enough canopy coverage. Also, they clustered samples of 1.0-m² quadrats. Thus their results are more indicative of microsite factors

within well-drained stands than factors operating among stands over the range of forest conditions.

The combination of indirect and direct gradient analysis revealed that these forests vary continuously along the drainage gradient, with open stands (approximately 35% cover) of predominantly Alaska cedar, red cedar, mountain hemlock, lodgepole pine, early blueberry, rusty menziesia (*Menziesia ferruginea*), Canadian dogwood, fernleaf goldthread, deer fern and skunk cabbage on very deep, very poorly-drained soils; to closed stands (approximately 85% cover) of predominantly western hemlock, Sitka spruce, Devil's club, Alaska blueberry, wood fern (*Dryopteris dilatata*), and five-leaf bramble on deep, well-drained soils.

An important conclusion from the comparison of direct and indirect ordination methods concerns the nature of vegetation response ver-

sus species response to environmental gradients. Many species showed a response to elevation, yet, when each stratum as a whole was subjected to ordination (DCA), only the herb layer showed a response to elevation. Thus, the interaction of species was not sufficiently correlated along the elevation gradient in the tree or shrub layers to be detected by DCA. It remains to be seen how prevalent this finding is in other areas.

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