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Relations Between Vegetation and Environment

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INTRODUCTION

The Coniferous Forest Biome program directed much of its early efforts to sampling, ordering, classifying, and describing forest communities. The formulation of hypotheses to explain vegetation diversity resulted, and correlations between environmental and vegetational gradients have emerged.

Most of the work relating vegetational and environmental gradients was conducted at the two intensive study sites (The Cedar River watershed, Washington, and the H. J. Andrews Experimental Forest, Oregon) and is discussed here. The vegetation of the intensive sites is discussed in detail in Chapter 1 so a brief description is sufficient here.

The principal vegetation zones of western Washington are represented in the Cedar River watershed. The *Tsuga heterophylla* zone occurs below about 600 m elevation, the *Abies amabilis* zone between 600 m and 1300 m, and the *Tsuga mertensiana* zone generally above 1300 m elevation.

Most of the lower watershed is covered by second-growth forests that date from logging or fires early in the century. *Pseudotsuga menziesii* is the dominant overstory species on all but the wettest sites; *Alnus rubra* occurs on these sites, the only forest stands not dominated by conifers.

Between 600 and 1000 m in elevation periodic disturbances, primarily fires, have been frequent enough to result in the dominance by *Tsuga heterophylla* on most sites. *Abies amabilis* is the principal species reproducing beneath the canopies of mature stands. At higher elevations *Tsuga heterophylla* disappears, leaving *Abies amabilis* as the principal dominant community.

Subzonal vegetational units on the Cedar River watershed have been identified (Table 2.1) and described by del Moral and Long (1977). Ten different community types were recognized, six of which represent old-growth stands on the upper watershed (above 600 m) and four that represent second-growth stands on the lower watershed (about 180 to 600 m). Extensive descriptions of

TABLE 2.1 Summary of the major factors characterizing the vegetation types of the Cedar River watershed.^a

Group	Community type ^b	Elevation (m)	Aspect	Slope	Age (yr)	Comments
A	Tshe-Abam/Xete	900-1200	W-SE	mod-steep	250	Not wholly homogenous; two groups joined by discriminant analysis
B	Tshe/Vaov	700-900	E-NW	gentle	250-300	Greater Abam dominance than C
C	Tshe/Vaal	600-1000	W-NE	gentle-mod	250	Well-developed Abam regeneration
D	Abam-Tsme/Xete	900-1200	various	mod	150-250	Regeneration mainly Abam
E	Abam/Vame-Vaov	700-900	various	steep	200-250	Strong Abam dominance
F	Abam-Tshe/Vame	900-1200	various	moderate	—	Differs from E in high amounts of Tshe
G	Psme/Gash	190-400	W-S-E	gentle	38-73	Characteristic of xeric habitats within the Tshe zone
H	Psme/Pomu	280-490	various	gentle-mod	31-50	Seral stands, hemlock regeneration
I	Psme/Pomu-Libo	190-550	various	gentle	40	Similar to H except in relatively high abundance of Libo
J	Alru/Pomu	170-520	various	gentle	39-50	Such stands are exceedingly common in Puget Sound Lowlands particularly on moist and recently disturbed sites

^aFrom del Moral and Long 1977; copyright © 1977 by the British Columbia Provincial Museum and the authors.

^bSee Table 2.2 for identification of abbreviations.

these plant communities are published elsewhere (Long 1973, 1976; del Moral and Long 1977).

Sampling of the H. J. Andrews site in Oregon was based on prior knowledge of general plant communities of the area (Dyrness 1965; Rothacher et al. 1967). Plots represented the majority of closed forest communities on both extreme and moderate sites. Other regional classifications were reviewed and incorporated into the classification of the H. J. Andrews site (Franklin et al. 1972; Dyrness 1973; Hawk and Zobel 1974).

The rationale, in part, for the biome studies of vegetation and community environmental interactions was to direct specific attention to testing hypothesized relations between floristic gradients and climatic gradients in moisture, temperature, snow depth, and snow duration. If community types or vegetation gradients are highly correlated with key environmental factors, the results of detailed process studies can be extrapolated over a much broader area where it

would be prohibitively expensive to install instrumentation. The objective of these studies were: (1) to describe the key structural and compositional features of forest ecosystems in order to relate these features to ecosystem function; (2) to ordinate the vegetation sample plots using solely vegetation characteristics; (3) to use the ordination results and environmental data to formulate hypotheses that might explain vegetation-environment interactions; and (4) to test the hypotheses.

The approaches used at the two intensive study sites varied though the same ultimate objectives were reached. On the Washington site, specific plant communities were selected according to the supposition that they represented different portions of the environmental spectrum. The plots were sampled, ordered, and then classified. On the Oregon site, previous classification studies were combined with our own sampling (Franklin et al. 1970) to develop the ordination and classification scheme.

VEGETATION CLASSIFICATION AND ORDINATION

Because of the broad spectrum of community and environmental variation in the study sites, a large number of stands was sampled to stratify the vegetation into relatively homogeneous and easily recognizable units. A rapid reconnaissance method for sampling vegetation was used (Franklin et al. 1970) that enabled data acquisition over a wide range of environments and ensured a reasonable degree of completeness in representing the different forest stand types. A total of forty-three mature and forty-five second-growth forest stands was sampled in the Cedar River watershed. Three hundred plots were sampled in and around the H. J. Andrews Experimental Forest.

In synecological studies, a common objective has been to describe apparently homogeneous vegetation units and to discuss their interrelationships (with regard primarily to floristics); however, ecosystem studies demand clarification not only of the relations between units but also between them and the environment. The approach used to determine these relations was indirect gradient analysis, that is, the use of vegetation ordination to infer environmental gradients (Whittaker 1970). This implies that vegetation gradients such as those generated in Washington and Oregon may or may not always correspond to actual environmental gradients.

A computer routine, SIMORD, was used to ordinate the vegetation data (Dick-Peddie and Moir 1970; Franklin et al. 1970; Hawk and Zobel 1974). The routine is similar to the Wisconsin comparative ordination techniques. SIMORD results in a two-dimensional reference stand ordination with the position of a stand in the ordination plane dependent on that stand's similarity (of vegetation characteristics) to other stands included in the analysis.

Ordination, in this context, is the arrangement of stands into one or more derived vegetation gradients. Floristic characteristics were used to delimit

portions of the gradients into relatively homogeneous plant communities. Environmental sampling was done in stands representative of particular community types or location along the vegetational gradient. The results of these investigations were then used to establish relations between vegetational and environmental gradients.

The ordination of plant communities of the H. J. Andrews Experimental Forest resulted in the separation of twenty-three plant communities over the vegetational gradient (Figure 2.1). Of the twenty-three communities, fourteen are in the *Tsuga heterophylla* (Tshe) zone, including the transition zone, and nine are in the *Abies amabilis* (Abam) zone or the lower part of the *Tsuga mertensiana* (Tsme) zone. The *Tsuga heterophylla* zone is at low elevation and dominated by *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*. Past studies and the ordination procedures used made it obvious that *Tsuga heterophylla* zone communities were displayed (Figure 2.1) along a complex moisture gradient with *Tsuga heterophylla* the climax dominant in all but the driest communities. The *Abies amabilis* zone is at high elevation and dominated by *Abies amabilis*, *Tsuga heterophylla*, and *Tsuga mertensiana* in mature

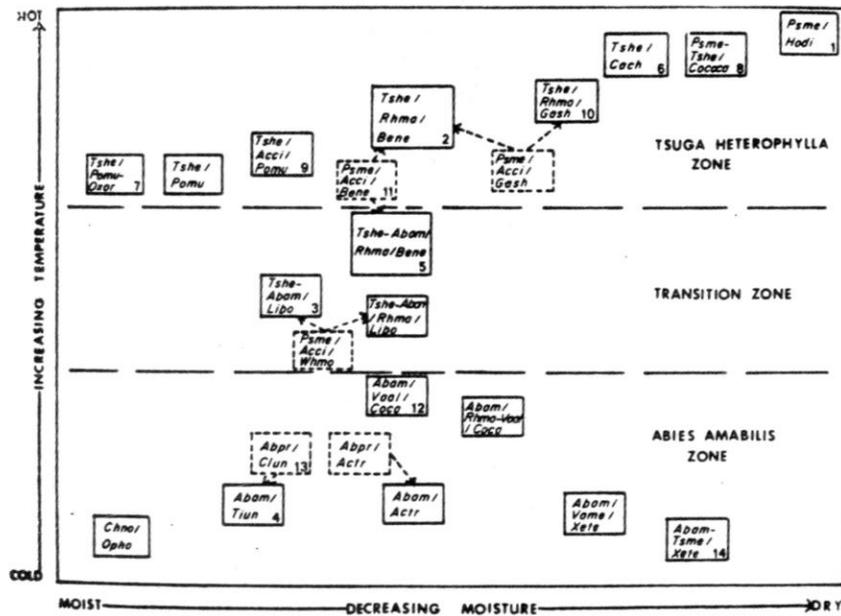


FIGURE 2.1 Hypothesized relations between forest communities and environment in the central western Cascades (Dyrness et al. 1974). This figure is based on their vegetation ordinations, somewhat modified by the intuition of the investigators. Communities enclosed with dashed borders are considered to be seral, the others to be climax. Communities sampled in this study are identified by the reference stand number in the box.

climax forest, and *Pseudotsuga menziesii* and *Abies procera* in subclimax stands. These upper elevation forests also appear to be arranged along a moisture gradient.

A large area of forest lies between the *Tsuga heterophylla* and *Abies amabilis* zones, representing a transition zone dominated by mixed young- and old-growth stands of *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Thuja plicata*, and *Abies amabilis*. The *Tsuga mertensiana* zone is not a major zone in the Cascades of central western Oregon; therefore its lower elevational components were treated as elements of the *Abies amabilis* zone.

Association tables were constructed as a result of the ordination analysis for stands in the H. J. Andrews Forest and these are presented in Dyrness et al. (1974). The tables illustrate the difficulty of classifying habitat types within an area that includes substantial landscape and species diversity. A diagrammatic display of plant communities over the observed temperature and moisture gradients (Figure 2.1) shows the *Pseudotsuga menziesii*/*Holodiscus discolor* (Psme/Hodi) community at the warm dry extreme, followed by communities in cooler and moister environments along the gradients. The sword fern communities of lower elevations are at the warm moist extreme. *Rhododendron* communities are mesic in terms of both the temperatures and moisture gradients. Beargrass communities occupy the cool dry areas and herb-rich communities occupy the cool moist extremes at upper elevations.

Ordination of communities resulted in development of community classification keys. Present communities are finer resolution classification units than those defined as habitat types by Pfister et al. (1977) or Daubenmire (1968). Some of our communities include both habitat types and phases that are presently being defined.

DISTRIBUTION OF SPECIES AND COMMUNITIES ALONG ENVIRONMENTAL GRADIENTS

Cedar River Watershed, Washington

Ordination of data from old-growth stands in the *Abies amabilis* zone of the Cedar River watershed suggests that two environmental complexes are primarily responsible for controlling the distribution of these forest communities. It was hypothesized that these factors of the physical environment, correlating with the x - and y -axes of the ordination (Figure 2.2, Table 2.2), are: (1) factor(s) strongly correlated with elevation (x -axis); and (2) available soil moisture (y -axis).

The ordering of the stands along the x -axis indicates that elevation accounts for the distribution of the montane forest communities in the upper Cedar River watershed. For example, on the low end of the x -axis is a *Tsuga heterophylla*-dominated stand at 700 m, while an *Abies amabilis*-dominated stand at 1300 m represents the upper end of this vegetational gradient.

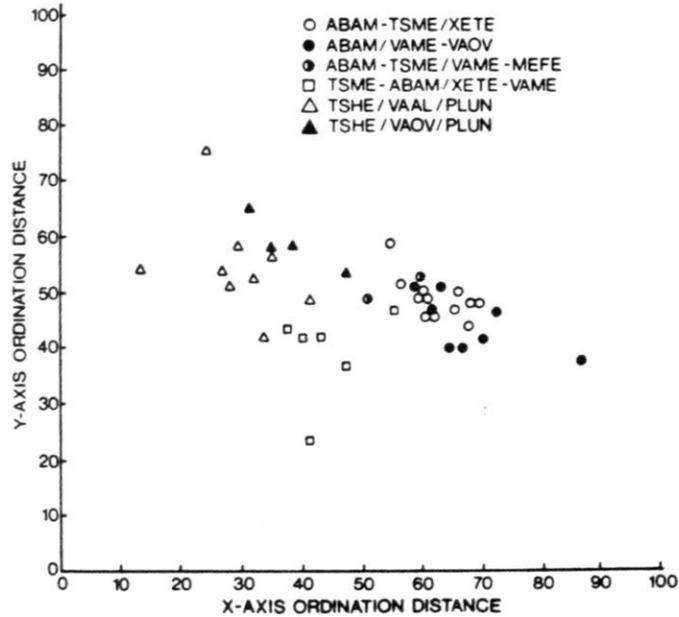


FIGURE 2.2 Relations between stands in the *Abies amabilis* zone of the Cedar River watershed based on a vegetation ordination (Long 1976). Community classifications follow del Moral and Long (1977); abbreviations for communities are identified in Table 2.2.

In the western Cascade Mountains of Washington there are several environmental factors strongly associated with elevation (del Moral et al. 1976). Some factors important in the distribution of vegetation include: (1) depth of snowpack; (2) air and soil temperature; and (3) precipitation and available soil moisture.

For community ordination on the Cedar River watershed, precipitation seems to be the least promising of the factors listed. The relation between mean annual precipitation and elevation for the entire watershed is not simple. The difference in precipitation at Seattle and Chester Morse Lake, corresponding approximately to the lower and upper elevational limits of the *Tsuga heterophylla* zone, is large in contrast to the difference in precipitation between Chester Morse Lake and Findley Lake, the elevations of which correspond closely to those of the lower and upper limits of the *Abies amabilis* zone (Figure 2.3). The implication is that within the Cedar River watershed there is a rather steep precipitation gradient associated with the *Tsuga heterophylla* zone and that this gradient is lacking in the *Abies amabilis* zone. The pattern of precipitation over the entire upper watershed is therefore a reflection of the orographic effect of high ridges on either side of the valley floor.

It was hypothesized that the most important environmental factor controlling distribution of forest communities within the *Abies amabilis* zone of the

TABLE 2.2 Mean cover (percentage) for common species in vegetation types of the Cedar River watershed.

Species	A	B	C	D	E	F	G	H	I	J	Avg.
Trees											
<i>Abies amabilis</i> (Abam)	25.8	28.0	10.5	41.8	76.2	35.0	0	0	0	0	19.2
<i>Abies procera</i> (Abpr)	17.5	0	0.1	0.8	0.1	1.6	0	0	0	0	1.4
<i>Acer macrophyllum</i> (Acma)	0	0	0	0	0	0	0	0	0.9	6.7	1.0
<i>Alnus rubra</i> (Alru)	0	0	0	0	0	0	0	1.6	0	74.6	10.4
<i>Pseudotsuga menziesii</i> (Psme)	12.7	4.2	17.8	0	0	3.3	76.4	71.4	78.1	3.4	27.4
<i>Tsuga heterophylla</i> (Tshe)	31.2	46.0	65.2	1.6	0.1	25.0	9.6	23.7	18.1	3.6	22.4
<i>Tsuga mertensiana</i> (Tsme)	0	0	0	34.0	9.6	5.3	4.5	0	0	0	6.3
Shrubs											
<i>Acer circinatum</i> (Acci)	4.7	0	3.0	0	0	0	3.6	2.6	2.5	7.8	2.7
<i>Berberis nervosa</i> (Bene)	0.2	0.2	3.9	0	0	0	2.7	0	1.3	3.8	1.6
<i>Gaultheria shallon</i> (Gash)	3.3	0	3.0	0	0	0	56.4	2.1	2.8	1.9	8.5
<i>Menziesia ferruginea</i> (Mefe)	0.2	3.0	1.7	6.9	3.5	17.0	0	0.1	0	0	2.3
<i>Oplopanax horridum</i> (Opho)	0	0	4.7	0.1	0	0	0	1.3	0	1.1	1.1
<i>Vaccinium alaskaense</i> (Vaal)	0.2	0	10.0	7.2	3.8	8.7	0	0	0	0	3.7
<i>Vaccinium deliciosum</i> (Vade)	0	0	0	4.7	0	0	0	0.3	0	0	0.6
<i>Vaccinium membranaceum</i> (Vame)	10.6	2.2	2.7	7.7	11.9	73.3	0.9	0.3	0	0	6.1
<i>Vaccinium ovalifolium</i> (Vaov)	0	46.0	5.0	1.3	9.4	0	0	0	0	0	4.6
<i>Vaccinium parvifolium</i> (Vapa)	1.2	3.2	3.1	0.1	0	0	2.4	2.4	3.4	1.1	1.8
Herbs and ferns											
<i>Achlys triphylla</i> (Actr)	4.5	0	3.2	0.2	0.2	1.6	0	0	0.1	0.6	1.0
<i>Clintonia uniflora</i> (Clun)	2.1	1.6	1.9	2.5	3.0	6.7	0	0	0	0	1.4
<i>Festuca</i> sp. (Fesp)	0	0	0	0	0	0	0	0.1	0.1	4.2	0.6
<i>Linnaea borealis</i> (Libo)	0.3	1.2	2.3	0	0	1.7	6.1	0.1	10.9	0.1	2.4
<i>Polystichum munitum</i> (Pomu)	0	0	0.3	0	0	0	3.7	65.0	23.0	58.3	15.9
<i>Pteridium aquilinum</i> (Ptaq)	0.3	0	0.1	0	0	0	8.0	1.8	1.8	8.4	2.5
<i>Rubus ursinus</i> (Ruur)	0	0	0.1	0	0	0	0	2.7	3.3	2.2	2.2
<i>Tiarella trifoliata</i> (Titr)	0	0.2	0.6	0.2	0.1	0	0	0.1	0	0.5	0.3
<i>Tolmiea menziesii</i> (Tome)	0	0	0	0	0	0	0	0	0	1.3	0.2
<i>Xerophyllum tenax</i> (Xete)	17.8	0.4	1.7	12.9	5.0	0	0	0	0	0.4	3.8
Mosses											
<i>Eurhynchium organum</i> (Euor)	0	0	1.9	0.8	0	2.0	39.1	18.5	27.5	9.3	10.8
<i>Hylocomium splendens</i> (Hysp)	0	0	1.1	0	0	0	3.1	1.0	12.2	1.4	2.0
<i>Mnium insigne</i> (Mnin)	0	0.2	0.1	0	0	0.3	0.5	1.4	0.8	0.8	0.4
<i>Plagiothecium undulatum</i> (Plun)	6.0	44.0	16.5	0.8	0.4	8.3	0	0	0	0	6.2

Note: Letters correspond to community types listed in Table 2.1.

Cedar River watershed is the depth and duration of winter snowpack. While there is apparently no great difference in the amount or timing of precipitation within the *Abies amabilis* zone, the form in which it falls varies considerably. At high elevations (Findley Lake, 1200 m) most precipitation falls as snow. The snowpack may be several meters thick and its duration may exceed seven

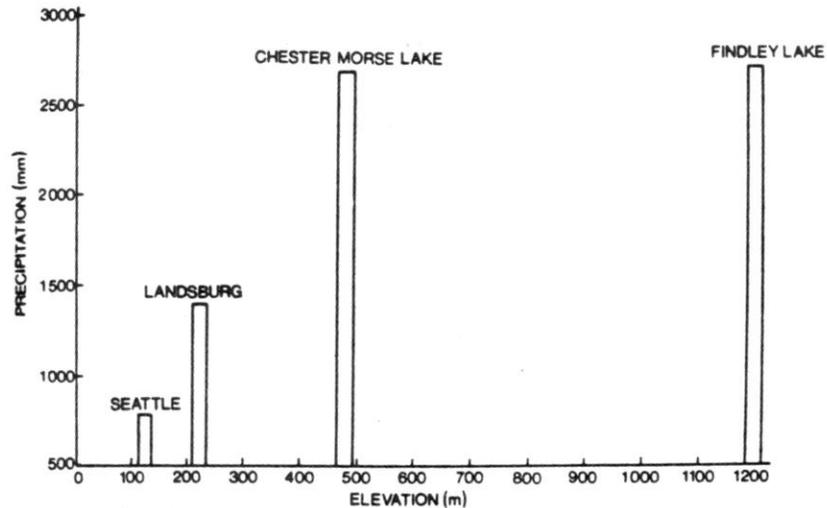


FIGURE 2.3 Relation between mean annual precipitation and elevation for four locations in western Washington.

months. In the Chester Morse Lake area the total annual snowfall is generally less than 120 cm, with snow remaining on the ground for less than thirty days.

We hypothesized that the y-axis of the Cedar River ordination represents a moisture gradient (this is inferred from the floristic gradient). For example, *Xerophyllum tenax*, a species indicative of dry habitats (Dyrness et al. 1974), is important only in those stands at the middle to lower end of this hypothesized moisture gradient. *Vaccinium ovalifolium*, a presumed mesic site indicator species, is important in stands at the middle to upper end of the moisture gradient.

Indirect gradient analysis thus yields the following hypotheses concerning the distribution of vegetation within the *Abies amabilis* zone on the Cedar River watershed: (1) a gradient in the winter snowpack depth and duration is responsible for much of the variability in the forest vegetation; and (2) a gradient in soil moisture during the growing season accounts for an additional component in the variability of the forests.

Population distribution of particular species along gradients may provide a starting point for determining the nature of particular plant-environment interactions. For example, snow depth, and by inference its duration, can be measured in each of several stands whose x-axis position is known. A high degree of correlation between these two variables can provide evidence for the existence of the hypothesized gradient as well as its association with the vegetational gradient. Similarly, correlation between seasonal development of water deficits and position on the y-axis may provide evidence of the hypothetical soil moisture gradient.

Limited access to high-elevation sites during the periods of maximum snow accumulation places a practical restriction on the direct measurement of snow depths in any of the sampled stands. Therefore the use of an apparent sensitivity of some epiphytic lichens to snowpack yields an indirect measure of relative snowpack accumulations. Corticolous lichens respond to environmental gradients on the boles of trees (Hale 1965; Gough 1975). Daubenmire (1974) suggests that under some circumstances the minimum height of lichens on tree boles is a function of the depth of winter snowpack. One of the most common of these lichens in the upper Cedar River watershed is *Alectoria sarmentosa*. It occurs from treetops to nearly ground level. Throughout the *Abies amabilis* zone it forms the major component of the epiphytic community. The lower distributional limits of the lichen on the boles is quite distinct; on each of the trees in a given stand the minimum height above ground to which the lichens extend is very nearly the same. It was concluded (Long 1976) that the average minimum height of lichens on the boles of trees in a stand represents a suitable indirect measurement of the maximum depth of the winter snowpack for that particular stand. Figure 2.4 relates the average minimum lichen height for each stand to that stand's x -axis ordination value. The regression of lichen heights, and presumably snow depth, against the x -axis ordination values is significant at the 0.01 level ($r^2 = 0.93$).

Time of snowmelt in the spring is a function of the depth of winter snowpack (Brooke et al. 1970). Data from 1968, 1973, and 1974 from nine weather stations in the western Cascades of Washington were used in an attempt to quantify this relation (Figure 2.5). These particular years were picked as they appear to represent a typical range of snow conditions for that area of the state.

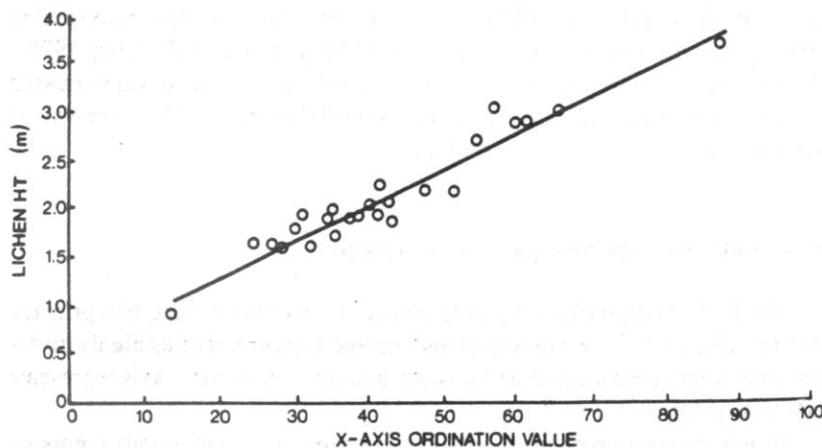


FIGURE 2.4 Relation between minimum lichen heights on the boles of trees and the x -axis ordination value for individual stands (height = $0.521 + 0.038X$, $r^2 = 0.93$).

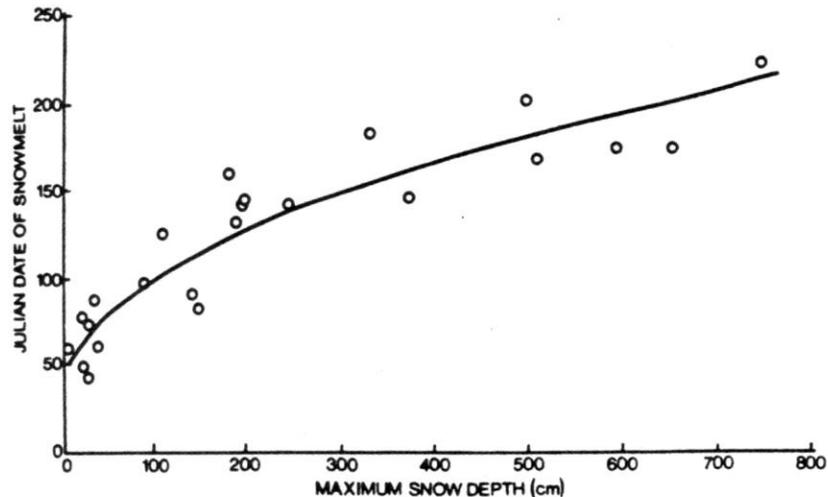


FIGURE 2.5 Relation between maximum snow depth and the date of snowmelt for nine U.S. Weather Bureau stations in the western Cascade Mountains of Washington. Data are for 1968, 1973, and 1974 (Julian date = $36.33 + 6.39 \text{ depth}^{-2}$, $r^2 = 0.86$).

The correlation of the Julian date for the beginning of the snow-free period against the maximum depth of snow is significant at the 0.01 level ($r^2 = 0.86$).

The hypothesized relation between the vegetational gradient represented by the y-axis of the ordination and available soil moisture was tested using measurements of plant moisture deficit (PMD), termed plant moisture stress (PMS) by Waring and Cleary (1967). Plant moisture deficit is the negative xylem sap pressure potential (Boyer 1967). A total of eight stands, representing various y-axis ordination values, was sampled for predawn PMD (Long 1976). The estimate of maximum seasonal predawn PMD for each stand was regressed against its corresponding y-axis ordination value (Figure 2.6). The regression is significant at the 0.01 level ($r^2 = 0.92$).

H. J. Andrews Experimental Forest, Oregon

The H. J. Andrews Experimental Forest ordinations yielded two primary gradients (Figure 2.1). We hypothesized that the x-axis represents highly divergent conditions along a complex moisture gradient, while the y-axis represents a thermal gradient.

In order to test hypothesized relations between forest community composition and environment, studies were concentrated in near-modal representative forest stands called *reference stands*. Within these stands environmental measurements were made. Sixteen of the twenty-three communities defined by

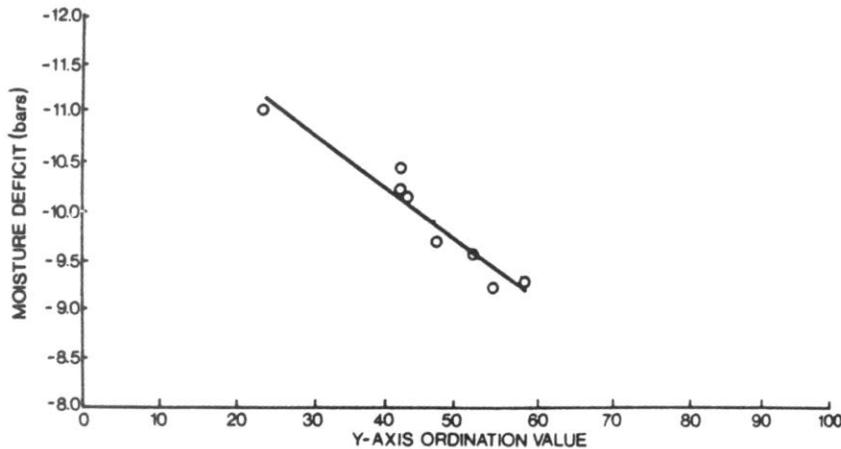


FIGURE 2.6 Relation between predawn PMD and the y-axis ordination value for individual stands ($PMD = 0.057Y - 12.52$, $r^2 = 0.92$).

ordination were chosen for intense analysis. Environmental measurements were made on small conifers, primarily Douglas-fir, western hemlock, and Pacific silver fir. Air and soil temperatures were recorded continuously for strata occupied by the foliage and roots of the understory trees. The moisture index used was PMD, and the predawn PMD was determined at the end of each growing season.

A temperature index for the growing season, called the *temperature growth index* (TGI), was determined from sapling phenology (Zobel et al. 1976) and a formula provided by Cleary and Waring (1969). The formula weighs temperature through its effect on Douglas-fir seedling production in controlled environments. The index yields a measure of growth conditions regulated by temperature. The TGI was summed up over the growing season for each site, and the growing season was defined as the period from conifer sapling budbreak to the date of the second fall frost. Subsequent studies (Chapter 3) set October 15 as the end of the growing season.

The PMD varied from 1970 to 1972 in response to changes in precipitation. Summers of 1970 and 1972 were dry, leading to high PMD values; however 1971 was relatively wet (Figure 2.7, Table 2.3). This test supported the hypothesis that at least in the lower *Tsuga heterophylla* and transition zones, the x-axis of the vegetation ordination corresponded to a moisture gradient. The PMD values of the *Abies amabilis* zone stands were measured in 1973 and 1974. The correlation of PMD with elevation is similar to that of the lower elevation zone, but the small number of samples resulted in nonsignificant regression coefficients.

The TGI in the reference stands showed considerable variation from 1971 to 1976 (Table 2.4). It was generally highest in 1973, particularly in the cooler stands, which had unusually late fall frosts. The relative positions of stands

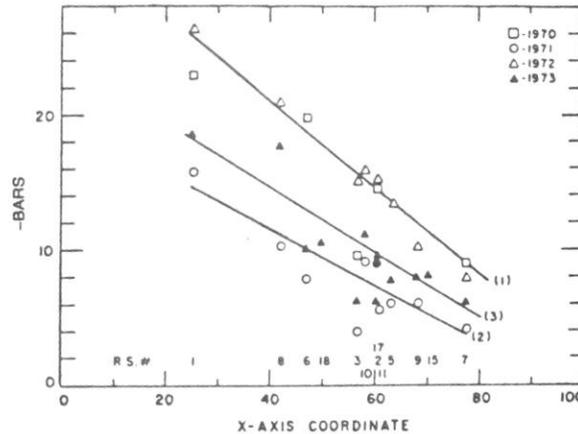


FIGURE 2.7 Relation of maximum yearly predawn PMD to position of the *Tsuga heterophylla* and transition zone communities on the x-axis of the vegetation ordination of Dyrness et al. (1974). The community represented by each reference stand is listed in Table 2.3. Linear regressions: (1) 1970 + 1972, $-Y = -33.96 + 0.319X$, $r^2 = 0.95$; (2) 1971 $-Y = -20.00 + 0.207X$, $r^2 = 0.83$; (3) 1973 $-Y = -24.31 + 0.241X$, $r^2 = 0.82$ (data from reference stand 3 were excluded from regression equations; from Zobel et al. 1976; copyright © 1976 by the Ecological Society of America).

from year to year remained similar; for example, correlation analysis yielded a coefficient of determination (r^2) of 0.98 ($n = 12$) for 1972 and r^2 of 0.96 ($n = 14$) for 1973. Communities in different vegetation zones were clearly separated by TGI in all years (Table 2.4). The differences among sites in unweighted temperature data were accentuated by TGI. Thus TGI is significantly correlated with elevation but there is great variation within elevational zones, indicating a temperature index other than that explained by elevation alone. This probably includes the effects of landform and aspect differences of the reference stands.

Distribution of species or communities along TGI and PMD gradients may reveal the fidelity with which either may be used to predict environmental variables if the predictions are made in the area where the correlations were made. Predictive value of some species may differ when they are found in different regions such as the central western Cascades and the Siskiyou Mountains (Zobel et al. 1976).

Most of the variation in community ordination in the H. J. Andrews Experimental Forest is associated with PMD and TGI gradients. Nutrient analysis of understory sapling needles taken in selected stands in early summer suggests that nutritional influences on community composition are important

TABLE 2.3 Characteristics of reference stands sampled by Zobel et al. (1976). Sample represents a 50- by 50-m area at each stand.

Zone	Reference stand no.	Community	Elevation (m)	Aspect	Slope (°)	Percent cover				
						Tree	Reproducing Shrub	Herb		
<i>Tsuga heterophylla</i>	1	<i>Pseudotsuga/Holodiscus</i>	510	SW	35	50	20	46	36	
	2	<i>Tsuga/Rhododendron-Berberis</i>	520	NW	20	105	10	30	24	
	6	<i>Tsuga/Castanopsis</i>	710	S	40	83	30	123	14	
	7	<i>Tsuga/Polystichum-Oxalis</i>	490	NW	18	110	42	17	41	
	8	<i>Pseudotsuga-Tsuga/Corylus</i>	500	W	40	81	25	64	27	
	9	<i>Tsuga/Acer/Polystichum</i>	490	WNW	45	100	35	72	48	
	10	<i>Tsuga/Rhododendron-Caulitheria</i>	670	SSW	5	89	60	118	7	
	11	<i>Pseudotsuga/Acer/Berberis</i>	1060	SSE	25	96	35	62	10	
	15	<i>Tsuga/Polystichum</i>	720	NW	45	108	43	14	18	
	16	<i>Tsuga/Castanopsis</i>	670	SW	40	107	48	108	7	
	17	<i>Tsuga/Rhododendron-Berberis</i>	530	NNW	18	102	47	43	37	
	Transition	3	<i>Tsuga-Abies/Linnaea</i>	950	SW	10	120	88	38	24
		5	<i>Tsuga-Abies/Rhododendron-Berberis</i>	920	N	8	90	27	125	5
		18	<i>Pseudotsuga/Acer/Whipplea</i>	1080	SE	30	81	24	92	23
	<i>Abies amabilis</i>	4	<i>Abies/Tiarella</i>	1440	SW	10	116	50	9	39
		12	<i>Abies/Vaccinium-Cornus</i>	1020	W	5	103	31	56	33
		13	<i>Abies/Clintonia</i>	1480	S	15	93	20	12	32
14		<i>Abies-Tsuga/Xerophyllum</i>	1570	NW	15	100	27	3	33	

TABLE 2.4 *Temperature growth index (TGI) for reference stands in 1971 through 1976.^a*

RD	1971	1972	1973	1974	1975	1976	Mean	SD
1	95	102	107	97	94	98	98.8	4.9
2	74	84	99	85	82	75	83.2	9.0
3	56	67	77	75	—	—	68.7	9.5
4	34	38	52	53	45	50	45.3	7.8
5	60	70	82	71	63	60	67.7	8.5
6	85	93	92	95	—	—	91.3	4.4
7	80	82	88	85	81	71	8.2	5.8
8	90	98	101	—	—	—	96.3	5.7
9	81	87	98	85	—	—	87.7	7.3
10	76	83	91	83	80	77	81.7	5.4
11	73	78	92	89	67	72	78.5	10.0
12	40	49	68	67	—	—	56.0	13.8
13	—	37	52	51	41	42	44.6	6.6
14	—	32	53	46	41	41	42.6	7.7
15	—	—	89	—	—	—	89.0	—
16	—	—	93	95	—	—	94.0	—
17	—	—	88	82	74	68	78.0	8.8
19	—	—	85	—	—	—	—	—

^aW.H. Emmingham, personal communication.

only in nitrogen-poor sites. The environmental field defined by PMD and TGI (Figure 2.8, Table 2.3) thus separates the plant communities in a useful manner. This illustrates the utility of TGI in separating various zones and PMD in arranging communities within at least the lower elevation and warmer zones. The array of plant communities (stands) generally supports the hypotheses of Dyness et al. (1974). The major difference is in the lack of sites with high PMD in the *Abies amabilis* zone. Such sites at high elevation are typically not forested, however, and no samples could be included from these sites.

SUMMARY AND CONCLUSIONS

Floristic gradients were constructed from two-dimensional ordination of plant communities in both the Cedar River watershed in Washington and the H. J. Andrews Experimental Forest in Oregon. In both sites there is a strong correlation between floristic gradients and environmental factors associated with elevation. In Washington the floristic gradient is apparently associated with a gradient in depth and duration of winter snowpack while in Oregon it is associated with a gradient in growing season TGI. The second floristic gradient in both the Cedar River watershed and the H. J. Andrews Experimental Forest is associated with a gradient in summer PMD, which was verified by predawn

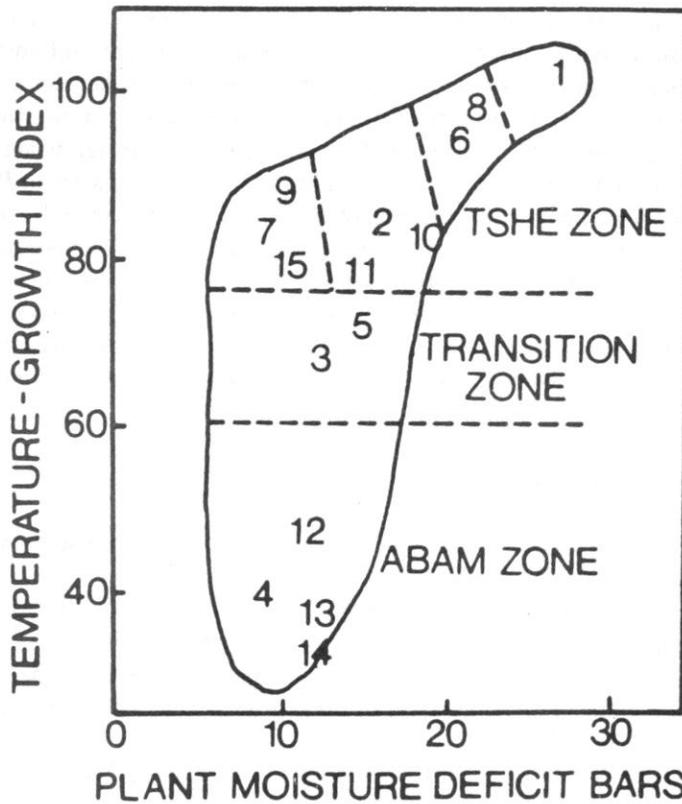


FIGURE 2.8 Position of reference stands in a two-dimensional environmental field. Temperature is represented by TGI computed by the method of Cleary and Waring (1969). Moisture is assessed as the late-summer predawn PMD of conifer saplings. Most data are for 1972. *Psme* = *Pseudotsuga menziesii*, *Tshe* = *Tsuga heterophylla*, *Abam* = *Abies amabilis*. The community represented by each reference stand number here is listed in Table 2.3 (after Zobel et al. 1976).

PMD measurements. At the Oregon site differences between vegetation zones are reflected in a temperature index, while within zones communities are distinguished by moisture deficits and to a lesser extent by temperature. In two cases in Oregon, vegetation differences appeared related to low needle nitrogen contents.

In further support of the classification scheme in Oregon, several investigations have provided evidence of gradient effects on producers, consumers, and decomposers; for example, Zobel et al. (1976) found that species diversity (the total number of vascular species) increased and dominance (Simpson's index) decreased toward either warmer-drier or colder communities. They also

found that dominance is concentrated in fewer strata of the vegetation on the colder sites. Wiens and Nussbaum (1975) found significant differences in population density and species composition within selected plant communities in their study of model estimation of energy flow in northwestern coniferous forest bird communities. Fogel and Cromack (1977) found significant differences in amounts and rates of decomposition of several size classes of *Pseudotsuga menziesii* litter within different plant communities (Chapter 7). Gholz et al. (1976) describe significant differences in productivity and biomass accumulation within several communities of the H. J. Andrews Experimental Forest. These studies tend to increase the utility of derived predictive models of terrestrial primary producer systems and the diversity of the studies makes interfacing with other major sections of the ecosystem studies more meaningful.

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