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RELATIONSHIPS OF ENVIRONMENT TO COMPOSITION, STRUCTURE, AND DIVERSITY OF FOREST COMMUNITIES OF THE CENTRAL WESTERN CASCADES OF OREGON[1]

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A bstruct. Temperature and moisture stress of conifer saplings and needle nitrogen content of conifer saplings were measured at reference stands representing 16 forest communities in the central portion of the western Cascades province of Oregon.

Most species occur over a wide range of temperature and moisture stress; many occupy a wider range of environments in the western Cascade than they do in the eastern Siskiyou Mountains of southwest Oregon. Differences between vegetation zones are reflected in a temperature index; within zones, communities are distinguished by moisture stress and, to a lesser extent, by temperature. In two cases vegetation differences appear to be related to low needle nitrogen contents. Use of complex gradients for vegetation ordination suggests certain environmental differences between communities which are contrary to the differences measured; therefore, we prefer the measured gradients over the complex gradients defined.

Species diversity (the total number of vascular species) increases and dominance (Simpson's index) decreases away from moderate environmental, conditions to warmer-drier and colder communities. Diversities of different strata are unrelated. Dominance is concentrated in fewer strata of the vegetation on the colder sites. However, discontinuities in the pattern of diversity with environment occur which are not related to major differences in our measured environmental indexes. Evergreenness of shrubs is highest in stands with the lowest foliar nitrogen levels.

Key words: Coniferous forest; diversity, vegetation; moisture stress, conifers; ordination, vegetation; Oregon; temperature stress, conifers.

INTRODUCTION

Studies of ecosystem characteristics and processes require some method of stratifying ecosystems and their subunits in all but the most homogeneous of areas. The intensity and timing of many ecosystem processes are in part determined by the type of vegetation. Because vegetation is such an important part of the ecosystem, and integrates the effect of the total environment (Billings 1952), changes in vegetation should be related to variability in many processes of interest. For these reasons a classification of forest communities was used as one of the major bases for stratifying the H. J. Andrews Experimental Forest, the Oregon Intensive Study Site of the Coniferous Forest Biome, US. International Biological Program. This forest classification for the central portion of the Western Cascades Province (Dyrness et al. 1974) was centered on the H. J. Andrews Experimental Forest and included an area 64 × 32 km in extent (Fig. 1). Along with their forest classification the authors included an interpretation of the major factors underlying the vegetational pattern. They believe that temperature differentiates vegetation zones, whereas intrazonal variation is thought to be primarily related to moisture stress.

A stratification system provided by vegetation analysis alone may not include all the information desired on environmental relationships. Plant communities may differ from ecosystem processes in their sensitivity to environmental factors, or they may react to factors not important to a particular process. To provide further data on the various stratification units in this area we made environmental measurements in selected stands representative of various forest communities. These measurements allow a firmer decision on how appropriate the vegetation units are as stratification units. They also allow a direct gradient analysis (Whittaker 1967) of the forest vegetation of this region, where we have observed environmental changes along a predefined vegetation gradient. This paper reports the environmental measurements made, and the gradients defined from them. We compared measured gradients with those inferred from the vegetation and from physiographic and edaphic conditions, and with

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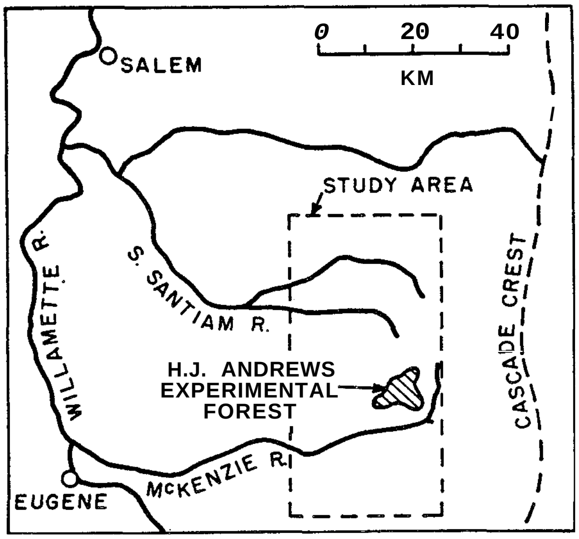

FIG. 1. Location of the study area in western Oregon.

gradients of vegetation composition, diversity, and structure; in this paper we present the relationship of the environmental patterns to distributions of species and of vegetation types. Comparisons are made with previous work of a similar nature, particularly that in mountainous western North America.

Vegetation data provided in Dyrness et al. (1974) include coverage only; tree dimensions and biomass for some communities we sampled were determined in separate studies, extensive in themselves, and will be reported elsewhere.

STUDY AREA

The western Cascades of Oregon are deeply dissected with generally well-developed soils on Tertiary volcanic substrates. Movement of moisture-laden air off the Pacific Ocean results in high precipitation, 2,000 to perhaps 4,000 mm annually in this area, and a relatively mild climate, although summers are very dry. Snow accumulates to great depths at higher elevations, but does not form a continuous cover over the lower slopes and valley bottoms. Dyrness et al. (1974) provide further climatic and edaphic data for the western Cascades, and Franklin and Dyrness (1973) place it in the overall context of the Pacific Northwest.

The forests of the western Cascades represent primarily two major vegetation zones: the *Tsuga heterophylla* zone (14 communities, 11 of them considered to be climax) and the *Abies amabilis* zone (9 communities, 7 of them climax). Dyrness et al. (1974) present individual plot data as well as summaries for each of the ,communities recognized. Stands of the three nonclimax units used in our study are almost all dominated by trees 100–150 yr-old, compared to > 300 yr for dominants of most stands of the climax communities. Four of the *Tsuga heterophylla* zone communities are considered transitional to the higher elevation *Abies amabilis* zone. In this paper, these are considered to represent a transition zone. Only one community is recognized which belongs to the *Tsuga mertensiana* zone of Franklin and Dyrness (1973), and Dyrness et al. (1974) include it in the *Abies amabilis* zone of this study. *Six* of the more important *Tsuga heterophylla* zone communities have also been described in Franklin and Dyrness (1973).

At lower elevations *Pseudotsuga menziesii* dominates most communities, and *Tsuga heterophylla* is the dominant reproducing tree on all but a few sites. In the *Abies amabilis* zone *Abies amabilis* accounts for most of the tree reproduction. Within zones community recognition is primarily dependent on shrubs and herbs. Most species are quite widely distributed, making shifts in species importance, rather than their presence, the basis for community differentiation except on the most extreme sites (Dyrness et al. 1974). The recognized forest communities are summarized in Table 1. Community names in the text include only genera; names on figures use four-letter abbreviations (Table 1). Nonforest vegetation and forests of the major alluvial areas are described in detail elsewhere, and are not included in this study (Hickman 1968, Hawk and Zobel 1974).

Relationships of vegetation units to environment inferred by Dyrness et al. (1974) are presented (Fig. 2) for comparison with our results. Dyrness et al. modified their original community ordinations, based on their intuition, to produce this figure. (However, our use of ordination coordinates from their work involves the original values produced by the ordinations; these coordinates were not determined from Fig. 2.)

From the vegetation classification 16 communities were chosen for further study. To include as many communities as possible in the sampling, only a single stand represented most communities (Table 2). (The two exceptions, *Tsuga/Rhododendron/Berberis* and *Tsuga/Castanopsis*, were sampled twice.) Such a stand was called a reference stand. Each reference stand was chosen, from among those areas sampled by Dyrness et al. (1974), to be close to modal in species composition and importance in the community it represented, thus hopefully eliminating stands nonrepresentative of, or transitional between, the community types recognized. The stands we used were chosen by C. T. Dyrness and J. F. Franklin after completion of their community classification. The only considerations used, besides being representative, were that stands should have reasonable accessibility and not be recently disturbed. These latter factors were not allowed to force use of non-

TABLE I. Forest communities recognized in the study area by Dyrness et al. (1974). NS = not sampled in this study

Community name	Abbreviation	NO. plots	Climax	Referemce stand no.
Tsuga heterophylla zone				
Pseudotsuga menziesii/Holodiscus discolor	Psme/Hodi	8	yes	*1*
Pseudotsuga menziesii-Tsuga heterophylla/Corylus cornuta	Psme-Tshe/Coco	15	yes	*8*
Tsuga heterophylla/Castanopsis *chrysophylla*	Tshe/Cach	16	yes	6, *16*
Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon	Tshe/Rhma/Gash	17	yes	*10*
Pseudotsuga menziesii/Acer circinatum/ Gaultheria shallon	Psme/Acci/Gash	13	no	NS
Tsuga heterophylla/Rhododendron *macrophyllum/Berberis nervosa*	Tshe/Rhma/Bene	18	yes	*2, 17*
Pseudotsuga menziesii/Acer circinatum/ Berberis nervosa	Psme/Acci/Bene	14	no	*11*
Tsuga heterophylla-Acer circinatum/ Polystichum munitum	Tshe/Acci/Pomu	12	yes	*9*
Tsuga heterophylla/Polystichum munitum	Tshe/Pomu	15	yes	*15*
Tsuga heterophylla/Polystichum munitum-Oxalis oregana	Tshe/Pomu-Oxor	8	yes	*7*
Transition zone				
Tsuga heterophylla-Abies amabilis/ Rhododendron macrophyllum/Berberis nervosa	Tshe-Abam/Rhma/ Bene	22	yes	*5*
Tsuga heterophylla-Abies ***amabilis/*** *Rhododendron macrophyllum/Linnaea borealis*	Tshe-Abam/Rhma/ Libo	12	yes	NS
Tsuga heterophylla-Abies ***amabilis/*** *Linnaea borealis*	Tshe-Abam/Libo	21	yes	*3*
Pseudotsuga menziesii/Acer ***circinatum/*** *Whipplea modesta*	Psme/Acci/Whmo	11	no	*18*
Abies ***amabilis*** zone				
Abies amabilis-Tsuga mertensiana/ Xerophyllum tenax	Abam-Tsme/Xete	8	yes	*14*
Abies ***amabilis/Vaccinium*** *membranaceum/ Xerophyllum tenax*	Abam/Vame/Xete	9	yes	NS
Abies amabilis/Rhododendron macrophyllum-Vaccinium alaskense/Cornus canadensis	Abam/Rhma-Vaal/ Coca	11	yes	NS
Abies amabilis/Vaccinium alaskense/ Cornus canadensis	Abam/Vaal/Coca	8	yes	*12*
Abies procera/Achlys triphylla	Abpr/Actr	6	no	NS
Abies ***amabilis/Achlys triphylla***	Abam/Actr	13	yes	NS
Abies procera/Clintonia uniflora	Abpr/Clun	7	no	13
Abies ***amabilis/Tiarella*** *unifoliata*	Abam/Tiun	12	yes	*4*
Chamaecyparis nootkatensis/Oplopanax horridum	Chno/Opho	7	yes	NS

representative stands. Vegetation data for the individual reference stands, and for the communities which they represent, are available from *the* National Auxiliary Publication Service.[3] Site characteristics for reference stands are given in Table 2.

The environmental characteristics as measured on the reference stands should describe the variation within the study area well. However, a measured difference between two communities surely includes variability induced by the exact choice of sample stands, and thus may not represent the average difference between the communities.

All except two reference stands were located on or immediately adjacent to the H. J. Andrews Experimental Forest; stands 13 and 14 were located at the Wildcat Mountain Research Natural Area, 7.5 km north-northwest of the center of the H. J. Andrews, in communities not well-represented on the H. J. Andrews Forest.

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[3] See NAPS document No. 02800 for 12 pages of supplementary material. Order from ASIS/NAPS c/o Microfiche Publications, 440 Park Ave- South, New York, N.Y. 10016. Remit in advance for each NAPS accession number $3.00 for microfiche or $5.00 for photocopies. Make checks payable to Microfiche Publications. Outside of the USA and Canada, postage is $2.00 for a photocopy or $1.00 for a fiche.

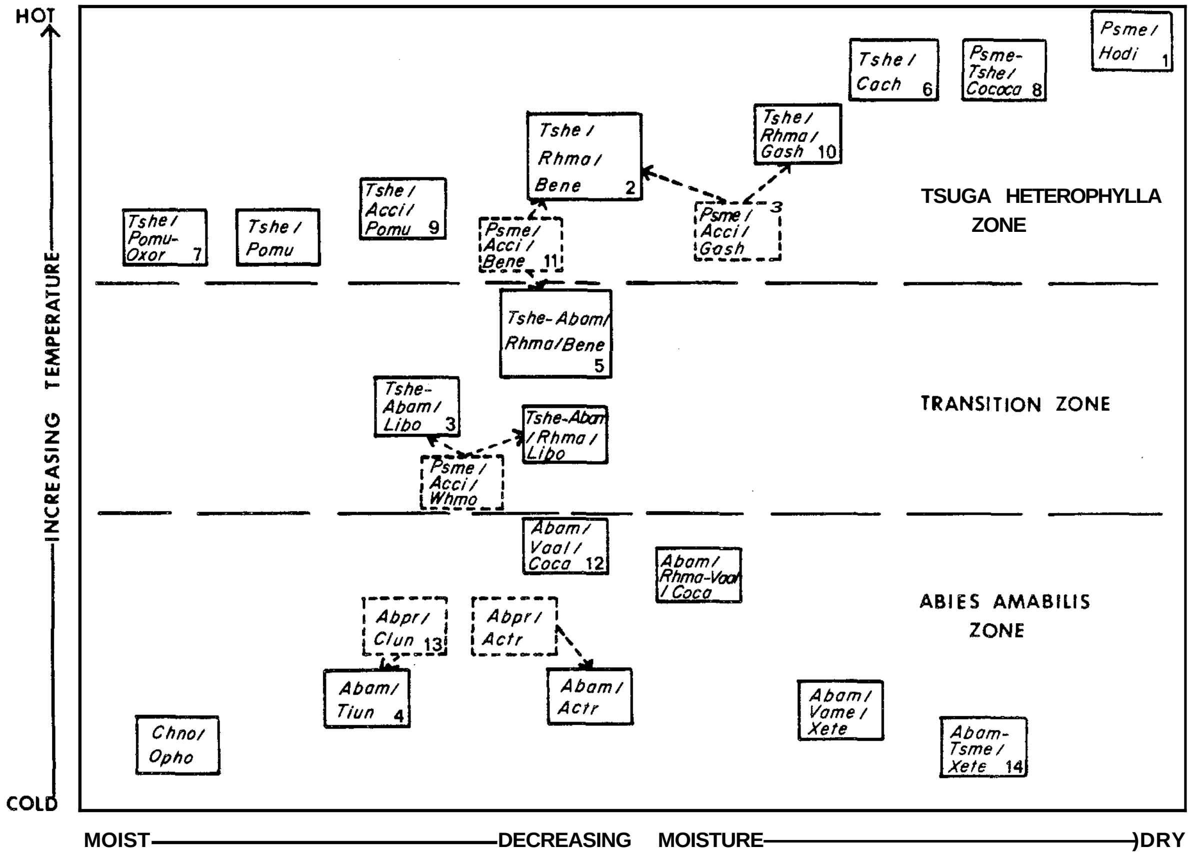


FIG. 2. Hypothesized relationships between forest communities and environment in the central western Cascades (Dyrness et al. 1974: Fig. 5). This figure is based on their vegetation ordination, somewhat modified by the intuition of the investigators. Communities enclosed with dashed borders are considered to be seral, the others, *to* be climax. Communities sampled in this study are identified by the reference stand number in the box. Abbreviations for communities are identified in Table 1.

MEASUREMENT OF ENVIRONMENTAL INDEXES

Methods

The environmental measurements we made were related to small conifer saplings in order to quantify the environment as integrated by trees of this size. Indexes of moisture and mineral nutrient availability were determined by direct measurements of plant moisture stress and needle nutrient content, respectively. Air and soil temperature were measured for major strata occupied by foliage and roots of these understory trees. The length of the summary season for the temperature index was partially determined by sapling phenology.

Temperature was measured continuously at one site in each reference stand, using a two-pen 30-day thermograph. Air temperature was taken at 1 m under an insulated A-frame shield which shaded the probe. The soil temperature probe was buried nearby at a depth of 20 cm. Air temperatures were digitized and each daily maximum, minimum, and mean was computed. Separate means were computed for daylight and night. Daylength for the 15th of each month was used to determine the day and night summation periods. Average daily soil temperatures were read from the charts manually. Monthly means, seasonal extremes, and other data were determined as needed.

In August 1933 soil temperature at 20 cm was measured at 11 points in each stand in order to assess how representative the sampling point was. One measurement was at the site of the thermograph probe, the others at the base of 1–3-m conifer saplings. Means for each stand were computed and compared with the measurement at the thermograph probe.

A temperature summing formula was used which weights temperatures by their effect on production of seedlings of *Pseudotsuga menziesii* in controlled environments (Cleary and Waring 1969). This calculates an index originally called "Optimum Temperature Days" which has been renamed Temperature Growth Index (TGI) by its originators. Average soil and daylight air temperature were used to compute the index for each day, and the daily

TABLE 2. Characteristics of reference stands sampled. Percent cover is for a 50 x 50-m area at each stand. Specific names of plants in the community names are given in Table 1

						Percent cover			
						Tree			
Zone	Reference stand no.	Community	Elevation (m)	Aspect	Slope (°)	Mature	Reproducina	Shrub	Herb
Tsuga heterophylla	1	*Pseudotsuga/Holodiscus*	510	SW	35	50	20	46	36
	2	*Tsuga/Rhododendron/Berberis*	520	NW	20	105	10	30	24
	6	*Tsuga/Castanopsis*	710	S	40	83	30	123	14
	7	*Tsuga/Polystichum-Oxalis*	490	NW	18	110	42	17	41
	8	*Pseudotsuga-Tsuga/Corylus*	500	W	40	81	25	64	27
	9	*Tsuga/Acer/Polystichum*	490	WNW	45	100	35	72	48
	10	*Tsuga/Rhododendron/ Gaultheria*	670	SSW	5	89	60	118	7
	11	*Pseudotsuga/Acer/Berberis*	1,060	SSE	25	96	35	62	10
	15	*Tsuga/Polystichum*	720	NW	45	108	43	14	18
	16	*Tsuga/Castanopsis*	670	SW	40	107	48	108	7
	17	*Tsuga/Rhododendron/ Berberis*	530	NNW	18	102	47	43	37
Transition	3	*Tsuga-Abies/Linnaea*	950	SW	10	120	88	38	24
	5	*Tsuga-Abies/Rhododendron/ Berberis*	920	N	8	90	27	125	5
	18	*Pseudotsuga/Acer/Whipplea*	1,080	SE	30	81	24	92	23
Abies amabilis	4	*Abies/Tiarella*	1,440	SW	10	116	50	9	39
	12	*Abies/Vaccinium/Cornus*	1,020	W	5	103	31	56	33
	13	*Abies/Clintonia*	1,480	S	15	93	20	12	32
	14	*Abies-Tsuga/Xerophyllum*	1,570	NW	15	100	27	3	33

indexes were summed over a growing season to obtain TGI. The definition of growing season in this study was from the date of budbreak of conifer saplings (A. McKee, *personal observations)* to the date of the second frost in the fall-

The moisture index used was Plant Moisture Stress (PMS), the reading of the pressure chamber (Scholander et al. 1965). Twigs of understory conifers were sampled before dawn near the end of the growing season (Waring and Cleary 1967). The PMS was determined on 4-6 trees at each reference stand, and was measured at least twice each season from 1970 to 1973. The highest average PMS for each reference stand for the several dates was the index for a given yeas. All measurements were made between midnight and dawn, At this time PMS should be at or near its minimum value, which is limited by the soil moisture conditions around the root system (Waring and Cleasy 1967). PMS is given in bars, and is the negative of the pressure potential of the xylem sap (Boyer 1967) Diurnal patterns of PMS were determined for contrasting sites in midsummer of 1970 and 1971.

Needle samples were collected for nutrient analysis from 1-yr-old needles of four to six understory conifers at selected reference stands in early summer. The nutrient stress on these needles should be the greatest at this time (Krueger 1967), Waring and Youngberg 1972). Samples were oven-dried at 70°C and stored in sealed containers until analysis. Nitrogen analyses were done by the Oregon State University Forestry Research Laboratory, using a, micro-Kjeldahl procedure.

Early results of this investigation are presented by Zobel et all. (1974)

Results and discussion

Temperature variation in time and space. Air temperature showed a definite July–August peak, considerably above both June and September levels (Fig. 3). Soil temperatures usually peaked in August (Fig. 4); their rise and decline was less precipitous than that of air temperature except on sites with late *snow* melt (as at the *Abies-Tsuga/Xerophyllum* stand in 1972).

Minimum air temperatures were relatively mild except in early December 1972 when record low temperatures of *-26°C* occurred at Eugene and Salem, Oregon, in *the* Willamette Valley; east of the Cascades, low temperatures were about -34°C. At that time low temperatures at our thermographs ranged from -16° to -22°C, well above the valley temperatures and the -27° to -29°C recorded with similar instruments at 1,100 m on the east flank of the high Cascades. In 1973 minima ranged from -7° to -9°C at lower elevations to -17°C at reference stand 14. The length of the frostless season within the area varied by a factor of about two, from 90 to 182 days in 1972, and from 130 to 286 days in 1973 when the first frost occurred as late as December on some sites. Extended soil freezing at 20 cm occurred

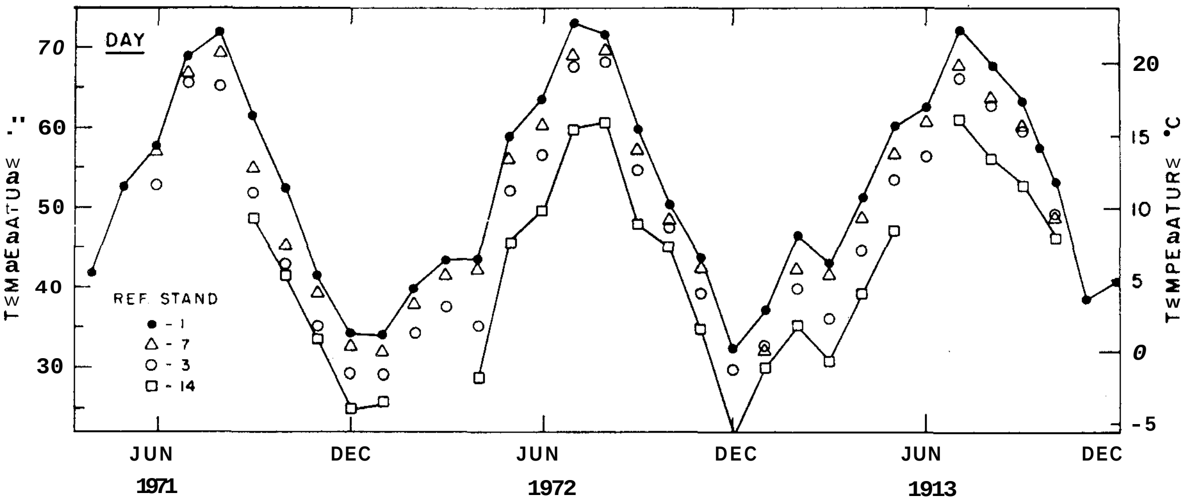


FIG. 3. Monthly averages of daytime air temperature at the *Pseudotsuga/Holodiscus* (reference stand I), *Tsuga/Polystichum-Oxalis (7)*, *Tsuga-Abies/Linnaea (3)*, and *Abies-Tsuga/Xerophyllum (14)* sites, representing most of the variability found in the study.

only in the winter of 1971-1972. One transition zone community (*Tsuga-Abies/Linnaea)* had soil at or below 0°C for 139 days, while at three *Abies amabilis* zone stands, it lasted 153, 137, and 213 days. Soil freezing in the *Tsuga heterophylla* zone communities did not exceed 31 days, and did not occur at most reference stands.

Annual maxima of air temperatures usually exceeded 38°C on the warmer sites; at reference stands 13 and 14 in 1973 they never exceeded 27°C.

Data from weather stations (Baker 1944) reveal a low July temperature lapse rate on the west slope of the Oregon Cascades, -0.42°C/100 m, compared to -0.64 for the mountainous western U.S. in general. Our data confirmed this low lapse rate up to about 1,100 m (Table 3). Night temperatures showed no significant decrease with elevation, and the minima actually increased up to 1,100 m, resulting in a mid-elevation thermal belt. Above 1,050 m the decline in temperatures was more rapid, although night temperatures dropped less with elevation than those during the day (Table 3). These temperature inversions probably arise partially from cold-air drainage. They may also result from advection from the more continental climate east of the crest of the Cascades. Steady, warm, dry east winds have been observed at higher elevations during some of the more extreme temperature inversions. January lapse rates were similar for both day and night temperatures, although the rates were considerably different in 1972 and 1973 (Table 3).

There is considerable variability in temperature at

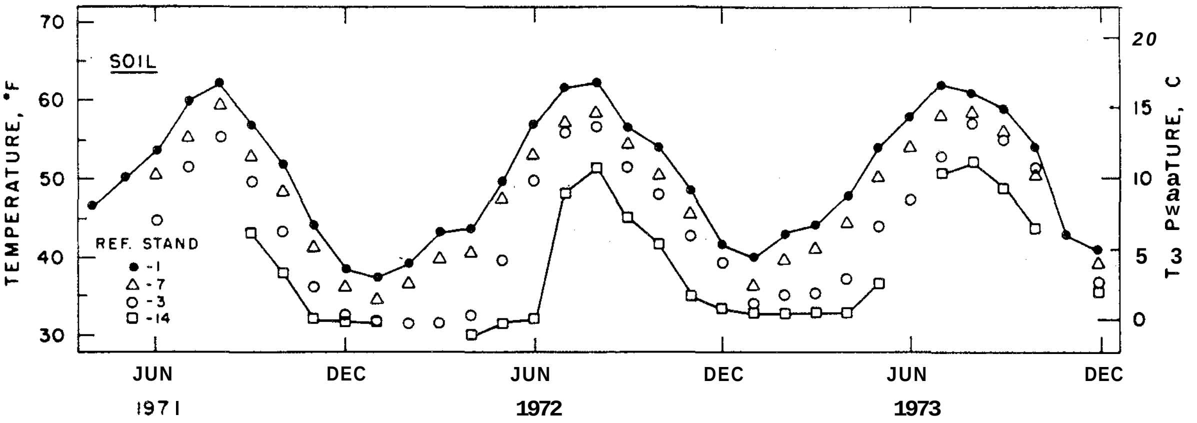


FIG. 4. Monthly averages of soil temperature at the *Pseudotsuga/Holodiscus* (reference stand I), *Tsuga/Polystichum-Oxalis (7), Tsuga-Abies/Linnaea (3),* and *Abies-Tsuga/Xerophyllum (14)* sites, representing most of the variability found in the study.

Table 3. Temperature changes (°C/100 m) with elevation on the study area. Two sites at lower elevations, adjacent to the H. J. Andrews Forest, are included in the data. Significant correlation of temperature with elevation at 0.05 and 0.01 levels are designated by the symbols * and **, respectively

	July					January	
	Below 1,100 m			Above 1,050 m		Below 1,100 m	
	1971	1972	1973	1942	1973	1972	1973
No. samples	11	16	16	5	6	9	17
Mean day	–0.26	–0.33**	–0.28*	–0.80*	–0.71*	–0.43**	–0.24*
Mean night	–0.09	-0.09	–0.17	–0.46	–0.40	-0.37**	-0.18*
Mean max	–0.38*	–0.54**	–0.54**	–1.13*	–0.98**	–0.46*	–0.22*
Mean min	+0.16	+0.18	+0.06	–0.47	–0.21	–0.28**	–0.24**
Mean range	–0.54**	–0.73**	–0.61**	–0.65*	–0.79*	–0.18	+0.02
Mean soil	–0.28	–0.47**	–0.37	–0.67	–0.43	–0.34*	–0.21**

a given elevation. For example, the seven stands with elevations ≈ 500 m had the following temperature ranges in July 1972: absolute minimum, 3-8°C; absolute maximum, 31-40°C; and daytime mean, 19–23°C.

Baker (1944) also noted a 18°C diurnal temperature variation in July for our region, which he said changed little with elevation. Our summer diurnal range approached this figure only at low elevations, and it declined 0.54°C or more per 100 m over all elevations (Table 3) Winter diurnal range was about 3-6°C; it showed little change with elevation (Table 3).

Variability within stands could lead to serious anomalies in our data if the sampling point were not representative. However, soil temperatures measured throughout the stand generally compared fairly well with those measured at the probe. On only 5 of the 18 reference stands did soil temperature at the probe site in August 1973 differ by more than 1.0°C from the mean of 11 points in the stand, and all were within 2°C of the mean. Means for the stand were almost always lower than the temperature at the probe. Correlation between soil temperature at the thermograph site and stand soil temperature mean was r =0.94.

Values for stands within the same vegetation type would also be expected to vary. We replicated only two communities, *Tsuga/Rhododendron/Berberis,* and *Tsuga/Casianopsis,* each at two sites (Table 1). Monthly averages of air and soil temperatures varied up to 2.2°C between replicate stands of the same community (Table 4). The temperature relationship reversed itself with season in most cases. For example, in April stand 2 was 1.1°C cooler than stand 17: in October it was 1.7°C warmer. The pattern of difference between replicate reference stands was not the same for soil temperature as for air temperature with stands 6 and 16; between stands 2 and 17 soil and air temperature varied in a parallel fashion.

Temperature growth index. Temperature growth index (TGI) at the reference stands varied considerably during 1971 to 1973 (Table 5). In 1973 the index was higher than for the other 2 yr, especially at the cooler sites, due to unusually late fall frosts. However, the relative positions of communities were similar from year to year. Correlation analysis of TGI of individual stands in 1971 with that in 1972 gave a coefficient of determination (r2) of 0.98 (n = 12) ;the comparison of 1972 TGI with TGI in 1974 had r^2 = 0.96 (n = 14).

Communities sampled in the different vegetation zones are clearly separated by TGI in all 3 yr (Table 5). However, variability in TGI does not correspond particularly well with vegetational changes within the Tsuga heterophylla and transition zones (Fig. 5). A major cause of the poor relationship between TGI and the Y-axis Coordinate is the position of reference stands 6 and 10; for the other stands, TGI generally decreases as the Y-coordinate increases, with a similar pattern repeated for the 3 yr represented in Fig. 5. A possible cause for the failure of stands 6 and 10 to conform to the general relationship is presented in the section on foliar nutrition.

Use of TGI accentuates the differences among sites seen in unweighted temperature data. There is rela-

TABLE 4. Differences between monthly means of day air temperature and soil temperature in replicate reference stands representing the same community. Data are for July 1972 through December 1973. Stands 2 and 17 represent the *Tsuga/Rhododendron/Berberis* community; stands 6 and 16 represent the *Tsuga/Castanopsis* community

	Day air temperature (°C)		Soil temperature (°C)	
Reference stand	(2-17)	(6-16)	(2-17)	(6-16)
Mean difference	+0.41	+0.91	+0.58	–0.23
Range of monthly differences	–1.9 to +1.9	–0.1 to +2.2	–1.3 to +1.7	–1.6 to +0.9

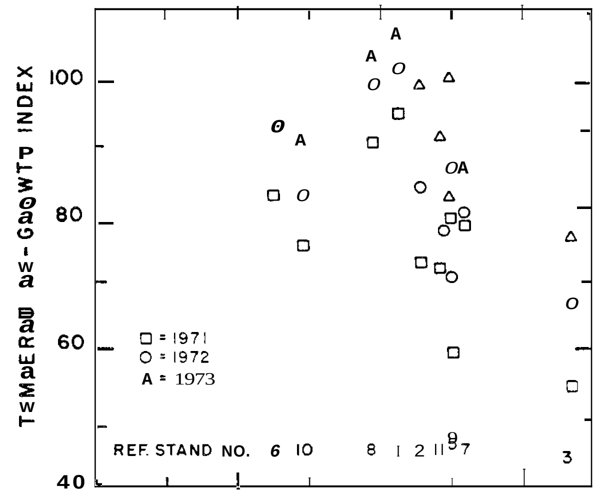


FIG. 5. Relationship of Temperature Growth Index of reference stands and the y-axis coordinate of the community the stands represent in a vegetation ordination, for *Tsuga heterophylla* zone and transitional communities. Communities represented by the reference stands are identified in Table 2.

tively more variation within elevational zones and the overall rate of decline with increasing elevation is considerably greater than any lapse rate for mean temperature. Although TGI is significantly correlated with plot elevation ($r^2 = 0.74$, 0.86, and 0.84 for 1971, 1972, and 1973), there is considerable variability within elevational zones, enough to justify use of a temperature index other than elevation itself. For example, vegetation at reference stand 12 at 1,020 m placed it in the *Abies amabilis* zone, whereas stand 11 at 1,060 m was in the *Tsuga heterophylla* zone. The TGI values conform to the zone determined by the vegetation and do not overlap (Table 5).

The large change in TGI from the transition to the *Abies amabilis* zone stands appears to be due partially to the steeper lapse rate at higher elevations, as well as possibly to sampling idiosyncracies. Another large environmental change seems to occur below the highest elevation stand in the study. The ***Abies-Tsuga/Xerophyllum*** community there would be placed into the *Tsuga mertensiana* zone in a regional of any of our sample sites. This situation may be analogous to southern British Columbia where snow accumulation increases and species composition changes abruptly above a certain elevation, with the loss of *Tsuga heterophylla* and *Pseudotsuga menziesii* (Brooke et al. 1970); this same shift in tree composition occurs from our *Abies/Clintonia* to the *Abies-Tsuga/Xerophyllum* stand.

At the replicate stands of the *Tsuga/Castanopsis* community (stands 6 and 16) the 1973 TGI differed only by 1 unit, despite the relatively larger differences in air and soil temperature means (Table 4). How-

TABLE 5. Temperature growth index (TGI) for reference stands in 1971 to 1973

Vegetation zone	Reference stand no.	Plant community	TGI 1971	TGI 1972	TGI 1973
Tsuga heterophylla	1	*Pseudotsuga/Holodiscus*	95	102	107
	2	*Tsuga/Rhododendron/Berberis*	74	84	99
	6	*Tsuga/Castanopsis*	85	93	92
	7	*Tsuga/Polystichum-Oxalis*	80	82	88
	8	*Pseudotsuga-Tsuga/Corylus*	90	98	101
	9	*Tsuga/Acer/Polystichum*	81	87	98
	10	*Tsuga/Rhododendron/Gaultheria*	76	83	91
	11	*Pseudotsuga/Acer/Berberis*	73	78	92
	15	*Tsuga/Polystichum*			89
	16	*Tsuga/Castanopsis*			93
	17	*Tsuga/Rhododendron/Berberis*			88
		Zone average	82	88	94
Transition	3	*Tsuga-Abies/Linnaea*	56	67	77
	5	*Tsuga-Abies/Rhododendron/Berberis*	60	70	82
		Zone average	58	69	80
Abies amabilis	4	*Abies/Tiarella*	34	38	52
	12	*Abies/Vaccinium/Cornus*	40	49	68
	13	*Abies/Clintonia*		37	52
	14	*Abies-Tsuga/Xerophyllum*		32	53
		Zone average	36	39	56

ever, the replicates of *Tsuga/Rhododendron/Berberis* (stands 2 and 17) had a TGI difference of 11 units. Much of this difference is attributable to a local late occurrence of fall frost at stand 2, allowing it 28 more days during which TGI units were accumulated.

Plant moisture stress. Rainfall during the four summers in which plant moisture stress was measured varied considerably. Summers of 1970 and 1972 were quite dry, leading to similarly high PMS levels late in the season. 1971 was relatively wet, with no dry spell longer than *3* wk. In 1973, although there was little precipitation and very low streamflows, there were only intermediate levels of moisture stress.

Dyrness et al. (1974) believe that the X-axis of their vegetation ordination represents a moisture gradient. X-axis coordinates from the ordination of *Tsuga heterophylla* zone and transition zone communitied correspond well with the late summer predawn PMS measured on the reference stands which represent them, especially in the driest years (Fig. 6). The only major exceptions to this are the *Tsuga-Abies/Linnaea* (stand 3) in 1970, 1971, and 1973, and the *Pseudotsugu/Acer/Berberis* (stand 11) in 1973. Both have PMS 3-6 bars below that predicted Prom their X-axis position in these years. These sites are within 1.4 km of each other, in different soil types and geologic substrates than the other reference stands compared in Fig. 6. The lower moisture stress at the *Tsuga-Abies/Linnaea* stand may reflect shading of the very dense tree canopy (Table 2). The *Pseudotsuga/Acer/Berberis* site is one of only two reference stands with an easterly aspect. A ridge rises rather steeply to the west, which may reduce after noon heating and evaporative stress somewhat. The only other east-trending slope is at the *Pseudotsuga/Acer/ Whippkea* site, which is below the regression line also. The *Tsuga-Abies/Linnaea* stand fit the regression (Fig. 6) in 1972, but this was immediately after salvage logging within *70* m west of the plot. The lower PMS level exhibited by this site during the other **3** yr is considered more characteristic of the community. Despite these exceptions the X-axis of the *Tsuga heterophylla* zone ordination is well-correlated with the influence of moisture on conifer saplings. This is a welcome contrast to many ordination axes, which are not interpretable directly in terms of environment in the field (Whittaker *1967).*

The PMS at all four reference stands in the *Abies amabilis* zone was measured only in 1973. The PMS varied only from 6.1 to 9.2 bars, but a correlation with the X-axis is present ($r^2=0.79$), similar to that in the lower zones. However, the regression coefficient of PMS on the X-coordinate is only -0.07 (not significant with the small sample), compared to -0.21 to -0.3% for the Iower zones.

The PMS was measured on different species at different stands, contributing a possible source of error. However, where two species were compared on the same sites, there. was no consistent difference betweem species, and use of different species appears to contribute no systematic error to the data (A. McKee and G.M. Hawk, *unpublished observations)*

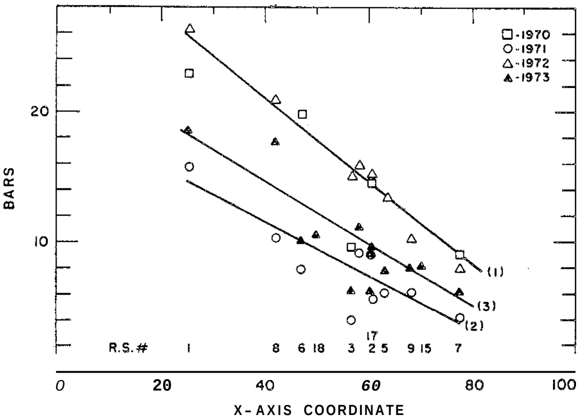


FIG. *6*. Relationship of maximum yearly predawn moisture stress to position of the Tsuga heterophylla and transition zone communities on the x-axis of the vegetation ordination of Dyrness et al. (1974). The community represented by each reference stand (R.S.) is listed in Table 2. Linear regressions: (1) 1970 + 1972-Y = -33.96 f 0.319 X, r2= 0.95, (2) 1971-Y =-20.00 -/- 0.207 X9 r2 = 0.83; (3) 1973--Y = -24.31 + 0.241 x, r2 = 0.82. (Data from reference stand 3 were excluded from the regression equations.)

The diurnal course of plant moisture :tress was followed on several days in 1970 and 1971. Maximum stress reached on clear, warm days was 6–10 bars drier than the predawn stress.

Plant moisture stresses have been measured similarly elsewhere in Oregon. The range of PMS sampled in the eastern Siskiyou Mountains, during 1967 (Waring 1969) was very similar to that of 1970 and 1972 on the H. J. Andrews Forest. In the South Umpqua Basin of the Oregon Cascades, communities varied from < 3 to 21 bars PMS in 1969 (Minore 1972), which was a somewhat moister year than 1970 and 1972 in this region, In the central western Cascades river terraces and open rocky slopes at high elevations support *Abies grandis* sapling populations which frequently have PMS more severe than the driest H. J. Andrews community (Zobel 1974, 19759.

Foliar nutrition. Foliar nutrient content varied with species, time of year and site. Sampling was not intensive enough to allow all communities to be ordered by nutrition, as they were by TGI or PMS. However, it did reveal certain stands to have very low foliar nitrogen contents.

Site differences in nutrient availability should be clearest following bud burst, when I-yr-old leaves lose some of their nutrients to developing shoots (Krueger

TABLE 6. Foliar nitrogen content following budbreak in 1971. Measurements were on needles produced in 1970. NA = budbreak dates were very late but were not observed

Reference stand	Community	Species	No. trees	Date	Days after bud-break	Percent N Mean	Percent N Range
6	Tshe/Cach	Psme	3	21 Jun.	33	0.68	0.65–0.72
I	Psme/Hodi	Psme	4	21 Jun.	33	0.87	0.85–0.91
8	Psme-Tshe/Coca	Psme	4	21 Jun.	33	0.87	0.78–1.00
6	Tshe/Cach	Tshe	3	21 Jun.	24	0.64	0.60–0.71
10	Tshe/Rhma/Gash	Tshe	4	23 Jun.	26	0.79	0.68–0.86
9	Tshe/Acci/Pomu	Tshe	4	21 Jun	17	0.86	0.75–0.99
2	Tshe/Rhma/Bene	Tshe	4	23 Jun.	19	0.86	0.81–0.92
7	Tshe/Pomu-Oxor	Tshe	4	23 Jun.	27	0.87	0.78–0.92
5	Tshe-Abam/Rhma/Bene	Tshe	4	23 Jun.	13	0.87	0.80–0.92
3	Tshe-Abam/Libo	Tshe	3	27 Jul.	33	1.24	1.16–1.39
12	Abam/Vaal/Coca	Abam	4	19 Jul.	NA	0.96	0.84–1.04
4	Abam/Tiun	Abam	4	22 Jul.	NA	0.99	0.95–1.04
14	Abam-Tsme/Xete	Abam	4	23 Aug.	NA	1.01	0.98–1.03
13	Abpr/Clun	Abam	4	23 Aug.	NA	1.05	0.95–1.11
3	Tshe-Abam/Libo	Abam	3	27 Jul.	33	1.13	1.04–1.19

19673, Waring and Youngberg 1972). Foliar nitrogen content of *Tsuga heterophylla* and *Pseudotsuga* averaged 0.86% or 0.87% at this time at several sites. The exceptions were the *Pseudotsuga/Holodiscus, Tsuga/Castanopsis,* and *Tsuga/Rhododendron/Gaultheria* communities, (stands I 6, and 10) with lower concentrations, and the *Tsuga-Abies/Linnaea* site (stand *3),* with higher nitrogen (Table 6). *Tsuga heterophylla* and *Pseudotsuga* were sampled only in the *Tsuga/Castanopsis* community; there, nitrogen contents of the two species were similar (Table 6). Foliar nitrogen levels of *Pseudotsuga* determined in this study are below most of those determined in previous foliar analyses (Krueger 1967a, van den Driessche 1969, Lavender 1970, Waring and Youngberg 1972).

The low foliar nitrogen content of Tsuga at the *Tsuga/Castanopsis* and *Tsuga/Rhododendron/Gaultheria* stands is reflected in the position of these stands on the vegetation-temperature correlation (Fig. 5). Their poor nutritional status may very well explain vegetational Y-coordinate values for these stands well below what would be expected from their TGI.

SPECIES DISTRIBUTION IN RELATION TO ENVIRONMENT

Many studies of vegetation and environment have as their objective the construction of relationships which will allow the environment (or timber site quality, or the most appropriate tree species to plant,

TABLE 7. Distribution patterns of tree species in the study area, with limits of Temperature Growth Index (TGI) and Plant Moisture Stress (PMS) in the communities studied. Other distribution refers to the occurrence of the species with importance less than that in its center of importance

Species	Mature (M) or reproduction (R)	Center of importance	Other distribution	Limits of TGI Min	Limits of TGI Max	Limits of PMS Min	Limits of PMS Max
Arbutus menziesii	M + R	Hot-dry		93	----	20	----
Libocedrus decurrens	M	Hot-dry	Moderate	78	----	10	----
Libocedrus decurrens	R	Hot-dry		83	----	17	----
Pinus lambertiana	M + R	Hot-dry		83	----	17	----
Acer macrophyllum	M	Hot-dry + Moderate		78	----	All	
Acer macrophyllum	R		Hot-dry + Moderate	75	----	10	----
Pseudotsuga menziesii	M	Hot-dry + Moderate	All	All		All	
Pseudotsuga menziesii	R	Hot-dry	Cold	(38)87	----	(8)17	----
Thuja plicata	M	Moderate	Cold + Med. Hot-dry	38	98	----	21
Thuja plicata	R	Moderate	Med. Hot-dry	67	98	----	21
Tsuga heterophylla	M + R	Moderate to Cool	All except extremes	38	98	----	21
Abies grandis	M		Moderate to cold		82	----	10
Abies grandis	R		Moderate	67	83	10	18
Abies procera	M	Cold	Moderate		72	----	17
Abies procera	R		Moderate to cold	37	78	9	18
Abies amabilis	M	Cold	Moderate	----	84	----	17
Abies amabilis	R	Cold	Moderate		78	---	18
Tsuga mertensiana	M + R	Cold		----	38	9	10

TABLE 8. Distribution patterns of shrub and herb species, central part of western Cascades, with limits of TGI and PMS in the communities studied. Species of little importance in any community are excluded

				Limits of			
				TGI		PMS	
Group	species	Center of importance	Other distribution	Min	Max	Min	Max
1	*Lathyrus polyphyllus*	Hot-dry	None	98	----	21	----
	Madia gracilis	Hot-dry	None	98	----	21	----
	Rhus diversiloha	Hot-dry	None	93	----	20	----
	Collomia heterophylla	Hot-dry	None	93	----	20	----
	Holodiscus discolor	Hot-dry	None	73	----	18	----
	Lonicera ciliosa	Hot-dry	None	83	----	(9)20	----
2	*Whipplea modesta*	Hot-dry	Moderate	67	----	10	----
	Synthris reniformis	Hot-dry	Moderate	67	----	10	----
	Corylus cornuta	Hot-dry	Moderate	67	----	All	
	Iris tenax	Hot-dry	Moderate	73	----	10	----
	Festuca occidentalis	Hot-dry	Moderate	73	----	10	-
3	*Berberis nervosa*	Hot, Dry + Moderate	All	38	----	All	
	Linnaea borealis	Hot, Dry + Moderate	All	38	----	All	
	Taxus brevifolia	Hot, Dry + Moderate	All	38	----	All	
	Acer circinatum	Hot, Dry + Moderate	All	All		All	
4	*Gaultheria shallon*	Medium hot, Dry	Moderate + Hot	67	----	9	----
	Castanopsis chrysophylla	Medium hot, Dry	Moderate + Hot	49	----	All	
	Cornus nuttallii	Medium hot, Dry	Moderate + Hot	49	----	All	
5	*Rhododendron macrophylum*	Medium hot, Dry	All	All		All	
6	*Hieraceum albiflorum*	Hot, Dry + Cold	Moderate	Absent 40–70			
7	*Polystichum munitum*	Warm-wet	Varies	All		All	
	Oxalis oregana	Warm-wet	Varies	38	83	8	15
8	*Coptis laciniata*	Moderate	Varies	48	98	8	2%
	Rubus nivalis	Moderate	Varies	All		9	21
9	*Viola sempervirens*	Cold + Moderate	All	All		All	
10	*Pteridium aquilinum*	Cold	All	38	-	All	
	Achlys triphylla	Cold	All	All		All	
	Campanula scouleri	Cold	All	All		All	
1%	*Listera caurina*	Cold	Disjunct moderate or Hot	All		All	
	Montia siberica	Cold	Disjunct moderate or Hot	38	90	8	21
	Galium oreganum	Cold	Disjunct moderate or Rot	38	73	8	15
	Arnica latifolia	Cold	Disjunct moderate or Hot	38	67	8	10
	Viola glabella	Cold	Disjunct moderate or Hot	38	73	8	15
12	*Osmorhiza purpurea*	Cold	None	37	38	8	9
	Streptopus roseus	Cold	None	38	48	8	9
13	*Rubus lasiococcus*	Cold	Moderate	----	73	----	18
	Clintonia uniflora	Cold	Moderate	----	83	----	18
	Pyrola secunda	Cold	Moderate	----	78	----	18
	Vaccinium membranaceum	Cold	Moderate	----	93	----	19
	Smilicina stellata	Cold	Moderate	----	98	----	21
	Cornus canadensis	Cold	Moderate	38	82	----	18
	Vaccinium alaskense	Cold	Moderate	38	84	----	15
	Tiarella unifoliata	Cold	Moderate	38	87	----	18
14	*Chimaphila umbellata*	Scattered	Varies	All		All	
	Smilacina racemosa	Scattered	Varies	All		All	
	Xerophyllum tenax	Scattered	Varies	All		All	
15	*Vancouveria herandra*	Wet fringe	All	38	----	All	
16	*Athyrium filix-femina*	None	Wet fringe	38	83	----	12
	Blechnum spicant	None	Wet fringe	49	83	----	12

TABLE 8. Continued

				Limits of			
				TGI		PMS	
Group	Species	Center of importance	Other distribution	Min	Max	Min	Max
17	***Fragaria** vesca* var. ***bracteata***	None	Dry fringe	All		**10**	----
18	***Pyrola asarifolia***	None	**2** of three extremes absent	**38**	**98**	----	**21**
	Pyrola picta	None	2 of three extremes absent	**38**	**93**	----	**19**
	Rosa gymnocarpa	None	2 of three extremes absent	**38**	----	All	
	Asarum ***caudatum***	None	2 of three extremes absent	**38**	**87**	----	**18**
	Corallorhiza ***mertensiana***	None	2 of three extremes absent	**38**	**82**	----	18
	Pachistima myrsinites	None	2 of three extremes absent	**38**	----	All	
	Disporum hookeri	None	2 of three extremes absent	**38**	**98**	----	**21**
19	***Galium triflorum***	None	All except coldest	**38**	----	All	
	Rubus ursinus	None	All except coldest	**38**	----	All	
	Adenocaulon ***bicolor***	None	All except coldest	**38**	----	All	
	Vaccinium parvifolium	None	All except coldest	**38**	----	All	
	Trientalis latifolia	None	All except coldest	**38**	----	All	
	Symphoricarpos *mollis*	None	All except coldest	**38**	----	All	
20	***Anemone deltoidea***	None	All	All		All	
	Chimaphila *menziesii*	None	All	All		All	
	Trillium *ovatum*	None	All	----	**98**	--	**21**
	Goodyera oblongifolia	None	All	All		All	

or the best silvicultural technique to use) to be predicted from the flora of the site. In many cases the environmental indexes derived from indicator plants are effective predictors of the measured environmental index (Waring and Major 1964, Griffin 1967, Waring et al. 1972, Minore 1972). However, it is stressed that their use should be confined to the region studied (Griffin 1967, Minore 1972, MacLean and Bolsinger 1973). Within our study area most species grow in a variety of habitats, although some preferential species are recognized (Dyrness et al. 1974). When species importance values are plotted on a TGI-PMS diagram, a number of distributional types emerge (Tables 7 and 8). Species with very low cover or low constancy in all communities were not considered in compiling these data.

The ranges of TGI and PMS within which a species occurs in our area were compared with the habitat ranges of the species studied elsewhere in the Northwest. Most species which Waring (1969) considered sufficiently restricted in distribution to have indicator value were less restricted in our area (Table 9). Most species used as moisture indicators occupied drier environments in our area than they did in the eastern Siskiyous. Several plants used as temperature indicators in the Siskiyous extended to both warmer and cooler environments in our study area and almost all occupied warmer habitats. General comparisons possible with other gradient analyses in southern Oregon (Whittaker 1960, Minore 1972) show the same type of difference, i.e., many species occupying environments relatively drier or warmer in our study area than they do further south. Such differences are not surprising. Higher rainfall and humidity, a shorter dry season, or different competitive pressures in our area may allow the expansion of species into the warmer, drier habitats, as defined by our indexes.

Comparisons with species distribution patterns from the redwood region of California (Waring and Major 1964) reveal no general pattern of differences. Many species have an apparently broader range in our area *(Gaultheria shallon, Achlys triphylla,* and *Acer macrophyllum,* for example). Some species *(Oxalis oregana* and *Polystichum munitum)* are more restricted to the wetter habitats here than they are in the redwood region. *Rhus diversiloba,* on the other hand, is more restricted to dry habitats in our study area. *Libocedrus decurrens* is limited to the warmest (and driest) habitats here, but to the coolest (and driest) in northwestern California.

Intsrpretation of the significance of these TGI and PMS limits (Tables 7, 8, and 9) is somewhat difficult, as the relative effects of biotic and abiotic factors on range limitation are unknown. Within one small area in the southern Appalachians, some tree species were apparently limited by environment, one by competition, and others by a combination of the two (Mowbray and Oosting 1968). The mix of com-

TABLE 9. Environments occupied in the central western Cascades by species with indicator value in the eastern Siskiyou Mountains (Waring 1969). TGI = Temperature Growth' Index; PMS = Plant Moisture Stress. (TGI is numerically equivalent to Waring's Optimum Temperature Days)

	TGI		PMS (bars)	
Species	Siskiyou	W. Cascades	Siskiyou	W. Cascades
Lathyrus polyphyllus			5–10	21 up
Rhus diversiloba	80–100	93 up	15–25	20 up
Whipplea modesta	60–90	67 up	5–10	9 up
Corylus cornuta	70–100	67 up		
Linnaea borealis	50–80	38 up	5–15	All
Viola sempervirens			5–10	All
Campanda scouleri			5–15	All
Viola glabella			5–10	8–9, 18
Arnica latifolia			5–15	8–10
Clintonia uniflora			5–10	8–18
Pyrola secunda	30–60	32–80	5–15	8–18
Tiarella unifoliata			5–10	8–18
Xerophyllum tenax	40–80	All		
Smilicina racemosa	30–60	All		
Pachistima myrsinites	40–80	38 up		
Disporum hookeri			5–15	8–21
Galium triflorum			5–15	All
Rubus ursinus	60–90	38 up		
Adenocaulon bicolor	70–90	38 up	5–15	All
Anemone deltoidea			5–15	All
Trillium ovatum			5–15	All
Goodyera oblongifolia			5–15	All

petitive and environmental limitation undoubtedly changes within a species' range as the flora and environment simultaneously vary from place to place. We have no basis for separating these two limitations. This confuses the interpretation of the meaning of the species limits given here and emphasizes the statement that their utility is strictly local.

COMMUNITY DISTRIBUTION IN RELATION TO ENVIRONMENT

Communities in relation to measured environmental gradients

Much of the variation in community ordinations in our area is associated with the temperature and moisture indexes, TGI and PMS. Nutrition influences community composition most obviously on the nitrogen-poor sites. A two-dimensional environmental field separates the reference stands (and therefore, presumably the communities they represent) in a useful manner (Fig. 7). It illustrates the importance of TGI in differentiating vegetation zones, and the usefulness of PMS in arraying communities within the warmer *Tsuga heterophylla* zone. The portion of this environmental field which is occupied in our area is similar to the eastern Siskiyou Mountains (Waring 1969), although vegetation composition differs appreciably between the two regions.

The array of communities in the two-factor environmental field (Fig. 7) generally reflects the conclusions based on synecological work alone (Fig. 2; Dyrness et al. 1974). The only major discrepancy between Figs. 2 and 7 is the lack of sites with high growing season moisture stress in the *Abies amabilis* zone, as originally had been predicted.

Past studies of vegetation along environmental gradients have shown that factors related to temperature, moisture, available nutrients, and mechanical stress often correlate with the observed vegetation pattern. Usually only two or three of these major factors are concluded to be of prime importance for any single area. Earlier work of this nature is reviewed by Waring and Major (1964); in this paper we consider the more recent work of particular significance to our area.

Chemistry of the soil plays an important role in distinguishing vegetation in the Klamath Mountain and redwood regions (Whittaker 1960, Waring and Major 1964, Waring 1969) and in the Bighorn Mountains of Wyoming (Despain 1973) In several western mountain systems soil differences are important only at a secondary level in accounting for the vegetation pattern (Whittaker and Nering 1965, Daubenmire and Daubenmire 1968, Fonda and Bliss 1969, Minore 1972). However, on Vancouver Island nutritional factors do apparently modify the moisture-induced pattern in *Pseudotsuga* forests (McMinn 1960). All these authors with others (Griffin 1967, Brooke et al. 1970, del Moral 1972) emphasize the role of moisture in influencing forest pattern; most also use a temperature gradient of some type.

At higher elevations snow plays an important role via mechanical force as well as modifying temperature and moisture regimes (Daubenmire and Daubenmire 1968, Fonda and Bliss 1969, Brooke et al. 1970, del Moral 1972). Rapid changes in vegetation may occur at the usual elevations of a winter freezing isotherm, presumably associated with snowpack accumulation (Brooke et al. 1970).

In our area a temperature index proved most important for distinguishing major vegetation zones, whereas moisture factors differentiated communities only within the warmer zone. Some minor exceptions apparently were due to soil nutrient availability. This appears similar to the Olympic Mountains (Fonda and Bliss 1969) and to the more mesic series of forest communities in northern Idaho and eastern Washington (Daubenmire 1956, Daubenmire and Daubenmire 1968), where weather bureau data

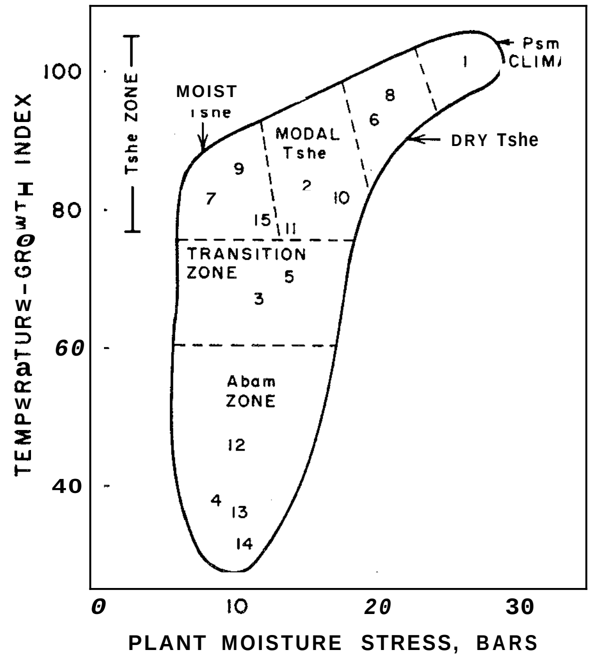


FIG. 7. Position of reference stands in a two-dimensional environmental field. Temperature is represented by Temperature Growth Index computed by the method of Cleary and Waring (1969). Moisture is assessed as the late-summer predawn moisture stress on conifer saplings (plant moisture stress). Most data are for 1972. Psme = Pseudotsuga menziesii, Tshe = Tsuga heterophylla, Abam = Abies amabilis. The community represented by each reference stand is listed in Table 2.

were correlated with vegetation pattern over a large area. Measurements of soil moisture confirmed that no differences in drought exist between the upper forest zones in the northern Rocky Mountains (Daubenmire 1968). There drought differentiates the lower forest zones from each other and from the *Tsuga heterophylla* series, but was not severe in the upper elevation zones. Extension of our study to the vegetation zone adjacent to the lower limits of our *Tsuga heterophylla* zone (the *Quercus-Pseudotsuga* forest and woodland of foothills surrounding the Willamette Valley) would almost certainly show a parallel difference in our area, with PMS differentiating most *Tsuga heterophylla* zone communities from most foothill woodland communities. Our *Pseudotsuga* climax community, drier than the other *Tsuga heterophylla* zone communities, is also a parallel situation in this way to the *Pseudotsuga* zone in the northern Rocky Mountains. Some of Waring's (1969) drier forest types in the eastern Siskiyous are differentiated from each other by PMS, although the majority differ primarily in temperature. Waring's type is a narrower unit than our zone, but broader than our community.

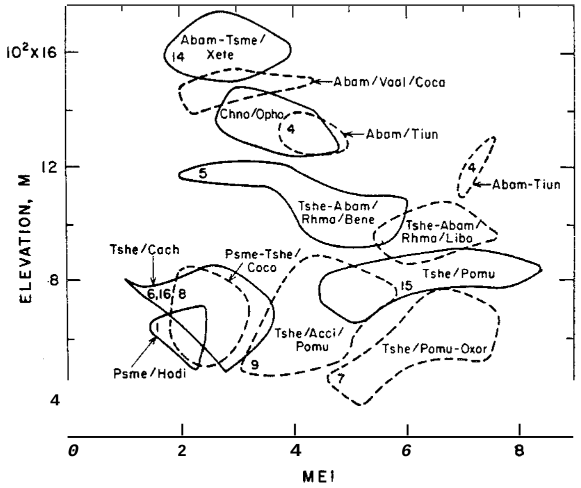


FIG. 8. Mosaic chart showing the usual location of climax forest communities in relation to elevation and a master environmental index (MEI) computed from topographic and soil characteristics (0 = xeric, 9 = mesic). These are the more restricted communities. Each enclosed figure includes at least 80% of the stands. A total of only 10 stands fall outside the figures shown. Numbers identify reference stands. Community abbreviations are identified in Table 1.

Communities in relation to complex gradients

The distribution of communities in relation to the temperature and moisture gradients may be compared with their distribution in relation to complex gradients (Whittaker 1967). C. T. Dyrness, J. F. Franklin, and W. H. Moir ***(unpublished observations)*** computed a Master Environmental Index (MEI) for their reconnaissance plots. Four environmental variables representing topography and soils were assigned scaling factors of from 1 to 10, where 1 represented the most xeric and 10 the most favorable condition of each factor.

$$\mathrm{MEI} = \tfrac{1}{2}\ \{X_1 + [(X_2 + X_3 + X_4)/3]\}$$

where X_1 = factor for topographic location,
X_2 = factor for soil series, incorporating effects of texture and other properties,
X_3 = factor for estimated rooting depth, and
X_4 = factor for soil stoniness.

A two-dimensional environmental field was again constructed, this time using elevation and MEI as the axes. Figures 8 and 9 show this relationship for the climax communities. The enclosed area shown for each community includes at least 80% of the stands measured. To be excluded from the enclosed figure for its community, a point, if included, would have had to increase the enclosed area by at least 30%. Most of the communities include only a small portion of the total field (Fig. 8), and in some cases

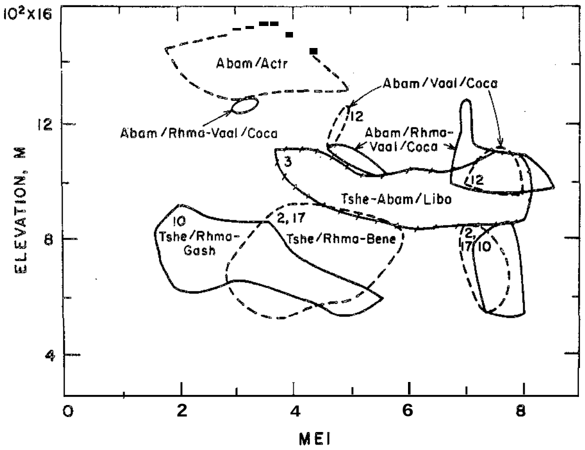


FIG. **9.** Same as Fig. 8, showing locations of five widely distributed climax Communities.

the overlap between communities is not very large. However, there are several communities with a broad or a bimodal MEI distribution (Fig. 9) which greatly overlap some of the more restricted communities. The bimodal nature is a consequence of variation in topographic location, not the soil factors included in MEI.

Comparison with the PMS-TGI ordination shows several differences between the two methods of defining the environmental field (Figs. 8 and 9 vs. Fig. 7). The complex-gradient diagram suggests that the mid- to high-elevation communities are mostly xeric, whereas the PMS at all those measured is quite low. At lower elevations the MEI axis shows differences between communities which are relatively smaller than those shown by PMS. The temperature differences between zones and the temperature patterns within zones are not as apparent using the elevational axis. Of course, some overlap in communities could be expected if several stands per community were measured for PMS and TGI, but this probably would not correct the distortions mentioned above. The MEI axis, constructed to represent a mesic to xeric scale, has different meanings at different elevations in terms of actual moisture stress.

The dispersion of the five climax communities which show a bimodal distribution on Figs. 8 and 9 is more restricted if one uses a Soil Profile Index (SPI = [X2 +X3 + X4]/3) as the X-axis, rather than MEI. All the seral communities are better separated by SPI than by MEI (Fig. 10). Their pattern of occurrence is probably greatly influenced by historical factors. The single community at low elevations occupies a very wide range of soil variation.

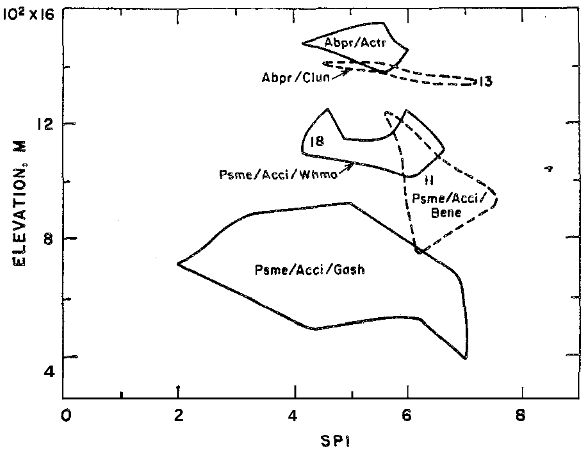


FIG. 10. Mosaic chart showing locations of five seral forest communities in relation to elevation and a soil profile index (SPI) (0 = xeric, 9 = mesic).

Advantages of measured environmental gradients

Using measured environmental gradients has several definite advantages, although many workers choose to identify only complex gradients rather than measuring one or a few factors to represent the environmental changes along these gradients. One would expect an elevational complex-gradient in our area to consist substantially of temperature-related factors, with modifications in intensity related to the depth and persistence of the snowpack. The complex gradient referred to in topographic terms is primarily a moisture gradient (Whittaker 1967). In many cases no single factor can be isolated which varies over the entire gradient of vegetation (Johnson and Risser 1972), making measurement of two or more factors imperative. That one or two measured factors do correlate well with the vegetation gradient does not necessarily imply that they are the sole causal agent(s) of the pattern, of course. For example, Mowbray and Oosting (1968) found the clay/sand ratio in the soil to be the factor best correlated with tree importance and growth. Their discussion emphasizes that besides direct influences on plants via soil aeration and moisture retention, this ratio integrated many microclimatic factors operating over a long time.

Despite the uncertainty as to the degree of causal influence that a measured environmental factor has, we believe that gradient quantification is a worthwhile endeavor. A working knowledge of the nature of effective environmental gradients is necessary to gain understanding of the adaptive strategies of the populations involved and to generate testable hypotheses about the specific competitive and selective forces acting on these populations. For example, a moisture gradient may involve either (or both) atmospheric and soil moisture. Adaptive responses to a moisture gradient vary depending on the exact nature of the gradient. Grand fir saplings on the more arid east slope of the Oregon Cascades are indeed subject to greater evaporative stress than west slope populations, but maximum measured plant moisture stresses are below those of west-slope populations, the reverse of the situation expected. These populations exhibit stomatal reaction patterns which are related to the differences in the type of moisture stress to which they are subjected (Zobel 1974, 1975).

Complex gradients are often defined in physiographic and elevational terms. However, topographic position does not effectively differentiate most vegetation types in our area (J. F. Franklin, C. T. Dyrness, and W. H. Moir, *personal observations).* Reversal of the aspect occupied by a forest type occurs as elevation increases on many mountain systems, as seen in complex-gradient mosaic charts from these areas (e.g., Whittaker and Niering 1965). This physiographic reversal of a vegetation type as elevation increases is well-developed in the southern Rocky Mountains. The reversal is absent from the upper vegetation zones of the northern Rocky Mountains which are especially affected by moist, westerly winds and it is suggested that it also should be absent on the western slopes of the Cascades (Daubenmire and Daubenmire 1968). In our *Tsuga heterophylla* zone communities the highest plots of each vegetation type are, indeed, only rarely on topography considered to be relatively xeric, nor are the lower ones consistently mesic (Figs. 8 and 9). In the *Abies amabilis* zone the patterns are less clear cut, about half the types having highest plots on relatively xeric topographic positions. The degree of aspect-elevation compensation is hardly consistent among mountain systems.

The mosaic chart with complex-gradients as its axes is a useful device for visualizing what a vegetation pattern looks like in the field. However, its use to decipher autecological relationships of species may lead to distortions. The environmental field of a mosaic chart includes all possible combinations of factors defining it. In studies using quantified gradients all possible combinations of two factors seldom, if ever, occur. Gradients such as wet-fertile to dry-sterile (Monk 1965) may be found, without the other possible combinations (dry-fertile, wet-sterile). Measured environmental fields lack many types of combinations of factors: low temperature-mesic and mesic-infertile (Waring and Major 1964), or cool-xeric and hot-mesic (Waring 1969 and this study). The few plots on which unusual conditions have been measured (e.g., cool-xeric in our area) have vegetation of limited extent, and of very little significance in a regional context (Zobel 1975 and *personal observations).* Thus, the implication of the full field mosaic chart is contrary to the observed environmental patterns. It is probably unusual to have all topographic and soil conditions occurring at all elevations.

The aspect-elevation relationships of vegetation which occur in many areas may lead to a shift toward the mesic with elevation for many species. This could be interpreted as a change in species response to moisture, when the explanation is more likely a shift in the moisture availability on a given topographic position. However, use of direct measurements as axes of an environmental field (Fig. 7) tends to prevent this ambiguity. Furthermore, the degree of aspect-elevation compensation varies, as discussed above, complicating the interpretations. Finally, the length of the complex moisture gradient may represent a very different plant moisture stress gradient at different elevations, as we found for our area.

The use of complex-gradients does avoid giving the impression that vegetation pattern responds to only one or two factors of the environmental complex. However, such distortions as mentioned above make formation of autecological hypotheses from vegetation patterns displayed in these charts more difficult than if measured gradients are used.

SPECIES DIVERSITY IN RELATION TO ENVIRONMENT

Species richness

Whittaker (1972) suggests species number per unit area as the most generally appropriate measure of diversity within a community (a-diversity): we use species number in this study. The stand samples analyzed by Dyrness et al. (1974) were not on measured quadrats, but should be uniform enough and large enough to eliminate any major errors in comparison of species numbers. Community descriptions are based on a composite of 7-22 stand samples per community. This variation in sample size could affect our estimate of species number in each community; however, it does not seem to have a great effect, as correlation of species richness with number of samples in a mean for a community gives $r^2 = 0.005$.

Alpha-diversity is presented here both as species number in the composite community sample and as the average number of species per stand sample within each community. These two measures vary in a somewhat parallel manner, with $r^2 = 0.66$. Comparison of richness to TGI-PMS coordinates shows approximately the same pattern whether composite species number or species number per sample is used (Fig. 11). In our area diversity increases away from the moderate environmental conditions, toward both cooler and more xeric environments, with the sole exception of the *Abies-Tsuga/Xerophyllum* community (TGI = 32).

Study of the relationship of species diversity to environmental conditions has not led to any widely acceptable generalities (Whittaker 1972). In some

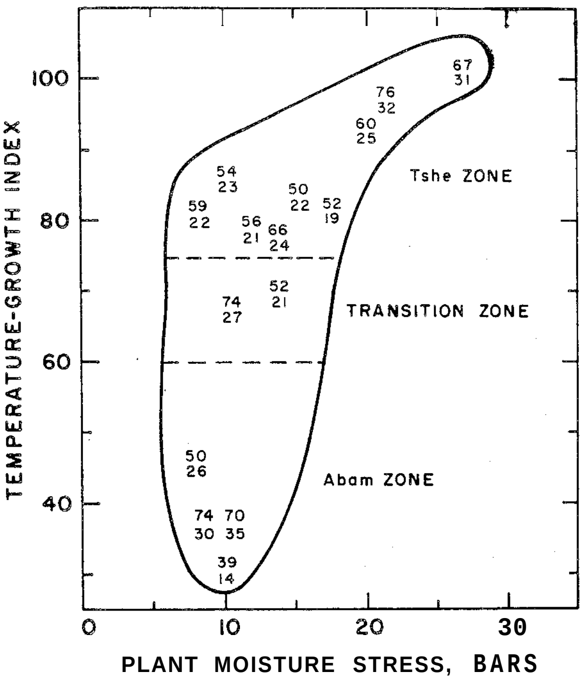


FIG. 11. Vascular species diversity (number of species) of forest communities in relation to temperature and moisture conditions at the reference stand representing it. The top figure is the species number in the composite sample; the bottom is the average species number per stand sampled. The reference stand at each position is identified in Fig. 7.

cases diversity is highest in more mesic communities; in others it is not. Terborgh (1973) states that the general case in temperate North American vegetation is to have greatest species number in the middle part of a moisture gradient, rather than in wetter or drier areas. This is contradicted by our study as well as several others (cited in Whittaker 1972, del Moral 1972). One must consider the relative xeric-mesic-hydric range which occurred in each study. In our area the wettest sites did not appear too wet for optimum growth of the dominants. This is probably also true in Whittaker's studies cited by Terborgh (1973) However, in other studies he cites very wet areas were included. A comparison of diversities at the midranges of moisture gradients which have greatly different end-points of hydrism and xerism (Terborgh 1973) should not, it seems, allow strong inference from the results.

Often, diversity in one stratum of vegetation cannot be predicted from the diversities of the other strata (Whittaker 1972). This is also true for this study. That diversities of different strata are unrelated is indicated by the r^2 between species richness of layers: tree-shrub = 0.01, shrub-herb = 0.02, and tree-herb = 0.06.

The dominance of one stratum (as opposed to its diversity) may affect the diversity of another (Whittaker 1972). The greater herb diversity on dry sites in our area contrasts to findings for some temperate forests (Daubenmire and Daubenmire 1968) but is similar to others (Rochow 1972). This pattern may result from a less dense canopy cover over these dry sites, leading to greater light intensities. The reduced tree density should also cause greater availability of nutrients and water, less chance of allelogathic influence, and a greater variety of available microhabitats (Daubenmire and Daubenmire 1968, del Moral 1972, Rochow 1972, Whittaker 1972). In our study the number of herbaceous species was inversely related to the percent cover of evergreen trees and shrubs in the community ($r^2 = 0.38$, $n = 22$, excluding the *Abies-Tsuga/Xerophyllum* community). Using seral communities alone this r^2 was 0.74 ($n = 5$). The model for control of forest species diversity (del Moral 1972) suggests that conditions on our *Pseudotsuga* climax and *Abies amabilis* zone sites are rigorous enough to cause a more open canopy, but are not rigorous enough to greatly deplete the flora. The net effect is increased diversity. The *Abies-Tsuga/Xerophyllum* community, on the other hand, apparently has an environment rigorous enough to delete many of the less hardy species, thus decreasing diversity.

On a given site in many temperate forests, species richness may increase for some time, and them decrease with canopy closure and establishment of strong dominance (Whittaker 1972). In our area the seral communities average more species than the old-growth communities (68 vs. 60 total; 29 vs. 25 per stand).

The degree to which species composition changes along environmental gradients within an area is termed ,@-diversity. A simple and generally appropriate measure of B-diversity is (BD - 1.0), where BD = Sc/S Sc being the number of species in the composite sample and S the average number of species in the communities (Whittaker 1972). The total vascular ,@-diversity of our study area is 1.473. ,@-diversity is somewhat lower for trees and shrubs (1.26 and 1.25) and higher for herbs (163)

Gamma diversity is the species richness in a particular range of habitats. The forests studied by Dyrness et al. (1974) include 153 vascular species. However, the total flora is much larger and is probably estimated best from Franklin and Dyrness (1971) who list 480 vascular plants in the H. J. Andrews Forest. This latter number includes a few introduced tree species and many species characteristic of meadows and disturbed areas (e.g., clearcuts)

Species dominance

Communities vary in the degree to which some measure of importance is shared among the species

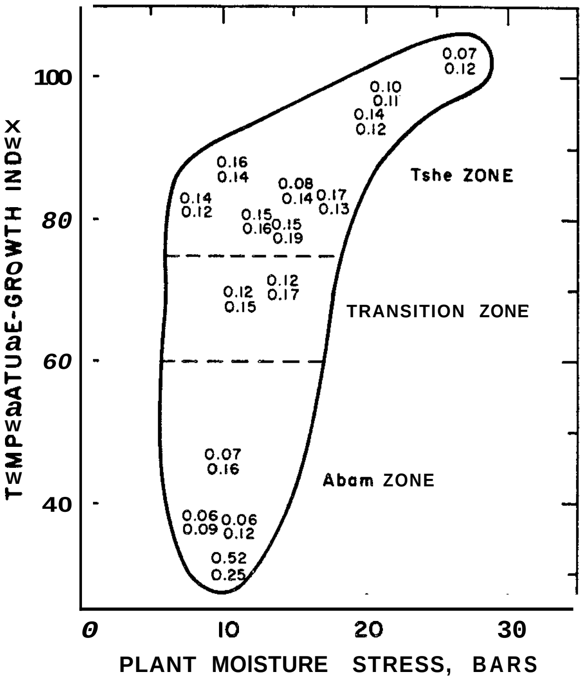


FIG. 12. Dominance (Simpson's index) in relation to temperature and moisture conditions of the reference stands representing each community. The top figure is calculated for all vascular species; the bottom for shrubs and herbs only. Percent cover is the measure of importance.

present, called equitability, or conversely, the concentration of dominance. We chose a simple measure of the concentration of dominance, Simpson's index (C).

$C = \sum_{i=1}^{s} p_i^2$, where s is number of species in the collection and p_i is the proportion of the importance value belonging to the ith species. Whittaker (1972) suggests that this index is appropriate for communities exhibiting strong dominance, as ours do. We used average percent cover in the composite community sample as our measure of importance.

Dominance varies considerably among communities (Fig. 12), generally being more pronounced in lower elevation and seral stands: *Abies amabilis* zone C = 0.115, *Tsuga heterophylla* zone C = 0.140; seral communities C = 0.148, climax communities C = 0.126. However, the *Abies-Tsuga/Xerophyllum* community, which is excluded from the means, has a very high dominance. When tree species are excluded from the calculations, the same generality holds for zones, but the understory dominance is similar in both seral and climax stands. Vascular dominance, and especially understory dominance, generally decrease away from the area of moderate environment toward the dry and the cold communities (Fig. 12). Thus, species richness and dominance are generally negatively related. C values are generally in the range of those found by del Moral (1972) for the Wenatchee Mountains.

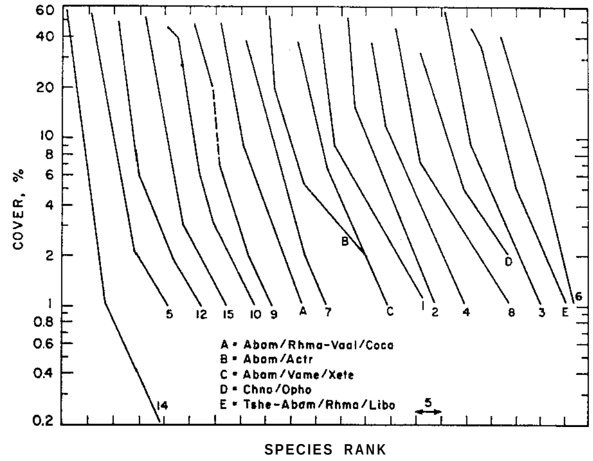


FIG. 13. Dominance-diversity curves for climax communities in the central western Cascades, constructed for the 20 most important species in the composite sample for each community. Curves are ordered by the percent cover of the 10th species, from lowest to highest (i.e., approximately the steepest to flattest slope in the top half of the line). Numbers refer to reference stands. Tables 1 and 2 identify communities.

DOMINANCE-DIVERSITY CURVES

Another way to look at dominance-diversity relationships is to plot the log of importance of species (cover, in our case) over species rank of importance. Different shapes of the resulting curve should theoretically arise depending on the type of theory one invokes for determining how niches are occupied (Whittaker 1972). Curves for the 20 most important species of each composite community sample (Dyrness et al. 1974) are of a form generated by a geometric series (Fig. 13), theoretically produced by the hypothesis of niche-preemption. Such a form is often exhibited by vascular plant communities of low diversity (Whittaker 1972). All our curves have a somewhat similar, steep initial slope. However, all except one have at least two parts with the slope decreasing after 3–10 species. This broken curve appears to represent two groups of plants: the first group is the dominant trees and the most important understory species, the other the rest of the lower strata. These groups have somewhat different dominance relationships as indicated by the slope of the lines, with the less important species groups having a smaller degree of dominance.

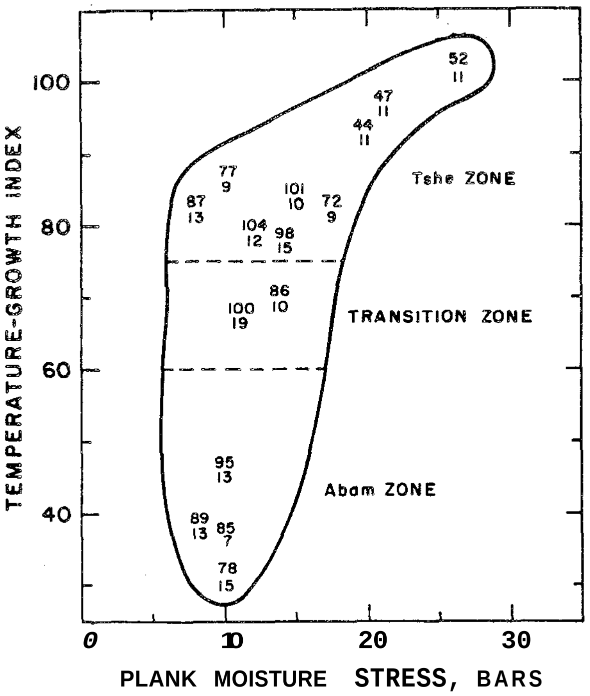


FIG. 14. Percent cover by mature trees (top figure) and tree reproduction (bottom figure), in relation to temperature and moisture conditions Cover figures are the sum of cover for individual species, and thus may exceed 100%.

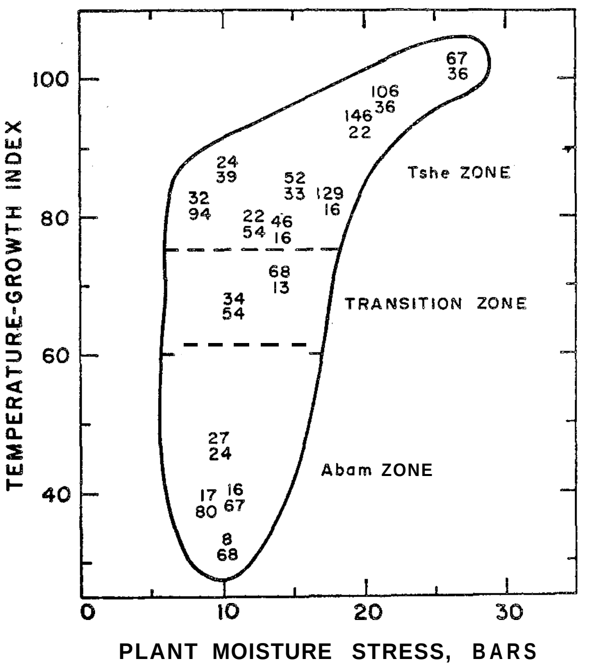


FIG. 15. Percent cover by shrubs (top figure) and herbs (bottom figure), in relation to temperature and moisture conditions. Cover figures are the sum of cover for individual species and thus may exceed 100%.

COMMUNITY STRUCTURE IN RELATION TO ENVIRONMENT

The coverage of each stratum has its own pattern in relation to the environment. Tree cover is greatest in moderate environments, decreasing toward all extremes, especially the dry stands (Fig. 14). Shrub cover is highest in the warm, dry stands, and lowest in the coldest communities (Fig. 15). This is very roughly the opposite pattern found in herbaceous cover (Fig. 15) which is high in cold and mesic stands. Siccama et al. (1970) attribute greater herbaceous importance with elevation in New Hampshire to factors related to a decrease in tree cover and the fact that environmental change with elevation may be more moderated for the herb layer than for the trees.

The communities studied vary considerably in the importance and relative importance of the various strata (Figs. 14 and 15); we summarized this property in a manner analogous to computing species dominance. Simpson's index was computed considering each of five vascular strata (mature trees, tree reproduction, tall shrub, low shrub, and herb) as a unit, using the total cover for each stratum from the composite community description. A definite pattern emerges from the data. Stratum dominance is greatest on the colder sites, intermediate on sites of moderate environment, and lowest on the dry sites (Fig. 16) The *Tsuga/Acer/Polystichum* community is the single exception to this trend. Thus, dominance is concentrated in fewer growth forms on colder and moister sites.

Acer *macrophyllum,* the only deciduous canopy tree in the study area, accounts for more than 3% tree cover in only three communities (maximum = 7%). However, evergreenness in the shrub layer is much more common, although it varies markedly from community to community. Most low shrub cover is evergreen (63%-100%), especially in warmer stands. Percent evergreenness of tall shrubs varies more, being highest in the moderately warm-dry stands, and decreasing in all directions. The absolute amount of evergreen tall shrub cover varies in a somewhat similar manner (Fig. 17). Interestingly, communities with the largest amounts of foliar nitrogen had the lowest evergreen shrub cover (Fig. 18).

The concentration of evergreenness on dry sterile sites in the western Cascades follows the pattern described by Monk (1965, 1966) for forests of northern Florida. He emphasizes the probable role of evergreenness in nutrient conservation; this role appears possible from our limited data (Fig. 18). Sclerophylly is often associated with evergreenness;

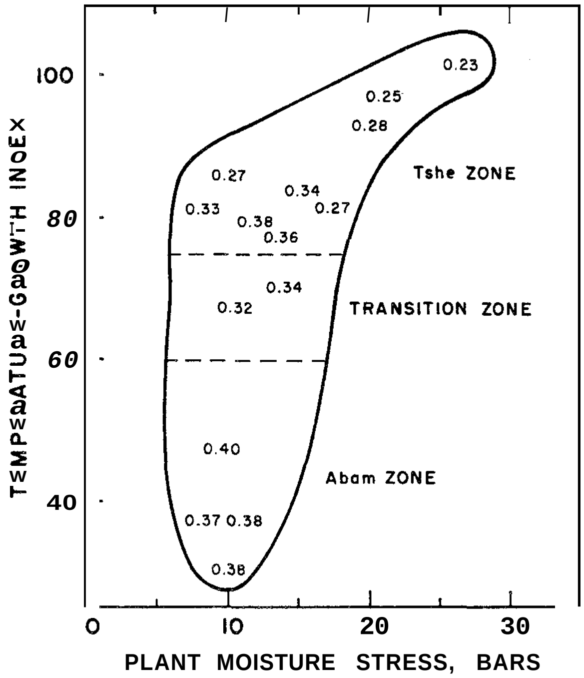


FIG. 16. Stratum dominance: Simpson's index computed for percent cover of five layers (mature tree, tree reproduction, tall shrub, low shrub, and herb), in relation to temperature and moisture conditions.

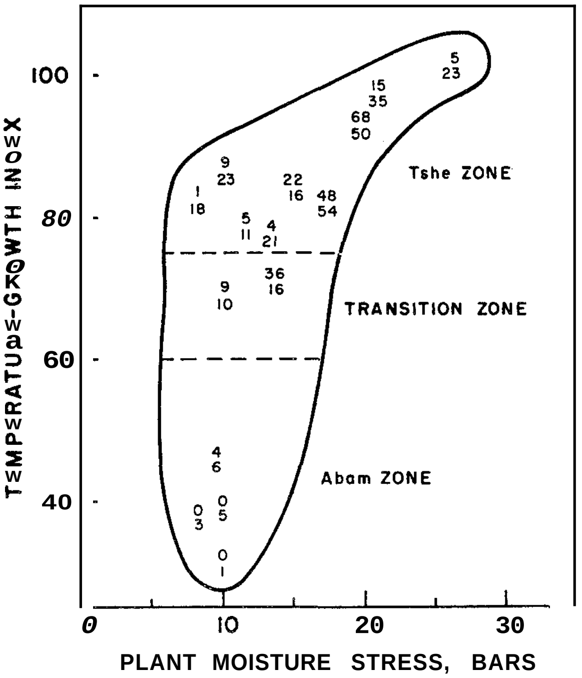


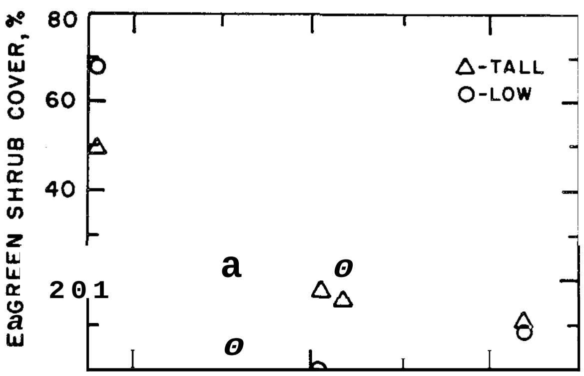
FIG. 17. Percent cover by tall (top figure) and low (bottom figure) evergreen shrubs, in relation to temperature and moisture conditions.

its importance in moisture conservation appears to be of secondary importance, or at least to be ineffective on our driest areas. The percentage of evergreenness is low in our two driest communities.

SOME IMPLICATIONS OF PATTERNS OF STRUCTURE AND DIVERSITY

The different community properties which we have examined exist in a variety of patterns over the environmental field we defined. Species richness increases toward our environmental extremes, whereas tree coverage and concentration of dominance decrease toward these extremes. Stratum dominance, shrub cover, and herbaceous cover vary in a more unidirectional manner across the environmental gradients. Shrub cover is highest on warm, dry sites, and the other two are highest on the cooler, moister sites. The pattern of diversity within a single stratum varies in a manner unrelated to diversity of other strata; however, herbaceous diversity is related to the coverage of evergreen shrubs and trees.

The *Abies-Tsuga/Xerophyllum* community (reference stand *14),* although the coldest we measured, still has environmental indexes not very different from the *Abies amabilis* zone stands. This is reflected in the pattern of structural characteristics: the trends set by the adjoining stands extend to stand 14 (Figs. 14, 15, and 16). However, this is not true for the general trends for diversity (Figs. 11 and 12), which reverse themselves at stand *14.* The sharp discontinuities which occur here reinforce the conclusion, based on composition, that this community really represents a different vegetational zone (the *Tsuga mertensiana* zone of Franklin and Dyrness 1973) and suggest that major changes occur here which are not reflected in our environmental indexes. If such dis-



continuities in the relationship of diversity to environment occur frequently in vegetation, generally applicable models of community diversity would be very complex and difficult to conceptualize. This may explain why widely acceptable models relating diversity to environment have not been developed.

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