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Title: VEGETATION ECOLOGY OF SELECTED MOUNTAIN

HEMLOCK (TSUGA MERTENSIANA) COMMUNITIES

ALONG THE EASTERN HIGH CASCADES, OREGON

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Tree diameter, understory plant cover, seedling
density, elevation, aspect, and slope steepness are re-
corded for 51 forest stands dominated by Tsuga mertensiana
(Bong.) Carr. along the eastern portion of the central
Oregon Cascades.

Species dominance based on prominence values for
trees and percent cover for shrubs and herbs are correlated
with elevational and topographic variables.

Community patterns are delineated in a two-dimension-
al ordination based upon similarity of composition between
stands. Four provisional community types are identified
along inferred length of snow free season and available
soil moisture gradients: (1) Abies amabilis-Tsuga
mertensiana/Vaccinium membranaceum; (2) Abies amabilis/
Vaccinium scoparium; (3) Tsuga mertensiana/Vaccinium; and
(4) Tsuga mertensiana/Luzula hitchcockii.

Three vegetation subzones are identified within the Tsuga mertensiana Zone based on tree size class relative frequency, seedling relative density, and species composition: (1) Subalpine subzone, where T. mertensiana dominates and is replacing itself; (2) Transition subzone, where T. mertensiana dominates and where A. amabilis development is suppressed during years of extreme snow accumulation; and (3) Montane forest subzone, where Abies amabilis is the potential climax species but where T. mertensiana currently dominates.

Vegetation Ecology of Selected Mountain Hemlock
(Tsuga mertensiana) Communities Along the
Eastern High Cascades, Oregon

by

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VEGETATION ECOLOGY OF SELECTED MOUNTAIN HEMLOCK (TSUGA MERTENSIANA) COMMUNITIES ALONG THE EASTERN HIGH CASCADES, OREGON

INTRODUCTION

The montane and subalpine Tsuga mertensiana (Bong.) Carr. forests of the Pacific Northwest provide a rich source for scientific study. The most extensive Tsuga forests in this region flank the crest of the central Oregon Cascades (Franklin and Dyrness, 1973). Stands along the eastern slope of the crest are the focus of this report.

The objectives of this investigation are to: (1) describe the vegetation of the study area; (2) analyze change in vegetative composition and structure as a function of elevation and topography; (3) infer directional trends in compositional change from size structure distribution; (4) delimit community types by ordination techniques and indirect gradient analysis; and (5) describe the composition and major environmental features of the community types.

Terminology

Composition, as used here, refers to the relative proportions of numbers of individuals of one species to all other species within a stand. Structure refers to the spatial distribution of individuals or species populations

(Mueller-Dombois and Ellenberg, 1974). Size structure is the distribution of above ground biomass in space (Goff 1968), and is used here to refer to species density across six size classes based on diameter at breast height (DBH). Aspect refers to the facing-direction of a sloping terrain surface. Slope steepness refers to the angle of inclination that a terrain surface departs from the horizontal and is measured in degrees.

All taxonomic nomenclature follows Hitchcock and Cronquist (1973). For the purposes of this research no differentiation was made between Abies magnifica var. shastensis and Abies procera. Individuals of this hybrid swarm were all designated as Abies magnifica var. shastensis.

DESCRIPTION OF STUDY AREA

Location

The major portion of the study area is located at roughly 44°N latitude, 121½°W longitude in T. 18 S., R. 8 E., and T. 18 S., R. 9 E., Willamette Meridian. Sampling sites cover an elevational range from 1580 m (5185 ft.) to 2220 m (7275 ft.). A few sample sites occur to the south of the major study area. Five plots occur along the eastern flank of Irish Mountain (T. 20 S., R. 6 E.), and seven plots occur along the eastern flank of Diamond Peak (T. 23 S., R. 6 E.).

Figure 1 shows the areal extent of the study area, a 55 by 8 km band along the east side of the Cascade crest, its eastern margin corresponding closely with the distributional range of Tsuga mertensiana on the eastern side of the central Oregon Cascades. Franklin (1965) places the area into the Three Sisters Ecological Province. The most southern sampling sites of this study are located along the northern margins of the Crater Lake Ecological Province.

Climate

Macroclimatic features of the central Oregon Cascades result from the interplay of wind circulation patterns and topography. About 70 percent of the annual precipitation in
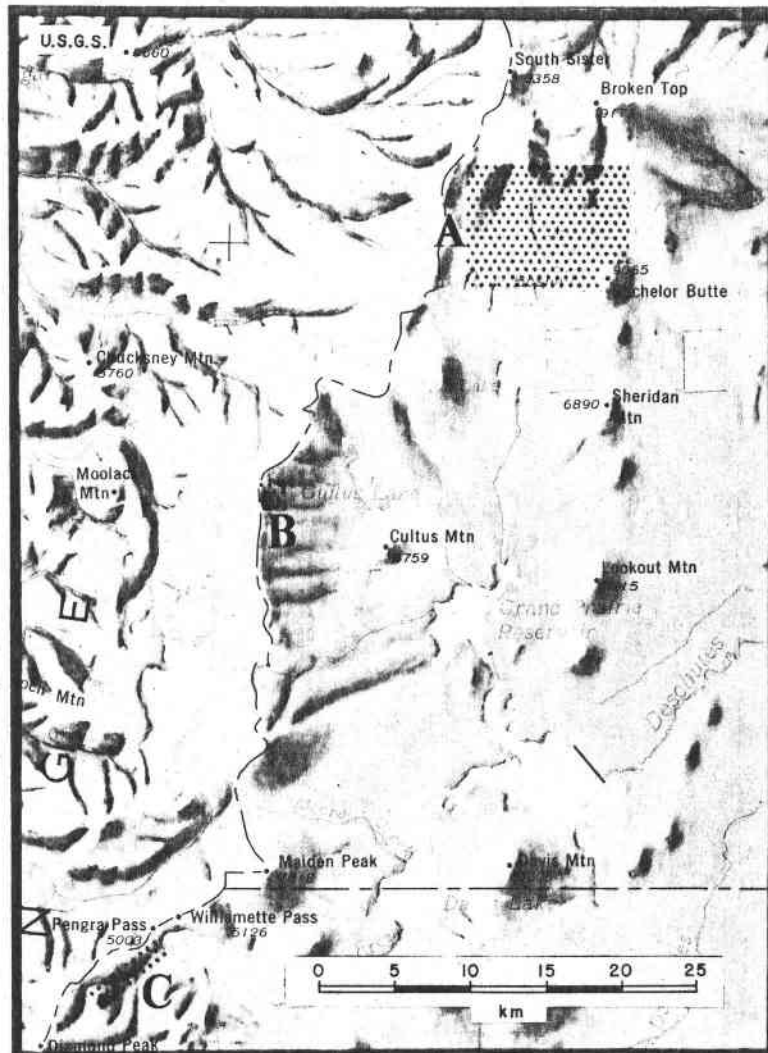
Figure 1. Study area: (A) major portion - 39 plots;
           (B) Irish Mountain - 5 plots; (C) Diamond Peak -
           7 plots.

the area occurs during the period November to March, mostly
as snow. Orographically induced precipitation characterizes
the west slope of the central Cascades while a rain shadow
effect prevails along the leeward flanks of the crest. The
summer months account for less than 10 percent of the annual
precipitation (Franklin and Dyrness 1973). Dry season con-
ditions are intensified on steep, south-facing slopes, and
mitigated on north-facing slopes.

The importance of meso- and microclimate in mountainous
areas cannot be overemphasized. In the mid-latitudes of the
Northern Hemisphere, great differences in meso- and micro-
climate exist between directly opposing slope exposures.
This is especially pronounced on southwest and northeast
slopes, where differences in insolation are the greatest
(Geiger 1965). As the sun rises, a large portion of the
insolation (on southeast slopes) is dissipated in evapora-
tion of surface soil moisture. As the sun crosses the
zenith, surface soil moisture decreases, resulting in a
larger portion of the insolation being directed toward
heating of the soil surface rather than evaporation.
A moisture gradient between aspects can be inferred. North-
east aspects are the most mesic, receiving less insolation
than the northwest, southeast, and southwest slope exposures.
The southwest aspect is the most xeric, receiving the
largest annual insolation budget directed toward heating.
These insolation differences are magnified with increasing

steepness of slope and changing seasons at mid-latitudes (Geiger 1965).

The study area is situated in the rain shadow, extending from the Cascade crest eight kilometers eastward. Across this area, a precipitation gradient is reflected in a decrease in average annual precipitation, warmer and drier summers, increasing length of snow free period, and colder winter temperatures (U.S. Weather Bureau 1960).

No climate stations exist within the study area. Although located 130 km to the south of the study area, the Crater Lake National Park Headquarters climatological station provides comparable data. The station, at 1975 m elevation along the summit of the Cascade axis, reports measurements for the 37 year period 1924-1961. Mean daily maximum temperature for January is 1.4°C. Mean daily minimum for January is -8.1°C. The mean maximum and minimum temperatures for July are 21.3°C and 5.7°C., respectively. Mean monthly precipitation for January is 275 mm; for July it is 16 mm (Sternes 1963). Crater Lake annual snowfall averages 13,970 mm, with a maximum recorded snowfall of 22,860 mm (N.O.A.A. 1974). Snow depth information has been collected intermittently over the past 30 years in areas more proximate to the study area. Monthly snow depth information over the winter and spring months has been recorded at the New Dutchman Flat 2 snow course (Sec. 21, T. 18 S., R. 9 E.), elevation 1,950 m. Snow depth averages 2,800 mm

on February 1, and 3,175 mm on May 1. This late accumula-
tion of spring snowpack is further evidenced by the late-
lying snowbanks, sometimes persisting into early August.

Geology

The most recent compilation on the geology of the
central High Cascades has been the work of Williams (1944,
1948).[1] The discussion presented here follows his narra-
tive.

The present day Western Cascades were formed by vol-
canic flows initiated in the middle and late Eocene. By
the middle Oligocene, a variety of ashes, agglomerates,
andesitic and basaltic lavas had accumulated to depths of
over 3,000 m. During the middle and late Miocene these
flows were uplifted as a unit to form the present day
Western Cascades. The uplifting produced a belt of north-
south fractures from which the High Cascades emerged.
Throughout Pliocene time, quiet, effusive eruptions formed
numerous shield volcanoes that are still evident today. The
gradual formation of shield volcanoes continued into the
Pleistocene accompanied by the formation of parasitic cones
composed of andesite and dacite. In the Recent period there
were eruptions of pumice and ash. Basalt and scoria

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[1]Dr. E. Taylor, Oregon State University, and Dr. B. Nolf,
Central Oregon Community College both have research under-
way in the study area.

flows also continued during this period from widely scat-
tered vents (Williams 1944). This chronology provides the
basis for the geologic mosaic evident in the study area to-
day. Devils Hill and Kaleetan Butte are composed of
glaciated dacites and andesites. Talapus and Katsuk Buttes
are scoria cones. In the Todd Lake area a mixture of scoria,
andesite, dacite, and basic lavas of old shield volcanoes are
exposed (Williams 1944).

Soils

Deposits of pumice, ash, and glacial till are wide-
spread throughout the study area. Soils developing from the
pumice mantle are coarse textured, generally having high
percentages of gravel-sized particles (Youngberg and Dyrness
1964). Williams and Dyrness (1967) characterize soils in
the _Tsuga mertensiana_ Zone of central Oregon as weakly
developed Haplorthids (Brown Podzolic soils), with a two to
five cm thick, densely matted, felty mor humus layer. The
Deschutes County S.C.S. Soil Survey classifies the area as
part of the Winopee-Moolack Association, composed primarily
of loamy sands and sandy loams (S.C.S. 1973). Older soils
are buried by a pumice mantle, varying in depth from 40 to
120 cm. Charcoal in the soil profile is either absent or
present in very small quantities (e.g., one to three mm
particle size).

Vegetation

A variety of classification systems exists for describing present or potential vegetation (Daubenmire 1968; Brooke et al. 1970; Franklin and Dyrness 1973). In mountainous areas, vegetation classification often comports to zonation based on elevation and topography. The zonal system employed by Franklin and Dyrness (1973), and following Daubenmire (1968) is used here. A zone is defined as an ". . . area in which one plant association is the climatic climax" (Franklin and Dyrness 1973; Daubenmire 1968). As a rule, the zonal name is based on the climax dominant within an area, although a number of exceptions may be found to this in the Northwest, one of them being the Tsuga mertensiana Zone. The montane or continuous forest subzone of the Tsuga mertensiana Zone has Abies amabilis as the potential climax dominant based upon size-class distribution in which Abies dominates the regeneration size classes (Franklin and Mitchell 1967; Franklin and Dyrness 1973). T. mertensiana dominates the larger size classes throughout the zone, but is regenerating at relatively low densities below 1,900 m. Abies lasiocarpa, Pinus monticola, and P. contorta var. contorta are minor components of the overstory in these forests. Vaccinium scoparium and V. membranaceum are the dominant shrubs, typically occurring with a sparse herbaceous understory.

The upper parkland subzone of the Tsuga mertensiana Zone has been characterized as ". . .a mosaic of forest patches and tree groups interspersed with shrubby or herbaceous subalpine communities" (Franklin and Dyrness 1973). Pinus albicaulis is often found in seral stands at the highest elevations. Abies lasiocarpa is commonly found layering on the outer margins of tree islands (Van Vechten 1960; Lowery 1972), especially on drier sites. Tsuga mertensiana is the major dominant and occurs in all size classes throughout the subalpine subzone. Ericaceous shrubs are generally absent above 1,900 m, where Luzula hitchcockii dominates the herbaceous understory.

LITERATURE REVIEW

Mountain Hemlock Studies

Tsuga mertensiana dominated vegetation has been re-
ported as a component of various synecological studies
throughout western North America. A review of the most per-
tinent research is included below.

Perhaps the most extensive research on T. mertensiana
yet completed has been in the subalpine forests of south-
western British Columbia (Brooke et al. 1970). A biogeo-
climatic classification system based on the interaction of
climate, soils, and vegetation is used to characterize the
Mountain Hemlock Zone (Krajina 1965). Climatic measurements
include precipitation and temperature, while phytosociologi-
cal analysis of vegetation in mesic habitats is combined
with a consideration of the dominant regional pedogenic pro-
cesses of zonal soils in producing a zonal classification
system for vegetation. The Mountain Hemlock Zone in British
Columbia extends from 900 to 1,000 m up to the limits of
tree growth around 2,650 m. Brooke et al. (1970) report
this Zone to correspond closely with the Tsuga mertensiana
Zone of Franklin and Dyrness (1969), and to the Hudsonian
Life Zone reported by Merriam (1899; Long 1976).

At least 12 plant associations have been identified in
the Mountain Hemlock Zone of British Columbia. Tsuga

mertensiana and _Abies_ _amabilis_ are common and widespread
overstory species, with _Chamaecyparis_ _nootkatensis_, _Thuja_
plicata, and _Abies_ _lasiocarpa_ occupying more restricted
habitats.

The montane and subalpine forests of the Olympic Moun-
tains, Washington support a diversity of tree species.
Fonda and Bliss (1969) used indirect gradient analysis to
infer compositional and structural patterns in this region.
A two-dimensional ordination led to the identification of
seven community types. Stands along the y-axis related to
a temperature gradient, while the x-axis corresponded to a
moisture gradient. _Tsuga_ _mertensiana_ was found to dominate
the cool, mesic subalpine environments along with _Abies_
amabilis. Forests of the _Abies_ _amabilis_-_Tsuga_ _mertensiana_
type occurred from 1,100 to 1,650 m along the western and
northern facing slopes. Basal areas of $109/m^2/ha$ and densi-
ties of 748 trees/ha were recorded for this type. Trees in
stands on steep slopes and ridge crests were much smaller
(up to 30 cm DBH) and more densely stocked (up to 1200
trees/ha). _T_. _mertensiana_ reproduction in the Olympics is
not nearly as vigorous as _A_. _amabilis_ in areas where the two
co-occur. _Abies_ _lasiocarpa_ dominates from 1,300 to 1,800 m
on the higher exposed ridges. The _Abies_ _lasiocarpa_ type
intergrades with the _Abies_ _amabilis_-_Tsuga_ _mertensiana_ type
at lower elevations, and in more mesic sites. This forest
type is floristically the richest of all the montane types

in the Olympics, attributed by Fonda and Bliss (1969) to the numerous small openings in the canopy which support an herbaceous vegetation similar to meadow communities. The floristic affinities of the herbaceous understory of the Olympic _T. mertensiana_ vegetation with the understory of the _Tsuga mertensiana_ stands on the eastern slopes of the Cascades, bears mention. A variety of species are mutually common to both areas: _Rubus lasiococcus_, _Valeriana sitchensis_, _Polemonium pulcherrimum_, _Xerophyllum tenax_, _Vaccinium membranaceum_, and _Lupinus latifolius_ var. _subalpinus_.

Along the moist, upper slopes (average elevation, 1,700 m) of the Bitterroot Mountains separating Idaho and Montana are found mixed coniferous forests of _T. mertensiana_, _A. lasiocarpa_ and _Picea engelmannii_. Habeck (1967) has examined the structure and composition of these forests, with particular attention given to successional relationships. He observed that the distribution and abundance of _Tsuga mertensiana_ closely relates to annual moisture. _Tsuga_ maintains the ability to regenerate over a variety of slopes and exposures that receive at least 100 cm of precipitation yearly. No single, predictable pattern of succession exists in seral stands developing toward _T. mertensiana_ climax. _Picea engelmannii_ and _Pinus contorta_ var. _contorta_ are major seral species in these communities. _Abies lasiocarpa_ retains some ability to reproduce in shade, and often persists into old-aged _Tsuga_ communities. Two shrubby species,

Vaccinium scoparium, and V. membranaceum, do not achieve
high cover values in any stand. There appears to be an
elevational stratification, with V. scoparium attaining high
cover above 1,750 m, and V. membranaceum having its highest
cover below 1,750 m. The majority of associated understory
species in western Montana are also present in the central
Cascades: Chimaphila umbellata, Pyrola secunda, Goodyera
oblongifolia, Pachistima myrsinites, and Xerophyllum tenax.

Franklin (1966) considers that T. mertensiana is either
seral or a minor climax component of the forests of the
southern Washington Cascades. The Tsuga mertensiana Zone
in southern Washington includes both the lower, continuous
(montane) forest subzone, and the upper parkland mosaic. It
covers an elevational range from 1,370 to 1,980 m in the
Mount Rainier Province, dropping to 1,220 m in the Mt. Adams
Province. Study of size class distribution in both Pro-
vinces indicates that Abies amabilis is reproducing heavily
in old-aged Tsuga stands, where T. mertensiana regeneration
is scattered and less abundant (Franklin 1965, 1966).

Del Moral (1973) has examined the vegetation of Find-
ley Lake Basin, Washington. Mid-elevation sites on steep
slopes are co-dominated by A. amabilis and T. mertensiana.
High elevation (1,350 m), ridge-top sites are dominated by
a Tsuga type, which represents a topographic modification of
Franklin and Dyrness' (1973) montane subtype in the Tsuga
mertensiana Zone. Size class analysis of the Tsuga type

indicates that Abies amabilis will eventually replace the currently Tsuga mertensiana-dominated stands. Total understory cover is dense, and species richness is relatively low. Understory dominants include: Xerophyllum tenax, Vaccinium deliciosum, V. scoparium, and Menziesia ferruginea.

Working in the subalpine parkland subzone of the T. mertensiana Zone in the North Cascades of Washington, Douglas (1971, 1972) recognizes the Tsuga mertensiana-Abies amabilis type as the single, climax association. Two phases of the association are recognized, an "open," and a "closed" phase. Tsuga is dominant in the closed phase, with Abies amabilis being an associate and A. lasiocarpa an occasional. In the "open" phase, Tsuga dominance decreases as A. amabilis increases (Douglas 1972). Stands differ markedly in structure and composition, with variations in the understory depending on the openness of the canopy (Douglas 1971). Floristically, the Tsuga mertensiana-Abies amabilis association is among the poorest in the Pacific Northwest, averaging only eight species per stand.

Lowery (1972) has investigated the structure and composition of tree "islands" in the subalpine Tsuga mertensiana Zone of the North Cascades. He notes that tree islands in drier habitats, such as steep, south-facing slopes, are dominated by A. lasiocarpa, while T. mertensiana, A. amabilis, and Chamaecyparis nootkatensis tend to occur in more mesic and moist stands on more gentle slopes,

and at lower elevations. Lowery (1972) argues that the current composition of upper elevation tree groups reflects the differential success of _Abies lasiocarpa_ seedling establishment.

Swedberg (1961, 1973) described the vegetation in the Mount Jefferson region along the eastern flank of the central Oregon Cascades, where "discontinuous" _Tsuga_-dominated forests are found from 1,670 to 1,770 m elevation. The forest floor in these stands is characterized by a densely compacted litter layer (0) up to 5 cm thick which makes seedling establishment difficult. Regeneration tends to occur in dense pockets along the margins of small openings rather than under the forest canopy. _Abies amabilis_, _A. lasiocarpa_, and occasionally _T. mertensiana_ seedlings are most abundant.

In the forests of the Mt. Jefferson Wilderness, _Tsuga mertensiana_ trees have been observed growing in clumps having three to eight stems that diverge above breast height (Swedberg 1961, 1973). This has been explained by Geiger (1965) to result from the "black body effect," where dark bodies such as vegetative surfaces differentially absorb insolation and transform energy into sensible heat. This heating results in the early melting of snow adjacent to the main stem, and produces a crater-like depression around it. The crater exposes the soil surface at an earlier date than adjacent areas providing a lengthened growing season for

seedling establishment to occur. The understory of the
mountain hemlock stands is extremely sparse. Poorly repro-
ducing individuals of _Luzula_ spp. and _Lupinus_ spp. are
sparsely scattered on the forest floor (Swedberg 1973).
Species common in mesic sites that are protected from direct
insolation and the effects of deep snow cover include _Pyrola_
secunda, _Hypopitys_ _monotropa_, _Nothochelone_ _nemorosa_, and
Polemonium _californicum_. _Polygonum_ _newberryi_ and _Aster_ spp.
are common in areas of deep snow that receive intense in-
solation following snowmelt (Swedberg 1961).

Van Vechten (1960) has studied the forests above 1,950
m of the Three Sisters Wilderness in the central Oregon Cas-
cades. Dense stands of slow-growing _T. mertensiana_ extend
to tree limit. Erect growth, with only slightly diminished
heights, characterize the tree island stands of _Tsuga_ _mer-_
tensiana, _Abies_ _lasiocarpa_, and _Pinus_ _albicaulis_ at the
upper elevations. _Abies_ _amabilis_ only rarely extends above
the 1,950 m level. The litter layer under semi-closed moun-
tain hemlock stands is a densely packed duff, 1 to 3 cm in
thickness.

When sufficient light penetrates the canopy, _Luzula_
glabrata, _Luetkea_ _pectinata_, and _Vaccinium_ _myrtillus_ often
occur (Van Vechten 1960). Larger openings in the forest
support a somewhat richer flora of _Lupinus_ _perennis_, _Micro-_
seris _alpestris_, _Aster_ _ledophyllus_, _Carex_ _phaecocephala_,
Phyllodoce _empetriformis_, _Cassiope_ _mertensiana_, _Vaccinium_

membranaceum, and Rubus lasiococcus. Meadow vegetation in this area typically occurs on gently sloping to flat slopes supporting a distinctive and much richer flora than the adjacent forests (Van Vechten 1960). Along the northern edge of meadows, where early snowmelt exposes the ground surface, dense thickets of T. mertensiana interspersed with A. amabilis are evident. Van Vechten (1960) observes that these stunted (less than 2 m high), slow-growing trees have invaded meadows during the last 50 years. A warming trend over the past 50 years has resulted in decreased snowpack and the opening of habitat conducive to tree growth. This pattern of meadow invasion in response to a shifting climatic regime has also been examined by Brink (1959) in the forests of British Columbia. Franklin et al. (1971), Franklin and Dyrness (1973), and Kuramoto and Bliss (1970) also observe this trend in the Washington and Oregon Cascades. Henderson (1973) sees meadow invasion occurring on Mt. Rainier, but attributes the explanation to a complex interaction of good seed years being followed by a favorable temperature and precipitation regime.

Dyrness et al. (1974) have identified an Abies amabilis-Tsuga mertensiana/Xerophyllum tenax association in the Western Cascades. Located from 1,400 to 1,620 m elevation along ridgetops having shallow soils, this association represents a cold, dry type in their ordination of forest communities of the Western Cascades. A. amabilis and T.

mertensiana are dominant in the overstory, with Abies reproduction being more abundant and vigorous. The poorest sites have Tsuga as the sole community dominant. Vaccinium membranaceum occurs with high constancy in the understory, but only averages six percent cover. Xerophyllum tenax dominates the herb layer, with 100 percent constancy and 40 to 60 percent cover (Dyrness et al. 1974). The very high dominance and low species richness of the Abies-Tsuga/Xerophyllum community reverses the compositional trend found in the lower Abies amabilis and Tsuga heterophylla Zones. Species richness typically increases in the more extreme environments. That this does not occur in the Abies-Tsuga/Xerophyllum association suggests that the Tsuga mertensiana Zone extends into the 1,400 to 1,620 m elevation band in particular habitats of the Western Cascades (Franklin and Dyrness 1973; Zobel et al. 1976).

The Abies magnifica shastensis Zone extends northward along the east side of the Cascades to roughly 43° North latitude. It is found below the Tsuga mertensiana Zone at elevations between 1,600 and 2,000 m (Franklin and Dyrness 1973). The forests are dominated by Abies magnifica var. shastensis and associates include T. mertensiana, Pinus monticola, P. contorta var. contorta, Abies concolor, and A. amabilis. Higher elevation stands find Tsuga mertensiana dominance increasing and Abies magnifica var. shastensis dominance decreasing. Abies amabilis is found along the

northern boundaries of this Zone, along with an occasional
A. lasiocarpa. Vaccinium scoparium is the dominant under-
story shrub in the T. mertensiana co-dominated forests in
this Zone. Chimaphila umbellata and Carex pensylvanica are
characteristic understory plants in these mixed forests
(Franklin and Dyrness 1973).

Jackson and Faller (1973) have examined the forest
structure and dynamics of plant communities on Wizard Island
in Crater Lake National Park, Oregon. Tsuga mertensiana was
found as a dominant in the north slope and lava flow commun-
ities. Tsuga co-dominated with Abies magnifica var. shasten-
sis in the lower cone community, and was sparsely evident in
the crater rim community, where Pinus albicaulis dominated.
Species richness varied between community types from a low of
three species in the south slope community to a high of twenty
species in the north slope community.

Ordination

One objective of ordination is to suggest interactions
between physical and biological phenomena (Bray and Curtis,
1957). The indirect gradient approach to ordination is a
useful heuristic tool, not an end in itself. A danger
exists that inferred gradients will be treated as the ef-
fects (Bray and Curtis 1957). Indirect ordination, then,
should be used as a first approximation technique that dis-
plays general correspondences between unmeasured environmen-
tal gradients and biological phenomena (Whittaker 1967,
1975).

Vegetation patterns are expressed by complex species
population distributions across environmental gradients.
When these population distributions are taken together to
form community gradients or coenoclines (Whittaker 1967),
it becomes possible to separate out segments of the
coenocline and group them into community types (Whittaker
1967; del Moral 1973). Existence of abrupt changes in popu-
lation distributions, or "steep gradients" in nature lends

credibility to the idea of referring to community types, while retaining the conceptual versatility of being able to describe species compositional changes across environmental gradients. In this paper, ordination will be used to classify community types and place them in relation to the environmental complexes.

Zobel et al. (1974) used direct gradient analysis on reference stands representative of community types suggested by Dyrness et al. (1974). The x-axis was found to correlate well with pre-dawn plant moisture stress, and thus supports the moisture gradient intuitively conceived by Dyrness et al. (1974). The y-axis was found to be generally correlated with both temperature and nutrient status and was not related to a single overriding environmental variable as initially hypothesized. Additional research by Zobel et al. (1976) showed that a Temperature Growth Index (Cleary and Waring 1969) differentiated communities in the Tsuga heterophylla Zone from those in the Abies amabilis Zone. Contrary to the intuitive predictions of Dyrness et al. (1974), a moisture gradient separated communities well in the Tsuga heterophylla Zone, but did not in the higher elevation Abies amabilis Zone.

Thornburgh (1969) used both direct and indirect gradient analysis in a study of vegetation in the Abies amabilis Zone southwest of Mt. Rainier, Washington. Elevation and slope exposure were considered the two complex environmental

variables forming the axes of the ordination. Elevation roughly corresponded to changes in temperature to form one axis, while snow depth and slope exposure together related to length of growing season (e.g., length of snow free period).

Long (1976) used indirect gradient analysis in his interpretation of the vegetation patterns of the Cedar River watershed within the Abies amabilis Zone in Washington. He interpreted depth and duration of winter snowpack as the primary gradient, with a secondary gradient being available soil moisture.

These examples of vegetation research in the Pacific Northwest suggest that regardless of the type of gradient approach used in the ordination, a variety of complex environmental patterns may influence vegetation patterns in different regions and Zones (Long 1976). Use of direct measurement techniques in forming composite environmental indices also suggests variability between subregions where the indices are suggestive of the distribution of vegetation (Zobel et al. 1976).

METHODS

Field Methods

Stand Selection

Stands were selected initially so as to fall within a 20 degree range of the aspects northeast, northwest, southeast, and southwest. These aspects were chosen because they represent the extremes of insolation and surface heating at 45°N. latitude in the Northern Hemisphere (Holland and Steyn 1975). Within a given aspect, efforts were made to represent the broadest range of Tsuga mertensiana communities possible by selecting sets of stands that varied by elevation and steepness of slope.

Vegetational characteristics further defined the selection of stands, e.g., stands were required to have Tsuga as a major component expressed in terms of density and/or total basal area. Stands were selected primarily on the basis of overstory homogenity, e.g., stands were rejected if there was a dominance of one species in one part of the stand and dominance of another species in a different part of the stand (Mueller-Dombois and Ellenberg 1974). Stands also were required to have habitat characteristics and reflect the kind of habitat variability representative of the area as a whole. Stands evidencing human disturbance were not

sampled. Finally, with all of the above criteria having been satisfied, circular plots were located in the most typical portion of the selected stands.

Plot Design

A circular plot of 12.6 m in radius and covering 500 m^2 was used as the standard plot size and shape (Figure 2). Within the plot, individual trees four centimeters diameter at breast height (DBH) or greater were recorded by species name and DBH. Shrub Cover was measured by four, 10 m line intercepts. Cover was measured along each linear meter by recording species name and the number of centimeters the species occupied below a tape (1 cm wide) held at waist height. This technique provided both cover estimates and frequency data for shrubs. Cover and frequency data were recorded for the herb layer by using 40, 2 x 5 dm microplots, cover being estimated in six Daubenmire (1968) cover classes. Ten microplots spaced at one meter intervals along the four line intercept radii (totaling 40 microplots) provided the sample for the herb layer. The radii for the line intercept and the microplots were laid out along the four cardinal directions using a Brunton pocket transit compass.

Four, two meter radius subplots were located systematically within the plot to record seedling regeneration. Within the subplots, the number of tree seedlings less than four centimeters DBH were recorded by species. Totals from
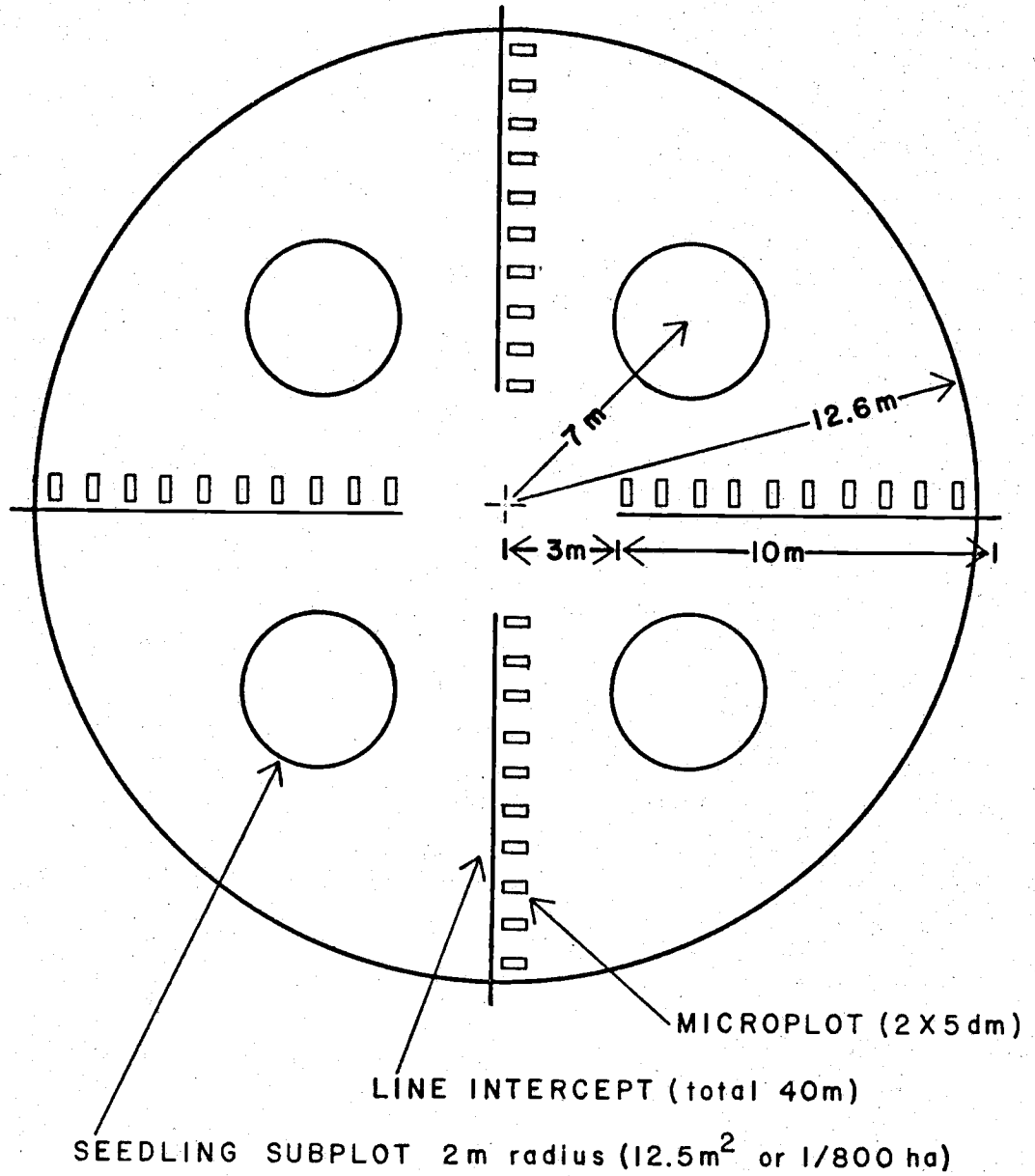
Figure 2. Sample plot (500 m² or 1/20 ha).

the four subplots provided the basis for absolute and relative density data.

Environmental Data

Selected environmental data were recorded in each sample stand. Location was determined by intersection of site lines from known landscape features. Elevation was interpolated using a U.S.G.S. topographic map. Aspect was recorded with a Brunton pocket transit and average slope steepness with a Suunto clinometer. Microtopography (e.g., shape of the slope in cross-sectional profile) and position of the stand on the slope were also recorded. Litter depth for each stand was averaged from four sampling points within the plot. Cover estimates for litter, bare ground, rock, and fallen log were tallied within the 40 microplots.

Laboratory Methods

Relative density is the ratio of the number of living stems of each species to the total number of living stems within a plot, and may vary from 0.0 to 1.0 for a given species within a plot. Relative basal area is a ratio of the basal area of a given tree species to the total basal area of all tree species within a plot, and may vary from 0.0 to 1.0 for a given species within a plot. A prominence

value is calculated for all tree species within a plot by averaging relative density and relative basal area so that 1.0 represents complete dominance of a species within a plot, and 0.0 represents the absence of a species within a plot. A prominence value, therefore, represents a synthetic measure reflecting the relative dominance of a tree species within a given plot.

A compositional change index measures the overall compositional change within a plot (Goff 1968) and is calculated by first calculating relative density and relative basal area for each tree species within a given plot. The sum of the absolute difference between the two values is averaged for each species, and the sums of the absolute differences for all species are added together and divided by two. The result is a single value on a scale from 0.0 to 1.0; the larger the value, the more compositional change taking place within a plot (e.g., the amount of change in relative proportions of tree species to one another). The compositional change index is calculated by the following equation:

$$C = \Sigma \frac{|Relden_i - Relba_i|}{2}$$

where: C = the compositional change index

    $Relden_i$ = the relative density for a species within a plot

    $Relba_i$ = the relative basal area for a species within a plot

An example of this calculation is given in Table 1.

Table 1. Calculation of compositional change within plot
#44 at elevation 1,580 m.

Species	Relden	Relba	Abs. Diff.
Tsuga mertensiana	.76	.54	.22
Abies lasiocarpa	.02	.004	.016
A. amabilis	.06	.002	.058
A. magnifica var. shastensis	.12	.36	.24
Pinus monticola	.04	.014	.036
	1.0	1.0	.57

$$C = \Sigma \left| Relden_i - Relba_i \right| / 2$$

$$C = .57/2 = .285$$

A Wisconsin-type ordination technique is used to compare similarity between plots based on floristic composition (Bray and Curtis 1957). Plot similarity is determined by calculation of a similarity coefficient using the computer program, subroutine SIMORD (Dick-Peddie and Moir 1970). Similarity is first computed using the Dick-Peddie and Moir (1970) index, where the similarity between any two plots, I and J, is computed as:

$$SIM(I,J) = \frac{1}{n} \sum_{k=1}^{n} \frac{2 \min (a_{ik}, a_{jk})}{a_{ik} + a_{jk}}$$

and a_{ik} and a_{jk} are cover measurements of the kth species in plots I and J. When presence-absence data are used, the Dick-Peddie and Moir index becomes the same as the Jaccard (1901) index. The second step of the two-dimensional ordination compares plot similarity values with selected reference plot values along x- and y-axes. Reference plots may be chosen by the investigator or selected by the SIMORD program. Reference plots for the ordination presented were chosen by the investigator. For a discussion of how SIMORD selects reference plots and ordination distances are computed, see Appendix I.

A variety of different vegetational characteristics was experimented with to determine which provides the best separation between plots within the two-dimensional ordination plane. For the purpose of classification, the best separation between plots was achieved using presence-absence data.

RESULTS

Vegetation Structure

Stem density, basal area, and average diameter per plot represent structural components that reflect the distribution of above ground biomass within a forest stand. Correlations among structural components, and between structural components and environmental characteristics of 51 sample plots are presented. Appendix IV lists plot structural and compositional characteristics. Appendix III lists plot environmental characteristics.

Absolute density refers to the number of living tree stems four centimeters DBH and larger for all species within a 500 m^2 plot. Total basal area is the total basal area for all tree species four centimeters DBH and larger within a 500 m^2 plot.

Figure 3 shows that the plots having larger average diameter (>56 cm DBH) have absolute densities less than 20. Plots having lower average diameters exhibit absolute densities from 30 to 70. A negative correlation (r = -0.73) exists between average diameter per plot and absolute density throughout the study area. The relationship between absolute density and average diameter has been treated as a linear relation, but obviously is nonlinear. No attempt has been made to fit a curve to this relation.
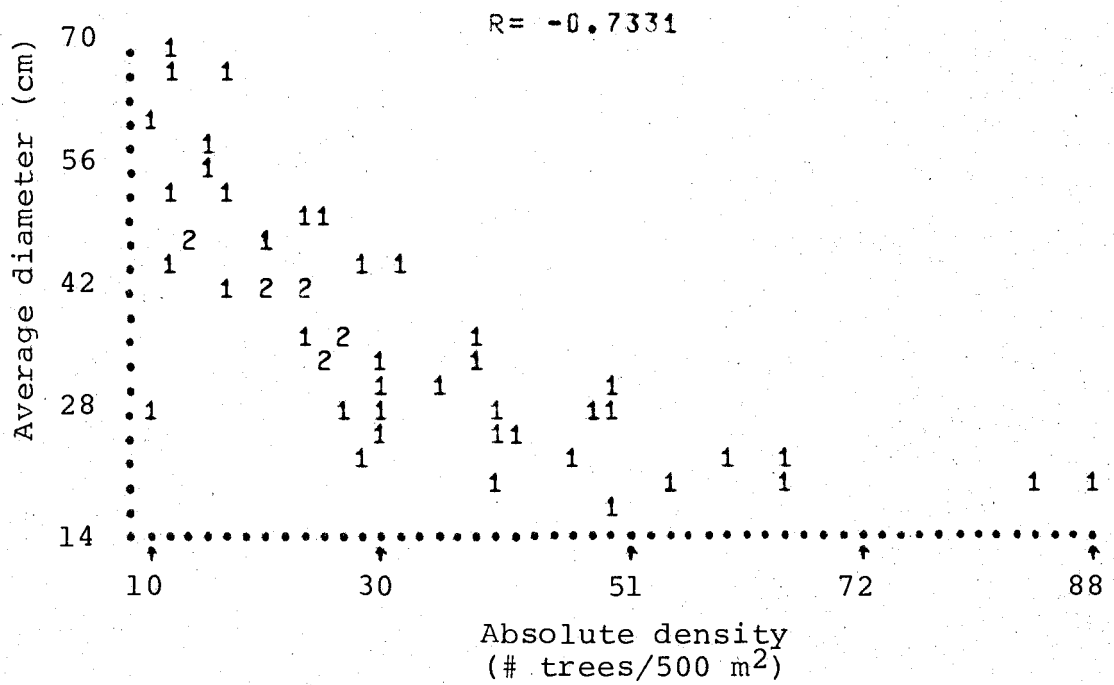
Figure 3. Correlation between absolute density and average
diameter for 51 plots.

Average diameter within a plot correlates positively with total basal area within a plot (r = 0.56). Figure 4 shows the tendency for plots with low average diameters to have low total basal area, and plots having high average diameters to have high basal area totals. The standard deviation in total basal area increases with increasing average diameter.

A weak positive relationship is evident between total basal area and plot elevation (r = 0.56). A positive correlation between average diameter and plot elevation is also weakly evident (r = 0.43). These two relations, together with the tendency for absolute densities to decrease with elevation (r = -0.38), suggest a tendency toward increasing dominance of the canopy by a few large trees at higher elevations.

General compositional change (for definitions see Laboratory Methods) within each plot was plotted along a variety of topographic and elevational gradients. No clear correlation between compositional change and elevation exists. Similarily, gradients of aspect and steepness of slope exhibited no clear relationship to the amount of compositional change taking place within a plot.
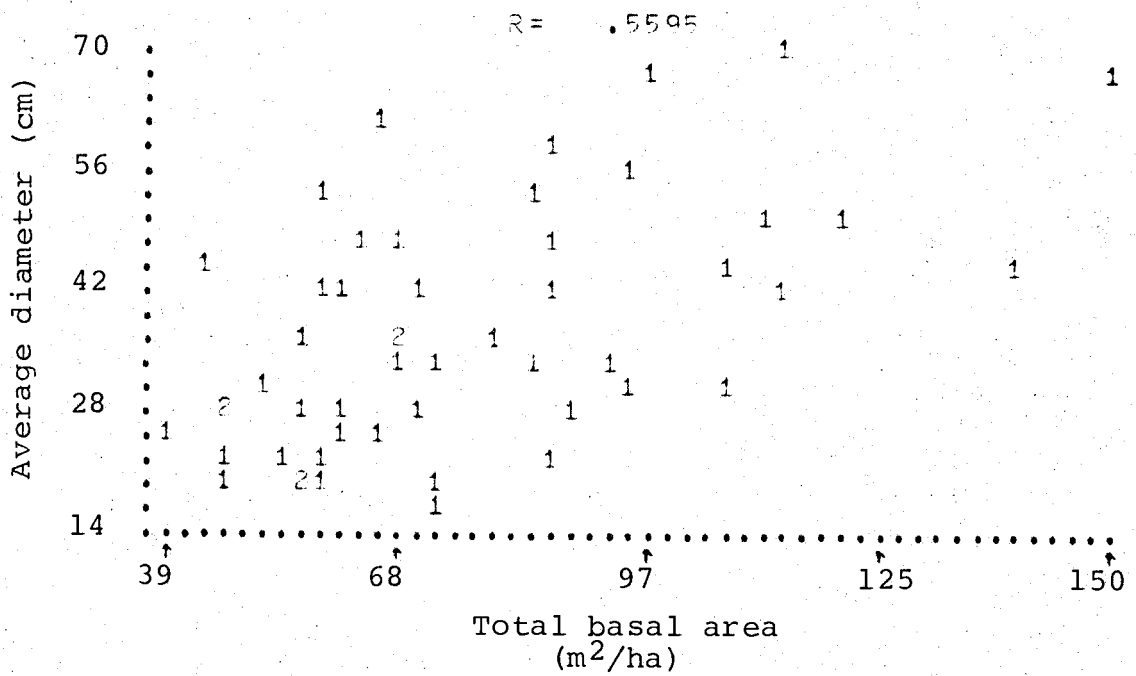
Figure 4.   Correlation between total basal area and average diameter for 51 plots.

Size Class Distribution

Size class refers to a range of DBH measurements by species. Six size-classes are employed: (1) seedlings (less than 4 cm DBH); (2) 4 to 10 cm DBH; (3) 10 to 20 cm DBH; (4) 20 to 40 cm DBH; (5) 40 to 60 cm DBH; and (6) over 60 cm DBH. A size class distribution of a plot shows the number of individual trees of each species in each size class in relation to all other species in each size class.

Table 2 shows the relative frequency of major tree species by size class within the 51 sampled plots. A shift in regeneration size class density and frequency occurs in mid-elevation plots. Figure 5 shows a shift in relative densities of Abies amabilis and Tsuga mertensiana seedlings across a 170 m elevational segment in mid-elevation (1860 to 2030 m) plots within the study area. Abies lasiocarpa, Pinus monticola, and P. contorta var. contorta seedlings are omitted in this analysis because of their seral status and low prominence values. Relative densities of A. amabilis seedlings are consistently high in plots below 1,950 m. An abrupt shift in seedling densities occurs between 1,980 and 2,000 m, where T. mertensiana seedling relative densities surpass A. amabilis relative densities. Abies amabilis seedlings drop out entirely above 2,030 m.
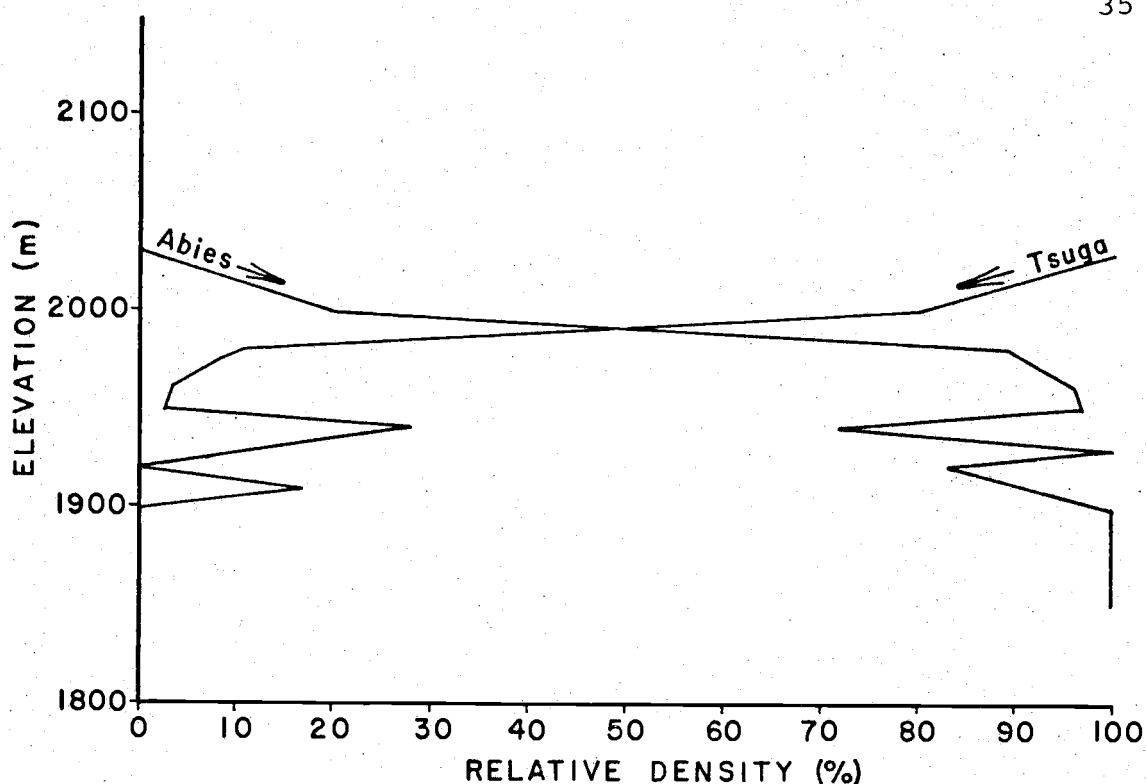
Figure 5. Relative density of Tsuga mertensiana and Abies amabilis seedlings in mid-elevation (1,860 to 2,030 m) stands.

Table 2. Relative frequency of major tree species by size class within 51 forest plots.

Species	Size class (cm) DBH					
	<4	4-10	10-20	20-40	40-60	>60
Tsuga mertensiana	.61	.65	.73	.90	.92	.87
Abies lasiocarpa	.37	.25	.20	.16	.06	.02
Abies amabilis	.47	.24	.20	.20	.16	.00
Pinus monticola	.12	.10	.06	.10	.08	.04

From 2,000 m to tree limit, seedling composition is primarily T. mertensiana with Abies lasiocarpa a minor component. A. lasiocarpa reproduces both by seed and vegetatively through layering in the upper elevation stands. Tsuga occasionally is found layering along rock outcroppings and on the margins of tree "islands" above 2,000 m.

Seedling densities in forests below about 1,900 m are highest for Abies amabilis, although Tsuga seedlings are present in low densities and with reduced vigor. Analysis of the entire size class distribution in the lower elevation (1,580 to 1,900 m) forests is shown in Figure 6. Absolute frequency is defined as the number of occurrences of a species within a given size class, and consequently emphasizes presence-absence while de-emphasizing dominance. Absolute frequencies have been accumulated for a given species for the number of plots in three elevational belts. Relative frequency of a species refers to the percentage of plots within the total sample that a species occurs within a given size class. Relative frequency in the seedling size class of Tsuga and Abies amabilis is roughly equal, being 55 to 60 percent in plots below 1,900 m. However, these relative frequencies do not take into account the relative seedling densities, e.g. A. amabilis is found as high as $314/12.5 \text{ m}^2$, as compared to $3/12.5 \text{ m}^2$ for Tsuga and A. lasiocarpa.
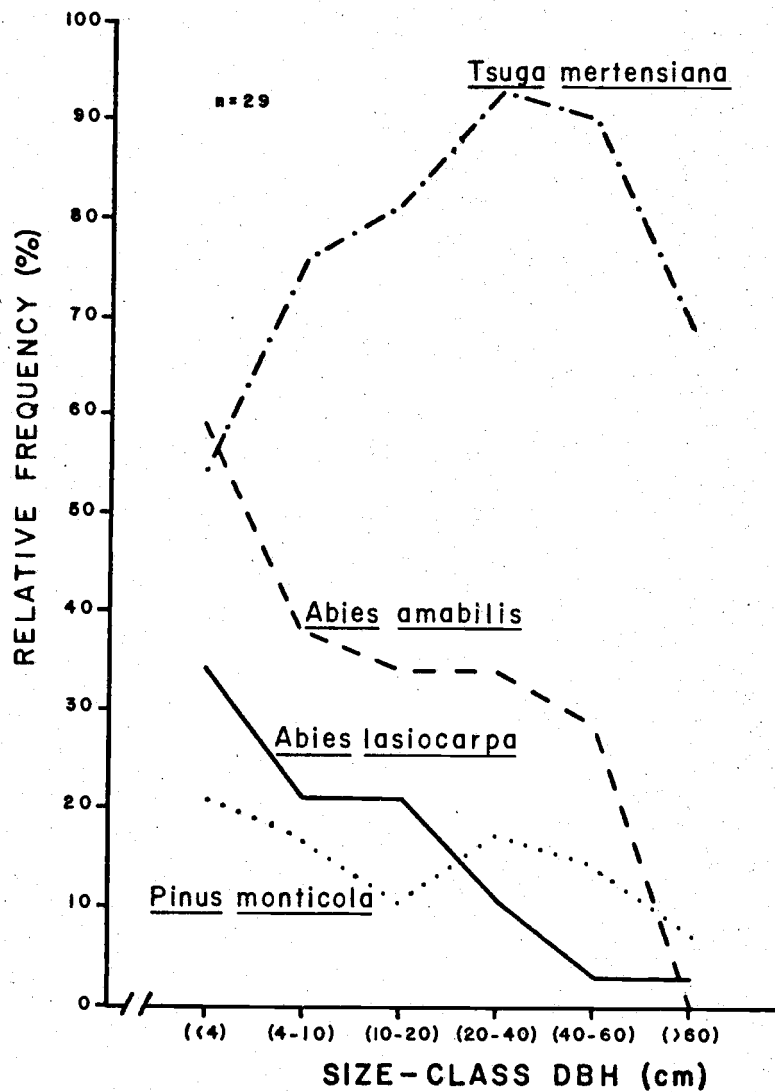
Figure 6. Relative frequency of tree species by size-class
in lower elevation (1,580 to 1,900 m) plots.

Abies lasiocarpa and Pinus monticola seedlings are less
frequent, occurring at 34 and 21 percent, respectively. The
relative frequency of these two species drops progressively
through intermediate size classes, until relative frequency
for A. lasiocarpa is 3 percent and P. monticola is 7 percent
in the >60 cm DBH size class. Abies amabilis occurs at 30
to 40 percent relative frequency through intermediate size
classes, but is not represented in the largest size class.
Tsuga occurs between 70 and 90 percent relative frequency
through intermediate and large size classes.

Figure 7 shows relative frequency of major tree species
as a function of size class in mid-elevation (1,900 to 2,000
m) plots. A. amabilis, A. lasiocarpa, and T. mertensiana
seedlings all occur between 45 and 65 percent relative fre-
quency, dropping to between 8 and 23 percent in the 4 to 10
cm DBH size class. Abies amabilis is not found in the
intermediate or large size classes in this elevational belt.
A. lasiocarpa occurs from 20 to 30 percent relative frequen-
cy through the 40 to 60 cm DBH size class, above which it
does not occur. T. mertensiana occurs at 30 percent rela-
tive frequency in the 10 to 20 cm DBH size class, and rises
abruptly to between 90 and 100 percent in the three size
classes above 20 cm DBH.
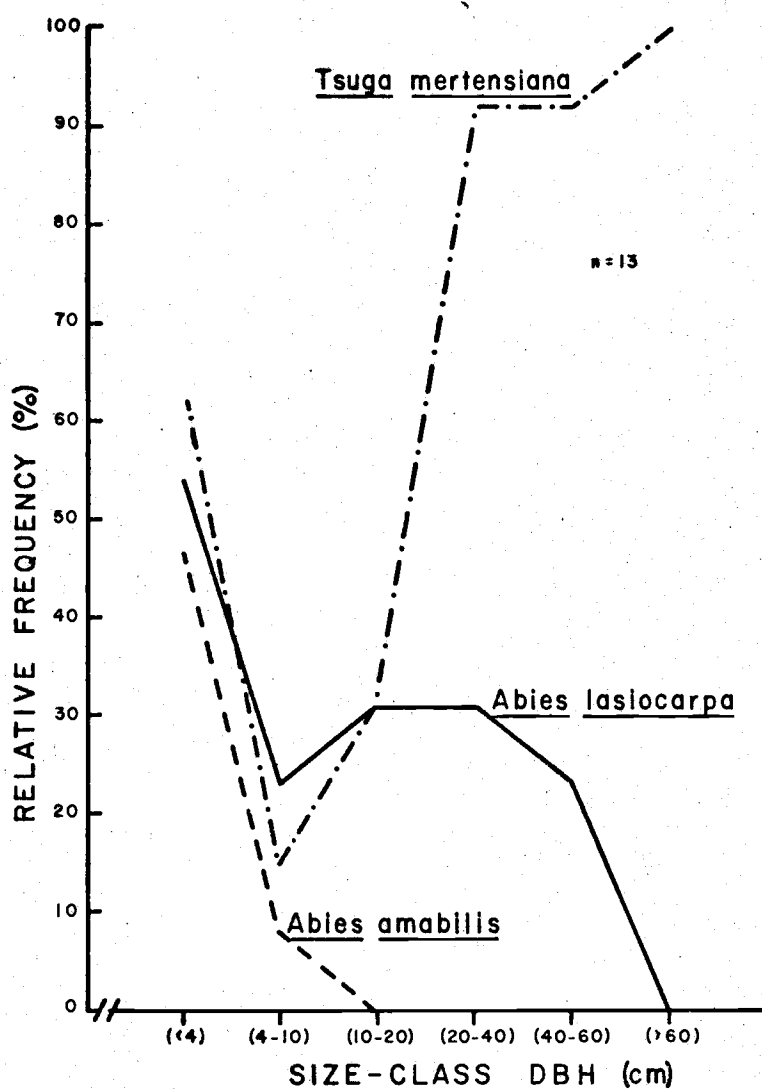
Figure 7. Relative frequency of tree species by size-class in mid-elevation (1,900-2,000 m) plots.

Species Distribution Patterns

Species Prominence Values

Tsuga mertensiana is a dominant or codominant in all sample plots throughout the study area. Absolute constancy refers to the number of plots in which a given species occurs. Relative constancy expressed in percent, is the proportion of plots in which a given species occurs divided by the total number of plots. The 100 percent constancy and high prominence values of Tsuga in all 51 sample plots argue for it's importance in the sampled forested areas above 1,600 m within the study area.

A prominence value (for definition see Laboratory Methods), based on relative density and relative basal area, provides one method for estimating the relative importance of tree species across environmental gradients in the study area. Tsuga is the sole overstory dominant in one third of the sample plots, and is a major dominant in one third of the plots, attaining prominence values of 0.80 to 0.95. In the remaining plots Tsuga has prominence values below 0.80 and occurs with A. amabilis, A. lasiocarpa, together with the seral species Pinus monticola, P. contorta var. contorta, and P. albicaulis.

Figure 8 shows the prominence values of major tree species by elevation. T. mertensiana has prominence values
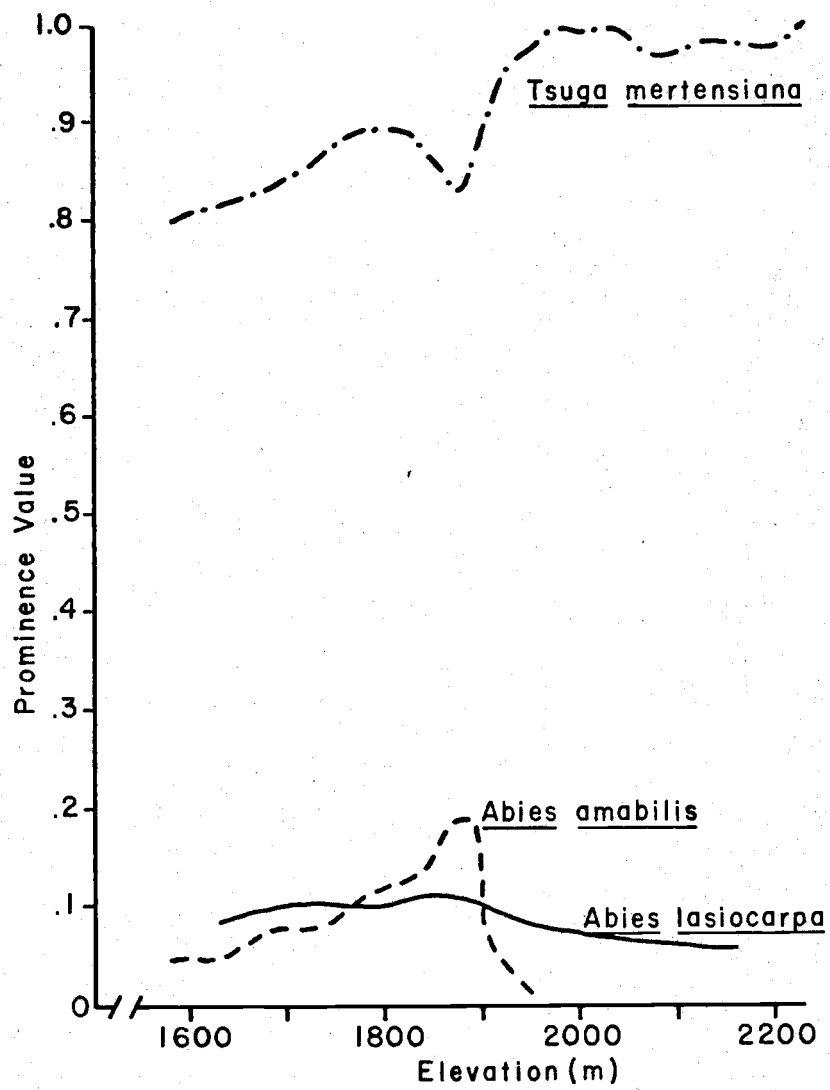
Figure 8. Prominence values of major tree species by elevation.

greater than 0.90 at elevations above 1,950 m. Below 1,950

m elevation, Tsuga prominence values range from 0.53 to 1.0,

with a mean prominence value of 0.85. Only in five plots

does Tsuga have a prominence value below 0.75.

Correlation between T. mertensiana and Abies amabilis

prominence values shows that Abies has it's highest pro-

minence where Tsuga drops in prominence (r = -0.81). This

relation is most clear at mid-elevations (1,800 to 1,900 m)

where A. amabilis prominence rises to 0.20 and T. merten-

siana drops below 0.80.

Abies lasiocarpa extends throughout the elevational

range of the study area as a minor component with promi-

nence values ranging from 0.06 to 0.12. The habitat pre-

ferences and competitive interactions of A. lasiocarpa are

not at all clear as the species is not restricted to any

particular aspect, topographic position, or elevation.

Species Distribution and Compositional Change

A compositional change index (for definition see

Laboratory Methods) was calculated for each plot. Composi-

tional change within a plot was correlated with species

prominence values within the plot. Tsuga mertensiana shows

a marked tendency to have high prominence values in plots

undergoing little compositional change (r = -0.91). Con-

versely, Tsuga achieves lower prominence values in plots

undergoing larger amounts of compositional change (Figure 9).
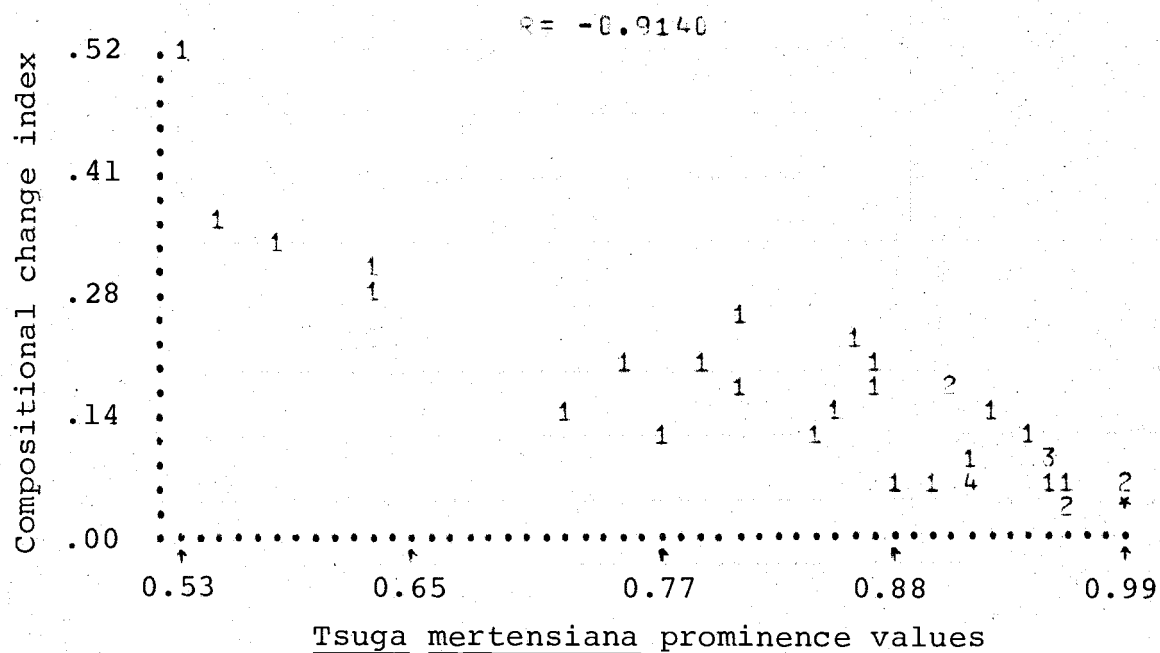
Figure 9. Tsuga mertensiana prominence values in relation
to sample plot compositional change index.

A tendency exists for A. amabilis to exhibit high prominence values in plots undergoing large (e.g., >0.28) amounts of compositional change (r = 0.74). Prominence values less than 0.12 are common for Abies in plots undergoing less (e.g., <0.28) compositional change (Figure 10).

Understory Species Distribution

The most salient feature of the understory in the 51 sample plots is the low number of species encountered. Including tree species less than 4 cm DBH, understory richness varied from three species in the most depauperate plot, to eleven species in the richest plot. Correlations between the number of species within a plot and selected environmental variables (see Field Methods) suggested no apparent relationships.

Vaccinium scoparium and V. membranaceum are the two most common shrub species in the study area. Within any particular stand one or the other of these species predominates, usually to the exclusion of the other. Luzula hitchcockii dominates the herbaceous understory at higher elevations.

Vaccinium membranaceum has 20 percent constancy throughout the 51 sample plots. Seldom exceeding three percent cover in any single plot, V. membranaceum is mainly restricted to drier sites at mid- and lower elevations. Vaccinium scoparium occupies mesic sites at elevations up
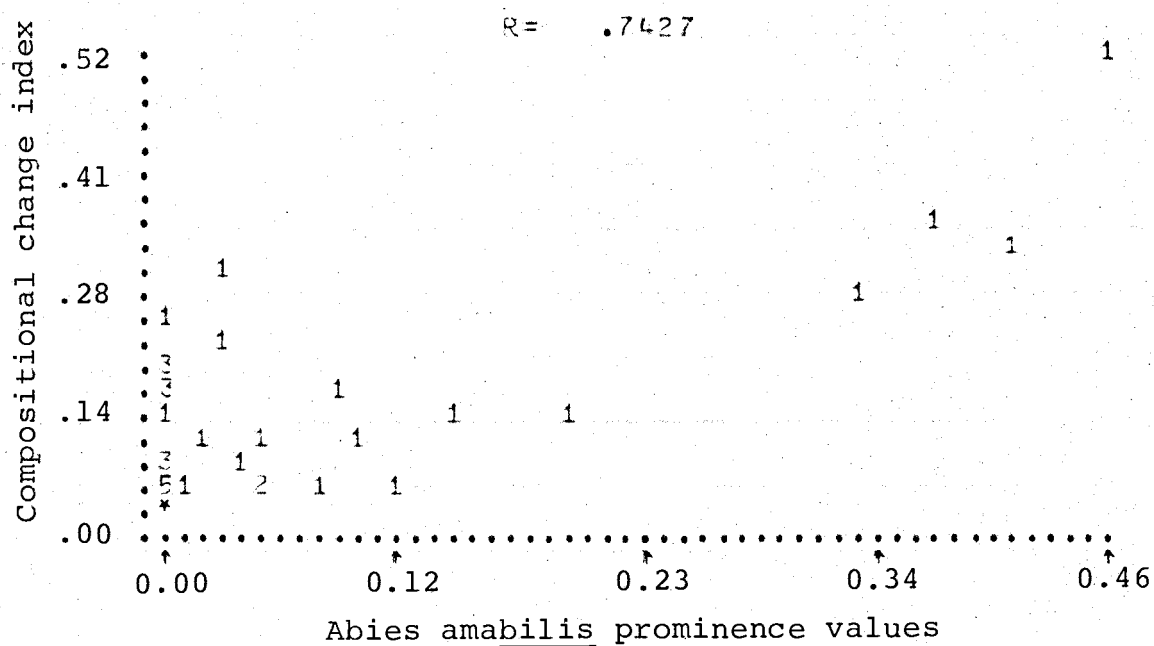
Figure 10. Abies amabilis prominence values in relation to sample plot compositional change index.

to 2,000 m. V. scoparium has 70 percent constancy, usually with a cover of less than 5 percent; however, cover values up to 30 percent are recorded within the study area. V. scoparium cover values are consistently higher in the seven sample plots taken in the Abies magnifica shastensis Zone, located along the eastern flank of Diamond Peak (area C on Figure 1). Luzula hitchcockii, with a few exceptions, is restricted to elevations above 1,900 m. Luzula has 95 percent constancy in plots above 1,900 m, and typically attains cover values from 5 to 10 percent, but, 30 to 60 percent coverage is not uncommon in the highest elevation plots.

Distribution of Community Types

Four community types are delimited by ordination based on presence-absence data combined with analysis of size class distribution of the 51 sample plots:

(1) Abies amabilis-Tsuga mertensiana/Vaccinium membranaceum

(2) Abies amabilis/Vaccinium scoparium

(3) Tsuga mertensiana/Vaccinium scoparium

(4) Tsuga mertensiana/Luzula hitchcockii

Figure 11 shows the distribution of community types within the ordination plane. Each of the 51 sample plots were assigned to one of the four community types. From this classification, relationships between community type (e.g., characteristics of all the sample plots having the same classification) and a number of environmental variables were made.

Figure 12 shows the relationship between community type and elevation. The Tsuga mertensiana/Luzula hitchcockii type is confined to elevations above 1,900 m, the T. mertensiana/Vaccinium scoparium type extends from 1,700 to 1,950 m, and the Abies amabilis/V. scoparium type occurs from 1,600 to 1,950 m. The A. amabilis-T. mertensiana/V. membranaceum type, the lowest, occurs from 1,580 to 1,880 m.

The relationship between the total basal area within a stand and community type is illustrated in Figure 13 where the Tsuga mertensiana/Luzula hitchcockii type exhibits the largest total basal areas.

The Abies amabilis-Tsuga mertensiana/Vaccinium membranaceum type is represented by six plots (12 percent of

A Abies amabilis – Tsuga mertensiana / Vaccinium membranaceum
• Abies amabilis / Vaccinium scoparium
+ Tsuga mertensiana / Vaccinium scoparium
■ Tsuga mertensiana / Luzula hitchcockii
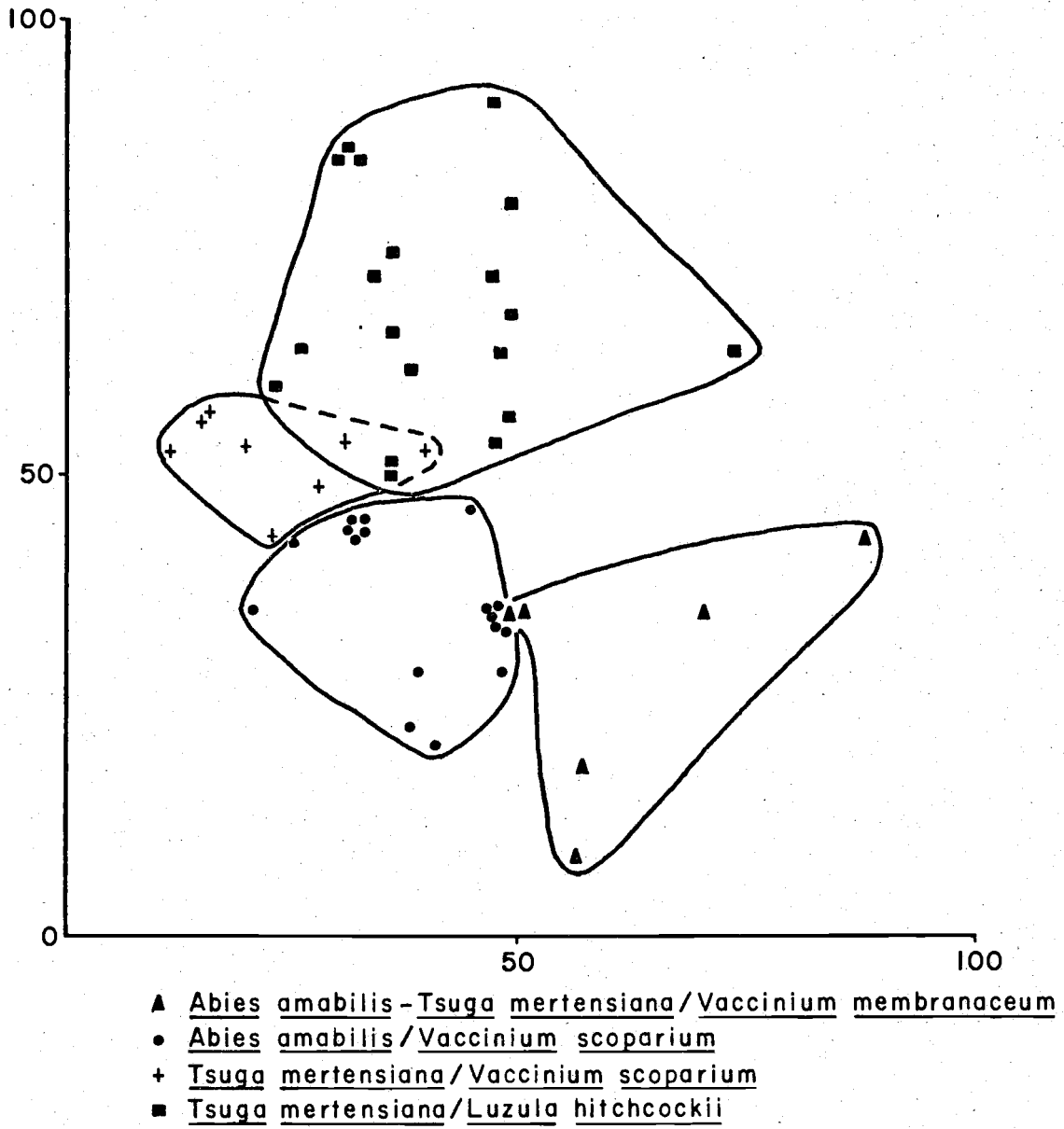
Figure 11. Ordination of 51 forest stands based on
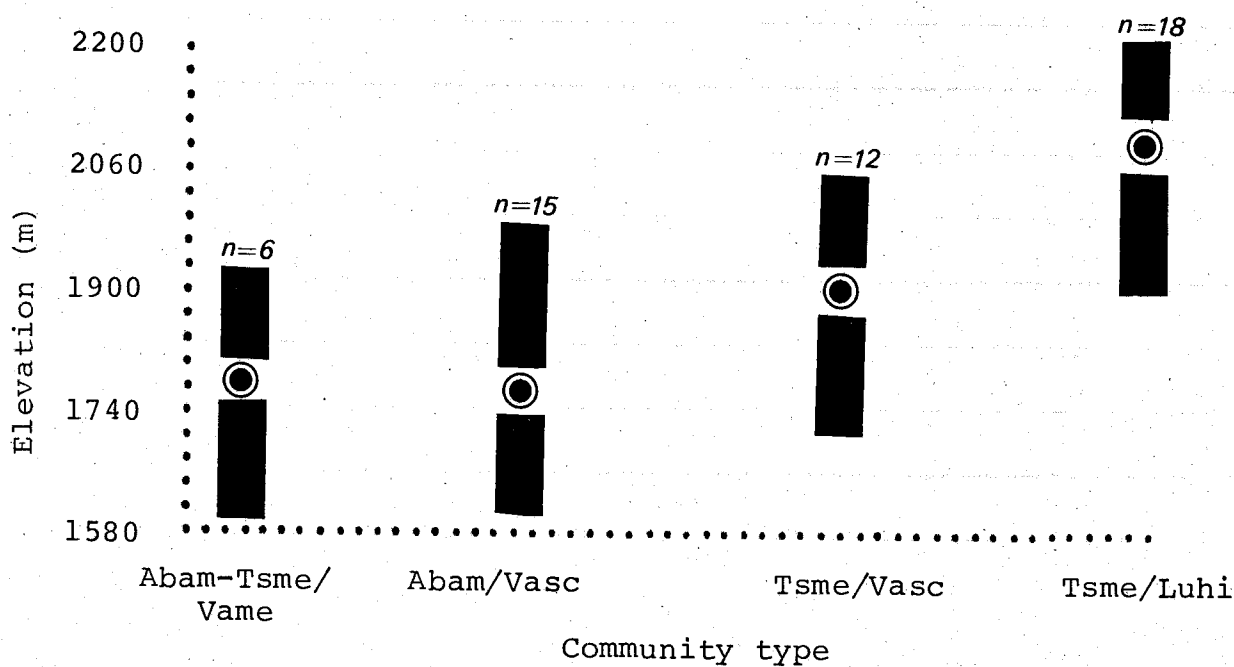constancy.

Figure 12. Relation between elevation and community
type for 51 plots.

Vertical bars indicate elevational range
of community type. ⊙ indicates average
elevation.
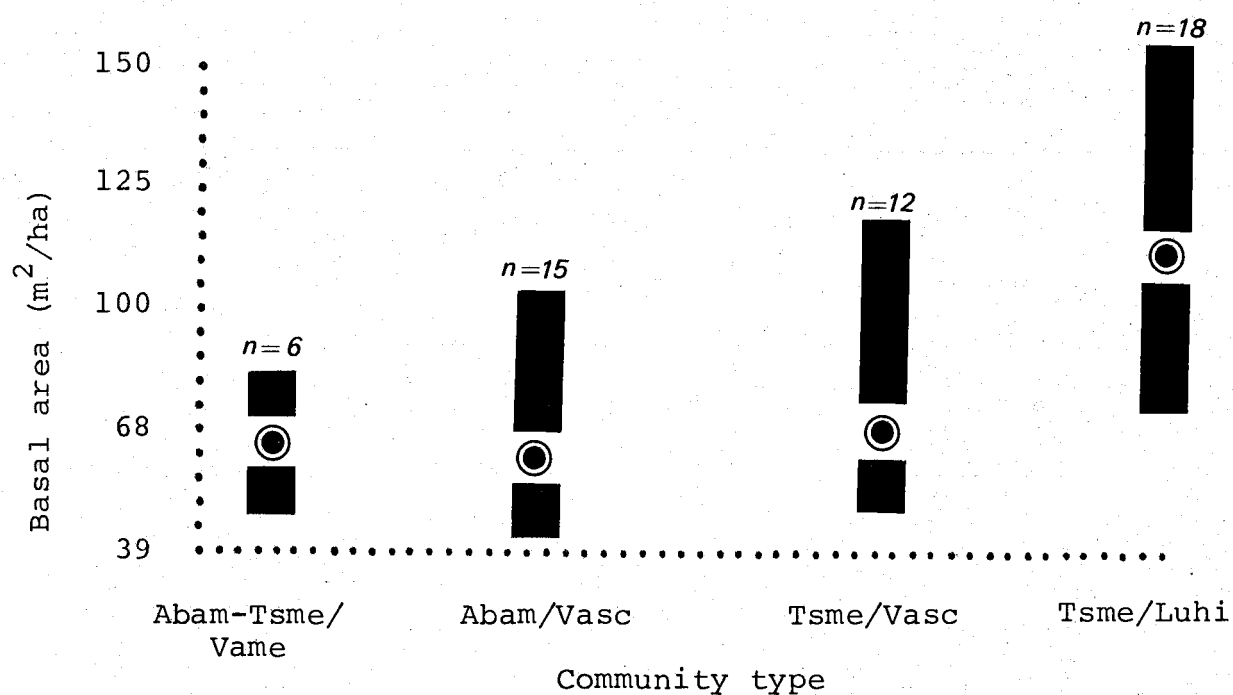
Figure 13. Relation between total basal area and
            community type for 51 plots.

            Vertical bars indicate elevational range
            of community type. ◉ indicates average
            elevation.

all plots). T. mertensiana is the major dominant with an
average prominence value of 0.87. Abies amabilis (average
prominence value of 0.09) and A. lasiocarpa average pro-
minence value of 0.04) occur as minor associates in this
type. Tsuga has 100 percent constancy within this type,
while both species of Abies exhibit 50 percent constancy
within the six plots. Vaccinium membranaceum is the domi-
nant shrub in this type, although V. scoparium attains one
percent cover in one plot. Pyrola secunda reaches one per-
cent cover in a few plots and Rubus lasiococcus occurs as a
minor element in the most western plots located along the
flanks of Irish Mountain. Chimaphila umbellata, Pyrola
picta, Nothochelone nemorosus, and Hypopitys monotropa are
also found in this type.

The Abies amabilis/Vaccinium scoparium type occurs in
17 plots (33 percent of all plots). T. mertensiana has 100
percent constancy and an average prominence value of 0.84
within this type. A. amabilis has a 60 percent constancy
and average prominence value of 0.13, and Pinus monticola
and Abies lasiocarpa occur as minor associates at prominence
values of 0.02 and 0.01, respectively. Vaccinium scoparium
typically occurs at cover values less than three percent and
often is the sole understory species in this type.

All seven of the sample plots taken within the Abies
magnifica shastensis Zone on the east side of Diamond Peak
belong to the Abies amabilis/Vaccinium scoparium type.

Abies amabilis seedling regeneration and occupance of inter-
mediate size classes suggest that A. amabilis is achieving
codominance with Tsuga from 1,600 to 1,830 m. Abies magni-
fica var. shastensis regeneration is sparse in these plots,
but has diameters up to 115 cm DBH. Shrub cover is typical-
ly Vaccinium scoparium ranging in cover from 2 to 30 percent.
Pachistima myrsinites occurs throughout this type in very
low quantities. Common herbs include a sparse cover of
Chimaphila umbellata, Pyrola secunda, and Lupinus latifolius
var. subalpinus.

The Tsuga mertensiana/Vaccinium scoparium type is
represented by eight plots, or 16 percent of the total
sample. Tsuga has an average prominence value of 0.91,
Abies lasiocarpa a 44 percent constancy and an average pro-
minence value of 0.08. An occasional Pinus monticola may be
found in valley bottoms or cold pockets. The understory is
primarily Vaccinium scoparium with low coverage. There are
no herbaceous species characteristic of this type although
Polygonum newberryi, Microseris alpestris, and Carex ros-
sii occur in openings and along the margins of the semi-
closed forests of this type.

The Tsuga mertensiana/Luzula hitchcockii type consists
of 18 plots (35 percent of the total) in the study area.
T. mertensiana occurs as a major dominant (prominence value
of 0.96) throughout this type. A. lasiocarpa is a minor
associate (prominence value of 0.03) in about one third of

the plots. *Pinus albicaulis* occurs in three plots with a
prominence value of 0.01. The major understory dominant is
Luzula hitchcockii, occurring at cover values ranging from
1 to 60 percent. An occasional *Vaccinium scoparium* shrub
occurs at the lower elevational limits (e.g., 1,900 m) of
this type.

DISCUSSION

Interpretation of Ordination

The distribution of forest community types within the ordination plane suggests interpretation of two complex environmental gradients. The composition of plots, and their location within the ordination plane is a reflection of the tolerance ranges and competitive abilities of the species present (Dyrness et al. 1974; Fonda and Bliss 1969).

The x-axis in the ordination seen in Figure 11 is interpreted to represent an available soil moisture gradient primarily affected by snow melt but also affected by aspect, slope steepness, slope position, microtopography, and soil drainage. No single combination of these factors are operative in all plots, and the usefulness of this inferred gradient must be born out by future direct gradient analysis.

The ordination y-axis is interpreted as corresponding to differences in temperature and snow depth and duration influenced by changes in elevation. A low position along this axis reflects lower elevation with less snow depth and increased snow free season. A high position along the y-axis reflects a colder, high elevation plot that receives more snow and a shortened snow-free season.

According to this interpretation, the Abies amabilis-Tsuga mertensiana/Vaccinium membranaceum type is sub-mesic,

and has the longest snow free season. These plots occur at elevations below 1,880 m on all aspects of varying steepness and position. The _A. amabilis/Vaccinium scoparium_ type occurs in an intermediate position along the x-axis at elevations below 1,900 m experiencing an intermediate to long snow-free period. The _Tsuga mertensiana/Vaccinium scoparium_ type is the most mesic, having intermediate to short growing seasons. The _T. mertensiana/Luzula hitchcockii_ type is intermediate in soil moisture relations and occupies plots above 1,900 m experiencing deep snow pack and short growing seasons.

Regeneration and Vegetation Development

Use of structural characteristics to infer compositional changes through time is most meaningful when supported by a knowledge of the autecology of the dominant species within a given area. The apparent morphological adaptations of tree species to the forces of snow illuminate successional trends within the study area. _T. mertensiana_ seedlings and saplings survive snow compaction and creep better than _Abies_ spp. or _Pinus_ spp. _Tsuga_ possesses the ability to "snap back" to vertical upon release from loading by snow, where _Abies_ and _Pinus_ are often broken off. In the Oregon Cascades, breakage tends to be less severe in _Tsuga_ than in other tree species partially because of it's supple stem, and partially because of an ability to form

compression wood growth in response to snow creep (Williams 1966; Fowells 1965).

The relative frequency of tree species by size class data suggests three subzones within the Tsuga mertensiana Zone in the study area:

    (1)   Subalpine Subzone;

    (2)   Transition Subzone; and

    (3)   Montane Forest Subzone.

Subalpine Subzone

Above 1,900 m, T. mertensiana is the major dominant with A. lasiocarpa a minor associate. Reproduction size class density for Tsuga is low, but apparently sufficient to regenerate by seed in a good year. Tsuga also is found vegetatively reproducing through layering occasionally within the Subalpine Subzone. This area conforms to the Subalpine Subzone of the Tsuga mertensiana Zone described by Franklin and Dyrness (1973).

Transition Subzone

The elevational span from roughly 1,800 to 1,900 m represents a transitional belt between the Subalpine Subzone and the Montane Forest Subzone. The upper margins of this transition mark the highest extent of Abies amabilis. Size class distribution reveals that A. amabilis regenerates in semi-openings throughout the subzone. Seedling densities

are much higher for A. amabilis than for Tsuga, and this has
been interpreted in other studies to suggest the eventual
replacement of Tsuga by Abies amabilis (Franklin 1966;
Franklin and Mitchell 1967; Franklin and Dyrness 1973).
However, the low densities of A. amabilis in size classes
larger than seedlings may be interpreted variously; (1) not
enough time for the development of Abies into larger size
class but, given enough time, development will occur because
A. amabilis has an ability to withstand suppression for long
periods in old-growth Tsuga-dominated forests; or, (2) the
process of directional change in vegetative composition is
periodically interrupted by environmental disturbances such
as unusually heavy snowfall. Habeck (1967) has observed the
first case in T. mertensiana communities in eastern Montana.
The second interpretation is offered as an hypothesis here.

Although snow course data has been collected for too
short a period to substantiate the hypothesis, it seems
plausible that unusually heavy snowpack years may result in
excessive damage to seedling- and pole-size tree species.
Morphological adaptations apparently differentially favor
T. mertensiana over A. amabilis during periods of heavy
snowpack with late snow-lie, and shortened growing season.
In addition to Tsuga's resistance to the mechanical forces
of snow, the species also appears to recover from snow-mold
quicker than other subalpine tree species (Fowells 1965).
The high relative densities of Abies amabilis seedlings

compared to Tsuga mertensiana seedlings might also account

for the differentially high mortality rates of A. amabilis

in heavy snow years. Dense regeneration pockets of Abies

typically occur on the margins of small openings (less than

10 m diameter) in the forest canopy created by heart-rot,

blow-down, or mechanical breakage by snow. The semi-open

habitat of A. amabilis seedlings exposes them to snow creep

more directly than the widely scattered Tsuga seedlings.

The habitat preferences of Tsuga mertensiana seedlings may

correspond to disproportionately low mortality rates. A

slight tendency exists for Tsuga to occur near the bases of

living or broken-off tree bases, which provide protection

from snow creep. Kotar (1972) has observed Tsuga hetero-

phylla becoming established in low densities on the convex

surfaces of fallen trees, while A. amabilis occurs with high

densities in regeneration pockets similar to those observed

in the study area. Comparable seed morphology between Tsuga

heterophylla and Tsuga mertensiana suggests that the loosely

packed duff and moisture regime on fallen logs are optimum

sites for seedling establishment to occur for both. On the

other hand, Abies amabilis seedlings are large and are

capable of deep radicle penetration in densely compacted O_2

litter common to the T. mertensiana forests of the study

area (Kotar 1972; Fowells 1965). Barring episodes of

catastrophic damage to seedlings and pole size Abies

amabilis, it seems likely that Abies would eventually

dominate the forests of the Transition Subzone; however, the hypothesis suggested here is that periodic episodes of heavy snow do occur, resulting in a disproportionately low mortality rate in Tsuga seedlings, compensating for the lower rates of establishment. Conversely, the differentially high mortality rate of A. amabilis seedlings may negate the effects of abundant seedling and sapling regeneration.

The resulting pattern of regeneration according to this hypothesis would be one of occasional establishment of Tsuga mertensiana in small openings (e.g., less than 10 m diameter). Vigorous A. amabilis regeneration would occur in semi-openings (e.g., 10 to 20 m diameter) through years of low-to-normal snow deposition. An unusually heavy season of snow accumulation would destroy seedling Abies amabilis (and A. lasiocarpa) and most Tsuga seedlings, leaving only enough Tsuga individuals for replacement to occur.

Montane Forest Subzone

The forests from 1,580 to 1,900 m are part of the Montane Forest Subzone of the Tsuga mertensiana Zone (Franklin 1966; Franklin and Dyrness 1973; Brooke et al. 1970; Thornburgh 1969). Abies amabilis occurs in all size classes but the largest, apparently replacing Tsuga mertensiana in stands where Tsuga regeneration is poor or absent. Other plots within the subzone exhibit moderate amounts of Tsuga regeneration through all size classes. A. amabilis is a

major co-dominant in these plots with prominence values sug-
gesting eventual replacement of Tsuga. The effects of snow
in this subzone are ubiquitous. Evidence of the bent stems
resulting from snow creep are common to all species in all
size classes but the very largest. Nonetheless, the lower
elevation plots receive proportionally higher amounts of
precipitation falling as rain, and consequently may escape
some of the catastrophic effects on vegetation manifest in
years of unusually heavy snow deposition in the Transition
Subzone above it.

Other Vegetation Patterns

Vegetation of "Openings"

Throughout the Montane Forest Subzone are numerous
openings in the canopy 20 to 40 m in diameter characterized
by much exposed pumice soil and a distinctive vegetation.
When present, the shrub layer is occupied by Arctostaphylos
nevadensis at one to five percent cover. Common herbaceous
associates above 1,900 m include Luzula hitchcockii and
Polygonum newberryi. Carex pensylvanica, Lupinus latifolius
var. subalpinus, Hieracium albiflorum, and Aster ledifolius
are typically found with varying cover in openings through-
out the study area. Carex, Aster, Lupinus, and Hieracium
also occur on the margins of and in, small openings within
the more open Tsuga (30 to 50 percent cover) stands.

These openings do not appear to be invaded by tree seedlings. A number of factors may be responsible for the maintenance of this pattern. The low specific heat and dead air spaces of the highly porous pumice soils result in poor temperature conductivity through the soil profile (Cochran et al. 1967). Insolational heat tends to intensify the temperature of the surface layer during the day. At night, very little heat is emitted from the cold layers beneath the surface, and the surface layer quickly releases it's heat to the atmosphere. This contributes to a "frost pocket" phenomenon where cold air collects in the basin of the forest opening and is dissipated upon warming by the morning sun. The fluctuating temperature regime of extreme cold followed by heat creates a "harsh" environment for establishment of seedlings (Cochran et al. 1967). Furthermore, cold damage to seedlings during the early part of the growing season may be severe (Billings 1969, Sakai 1968). Following snow release, soils may be subjected to diurnal freeze-thaw activity resulting in uprooting or damage to seedlings (Heidmann 1976). The lower margins of the openings below snowbanks receive cold meltwater by overland flow and interflow, saturating the soil and resulting in periods of poor aeration, which inhibit seedling germination (Canaday and Fonda 1974; Holway and Ward 1963; Billings and Bliss 1959). In late summer, these pumice soil openings are subjected to intense heating of the surface layers. Moreover, because of

the porous nature of the soils, high moisture stresses at the root-soil interface may develop (Horn 1968). The seasonal fluctuations between the two harsh environmental extremes appear to inhibit seedling invasion, and also keep species richness low.

Seedling invasion into openings is further discouraged by the extremely deep snow deposition and subsequent late snow release in tree-protected pockets. Seeds of both A. amabilis and T. mertensiana have been observed to germinate prematurely on top of late-persisting snowbanks; however, the success rate of these seeds is low and it is doubtful that invasion into openings can be accomplished through a strategy of premature germination on snow (Franklin and Krueger 1968).

Riparian Vegetation

Riparian communities represent another distinctive assemblage of plants within the study area. Clintonia uniflora, Valeriana sitchensis, Spiranthes romanzoffiana, and Listera cordata occurred along stream courses on the east side of the Cascade crest. All four species are more widespread on the west side of the Cascades, occupying mesic to hydric habitats in, or adjacent to Tsuga-dominated stands. Senecio triangularis, Microseris alpestris, Mitella breweri, and Rubus lasiococcus are most abundant along streams but are also sparsely scattered throughout the

forests of the eastern flank of the Cascades. These species likewise grow more vigorously and with higher cover on the west side of the Cascades. Whether this pattern reflects the limitations of available moisture on the east side or reflects longer growing seasons due to early snowmelt along stream courses remains to be determined.

SUMMARY

The relationships between vegetative composition and structure of Tsuga mertensiana stands as they vary across elevational and topographic gradients along the eastern flank of the central Oregon Cascades has been analyzed. Emphasis has been placed on tree species distribution and distribution of plant community types. Compositional change within three different subzones in the study area was inferred from tree size structure data.

Tsuga mertensiana occurs as a dominant in all 51 sample plots within the study area. It attains prominence values approaching 1.0 at elevations above 1,900 m and has average prominence values of 0.85 below 1,900 m. Abies amabilis is found from roughly 1,600 to 1,900 m elevation. At lower elevations, A. amabilis occupies all but the largest size classes. In 10 percent of the plots, Abies amabilis has prominence values approaching those of T. mertensiana (0.40 to 0.50). Abies lasiocarpa occurs on all aspects over the entire elevational extent of the study area, but typically with prominence values of less than 0.10. Pinus monticola, P. contorta, var. contorta, and P. albicaulis appear as minor seral species occupying limited ranges within the study area.

Two dimensional ordination (SIMORD) distinguished four
natural groupings along coenoclines within the ordination
plane. The independent mode (see Appendix I) of SIMORD
(Dick-Peddie and Moir 1970) differentiated plots based on
composition similarity. Presence-absence data produced the
best separation of sample plots into four clusters called
community types: (1) the Abies amabilis-Tsuga mertensiana/
Vaccinium membranaceum type in which Tsuga is the major
dominant and Abies amabilis a minor associate, vigorously
reproducing in smaller size classes. Vaccinium membranaceum
is the dominant shrub, with Pyrola secunda occurring with
moderate constancy in the herb layer, (2) The Abies amabilis/
Vaccinium scoparium type is currently dominated by Tsuga
mertensiana, with Abies amabilis occupying a major portion
of the reproduction size classes. Vaccinium scoparium typi-
cally is found at less than three percent cover, and often
is the only understory species present, (3) The Tsuga
mertensiana/Vaccinium scoparium type occurs at mid-eleva-
tions (1,750 to 1,900 m) above the Abies amabilis/V.
scoparium type. Tsuga dominates the overstory with pro-
minence values of 0.91, and is reproducing in minor amounts
occupying the smaller size classes. V. scoparium is the
dominant shrub but has low coverage values, (4) The Tsuga
mertensiana/Luzula hitchcockii type occurs in the higher
elevation plots above 1,900 m. Tsuga is the major dominant
(prominence value of 0.96) with A. lasiocarpa occurring as

a minor associate. No shrub species are found in this type, and Luzula hitchcockii is often the only herbaceous species present, ranging from 1 to 60 percent coverage.

Three subzones have been identified in the study area on the basis of size class distribution: (1) The Subalpine Subzone, where T. mertensiana dominates and is replacing itself; (2) Transition Subzone, where T. mertensiana domi-nates and where A. amabilis development is suppressed during years of extreme snow accumulation; and (3) Montane Forest Subzone, where Abies amabilis is the potential climax species but where Tsuga mertensiana currently dominates.

The study area occurs within the Tsuga mertensiana Zone that has been recognized by previous studies as one of deep snow accumulation and having an extremely depauperate flora. The T. mertensiana forests on the eastern flank of the central Oregon Cascades are distinctive in supporting the floristically sparsest forest vegetation in the Pacific Northwest.

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APPENDICES

APPENDIX I: SIMORD

The discussion below is taken directly from Dick-Peddie
and Moir (1970).   The independent mode (I mode) option of
choosing reference stands for the y-axis was used in this
study.   In the independent mode, the reference stands defin-
ing the extremes of the y-axis are sought from the stands
clustered near the center of the x-axis.   Thus, the pair of
reference stands have the least mutual similarity to those
of the first axis.

> Vegetation stands are compared on a phyto-
> sociological basis and are ordered in two-dimen-
> sional space according to their degree of similarity
> to reference stands at each end of the x and y axes.
> Similarity is computed by one of four functions
> available.   Ordination distances along the x and y
> axes are found by comparing each stand, I, with re-
> ference stands, R1 and R2, of each axis.   The ordi-
> nation distances, DX and DY are computed as follows:

> X = 1 - SIM(I,R1)

> Y = 1 - SIM(I,R2)

> DX = 50 + 50 * (X*X - Y*Y), where R1 and R2 are
>   X axis ref stands,

> DY = 50 + 50 + (X*X - Y*Y), where R1 and R2 are
>   Y axis ref stands,

> D = SQRT(DX*DX + DY*DY).

> Reference stand R1 of the X axis is that stand
> having least similarity to all the stands taken as
> a whole.   It is found by summing the columns of a
> stand similarity matrix and choosing that column with
> the lowest sum.   All stands are then partitioned into
> sets U1 and U2.   Stands in U1 have nonzero or a high

similarity to R1, and stands in set U2 have zero or
low similarity to R1. The summed similarities of
each stand in U2 with all stands in U1 are computed,
and the second reference stand of the X axis, R2,
is chosen as that stand having least similarity to
the stand set U1, and (in case more than one stand
qualifies), with lowest column sum from the simila-
rity matrix.

APPENDIX II: PLANT SPECIES LIST

Family/Genus/Species	Common Name
Caryophyllaceae - Pink Family	
Arenaria macrophylla Hook.	Bigleaf sandwort
Celastraceae - Staff-tree Family	
Pachistima myrsinites (Pursh) Raf.	Mountain lover
Compositae - Aster or Sunflower Family	
Aster ledophyllus Gray	Cascades aster
Hieracium albiflorum Hook.	White hawkweed
Microseris alpestris (Gray) Q. Jones	Alpine microseris
Senecio triangularis Hook	Arrowleaf groundsel
Cyperaceae - Sedge Family	
Carex pensylvanica Lam.	Long-stoloned sedge
Carex rossii Boott	Ross sedge
Ericaceae - Heath Family	
Arctostaphylos nevadensis Gray	Pinemat manzanita
Chimaphila menziesii (R. Br.) Sprenq.	Little prince's pine
Chimaphila umbellata (L.) Bart.	Prince's pine
Hypopitys monotropa Crantz.	Fringed pinesap
Pyrola picta Smith	Whitevein pyrola
Pyrola secunda L.	One-sided wintergreen
Vaccinium membranaceum Dougl. ex Hook	Big huckleberry
Vaccinium scoparium Leiberg	Grouse huckleberry
Juncaceae - Rush Family	
Luzula hitchcockii Hamet-Ahti	Smooth woodrush
Leguminoseae - Pea Family	
Lupinus latifolius Agardh. var.	
subalpinus (Piper & Robbins)	
C.P. Smith	Arctic lupine
Liliaceae - Lily Family	
Clintonia uniflora (Schult.) Kunth.	Queen's cup beadily
Xerophyllum tenax (Pursh) Nutt.	Beargrass
Orchidaceae - Orchid Family	
Listera cordata (L.) R.Br.	Twayblade
Spiranthes romanzoffiana Cham.	Ladies-tresses

Family/Genus/Species	Common Name

Pinaceae - Pine Family
    Abies amabilis (Dougl.) Forbes — Pacific silver fir
    Abies lasiocarpa (Hook.) Nutt. — Subalpine fir
    Abies magnifica Murr. var. shastensis
      Lenn. — Shasta red fir
    Pinus albicaulis Engelm. — White bark pine
    Pinus contorta Dougl. var. contorta — Lodgepole pine
    Pinus monticola Dougl. — Western white pine
    Tsuga mertensiana (Cong.) Carr. — Mountain hemlock

Polemoniaceae - Phlox Family
    Polemonium californicum Eastw. — Low polemonium

Polygonaceae - Buckwheat Family
    Polygonum newberryi Small — Newberry's fleece flower

Ranunculaceae - Buttercup Family
    Anemone deltoidea Hook. — White anemone

Rosaceae - Rose Family
    Luetkea pectinata (Pursh) Kuntze. — Partridgefoot
    Rubus lasiococcus Gray — Dwarf bramble

Saxifragaceae - Saxifuage Family
    Mitella breweri Gray — Brewer's mitrewort

Scrophulariaceae - Figwort Family
    Nothochelone nemorosa (Dougl.) Straw. — Woodland beard-tongue

Violaceae - Violet Family
    Viola glabella Nutt. — Wood violet

APPENDIX III: SAMPLE PLOT CHARACTERISTICS

Plot[a] No.	Aspect (°)	Elevation (m)	Slope (°)	Location
1	225	1950	27	NW¼NW¼ Sec. 8,T18S,R9E
2	305	1800	8	SE¼NW¼ Sec. 15,T18S,R8E
3	225	2075	28	NE¼ Sec. 3, T18S,R9E
5	140	1740	27	NW¼NE¼ Sec. 10,T18S,R8E
6	045	1770	17	NE¼NW¼ Sec. 10,T18S,R8E
7	222	1670	14	NW¼NW¼ Sec. 10,T18S,R8E
8	140	1740	15	NW¼NE¼ Sec. 10,T18S,R8E
9	218	2000	15	SW¼NE¼ Sec. 9,T18S,R9E
10	130	1900	12	SE¼NE¼ Sec. 7,T18S,R9E
11	045	1700	26	SW¼NE¼ Sec. 10,T18S,R8E
12	220	1850	16	NE¼NW¼ Sec. 18,T18S,R9E
13	310	1940	12	SW¼SW¼ Sec. 8,T18S,R9E
14	232	1940	20	SE¼SE¼ Sec. 7,T18S,R9E
15	055	1930	24	SE¼SE¼ Sec. 7,T18S,R9E
16	125	1700	14	NW¼NE¼ Sec. 11,T18S,R8E
17	050	1950	16	NW¼SE¼ Sec. 7,T18S,R9E
18	305	2100	25	NE¼SW¼ Sec. 7,T18S,R9E
19	322	1975	15	NW¼NE¼ Sec. 7,T18S,R9E
20	145	1980	11	NW¼NE¼ Sec. 18,T18S,R9E
23	308	1740	29	SE¼NW¼ Sec. 10,T18S,R8E
24	235	1920	16	NE¼SW¼ Sec. 8,T18S,R9E
25	220	2200	22	NE¼NE¼ Sec. 5,T18S,R9E
26	145	2080	18	SE¼NE¼ Sec. 5,T18S,R9E
27	042	1750	34	SW¼NE¼ Sec. 10,T18S,R8E
28	310	1820	22	SE¼NW¼ Sec. 10,T18S,R8E
29	325	1780	24	SE¼NW¼ Sec. 10,T18S,R8E
30	045	1960	25	NE¼NW¼ Sec. 20,T18S,R9E
31	325	1740	13	Sec. 13,T20S,R6½E
32	145	1830	21	Sec. 12,T20S,R6½E
33	050	1880	22	Sec. 12,T20S,R6½E
34	142	1860	22	Sec. 12,T20S,R6½E
35	315	2000	23	SW¼SE¼ Sec. 7,T18S,R9E
36	035	2160	18	NW¼NE¼ Sec. 29,T18S,R9E
37	325	2160	31	NW¼NE¼ Sec. 29,T18S,R9E
38	040	2030	30	SW¼NW¼ Sec. 20,T18S,R9E
40	320	1850	15	SE¼NE¼ Sec. 18,T18S,R9E
41	325	1600	19	NW¼SW¼ Sec. 17,T18S,R7E
42	045	1720	13	SW¼SE¼ Sec. 23,T24S,R5½E
43	215	1725	5	Sec. 28,T24S,R6E
44	055	1580	15	Sec. 33,T24S,R6E
45	155	1850	3	SW¼NW¼ Sec. 3,T18S,R8E

Appendix III (continued)

Plot No.	Aspect (°)	Elevation (m)	Slope (°)	Location
46	125	2030	30	NW¼NW¼ Sec. 3,T18S,R8E
47	049	1940	7	Sec. 8,T18S,R9E
48	240	2220	17	Sec. 32,T17S,R9E
49	140	1620	9	Sec. 13,T23S,R6E
50	050	1700	6	NW¼NW¼ Sec. 24,T23S,R6E
51	050	1850	1	Sec. 27,T23S,R6E
52	130	1860	7	Sec. 27,T23S,R6E
53	130	1730	3	Sec. 23,T23S,R6E
54	035	1700	10	Sec. 23,T23S,R6E
55	315	1600	18	Sec. 18,T23S,R6½E

[a] Plot numbers 4, 21, 22, and 39 were environmentally heterogeneous stands and were not analyzed.

APPENDIX IV: SAMPLE PLOT STRUCTURAL AND
COMPOSITIONAL CHARACTERISTICS

Plot[a] No.	Avg. DBH (cm)	Stand Density number trees/ha	Total BA (m^2/ha)	Compositional Change Index [b]	No. Species
1	31	700	96	18	8
2	18	300	73	23	3
3	21	580	87	1	6
5	42	400	71	0	6
6	27	980	71	0	3
7	33	520	67	19	7
8	22	940	59	14	5
9	33	520	94	2	4
10	68	340	155	20	8
11	26	220	56	0	4
12	50	480	113	16	3
13	68	240	98	7	4
14	45	580	107	0	2
15	45	240	44	0	3
16	35	540	67	0	4
17	57	300	86	0	2
18	47	400	86	5	3
19	71	260	114	0	3
20	52	340	84	0	4
23	19	800	48	3	10
24	40	480	87	17	5
25	29	1000	107	7	7
26	51	500	121	8	3
27	33	780	72	5	9
28	34	780	80	5	8
29	25	840	60	4	8
30	36	560	69	0	6
31	32	620	85	55	3
32	27	600	47	12	6
33	48	280	64	31	5
34	52	240	58	8	5
35	55	320	95	0	4
36	40	360	62	0	7
37	14	1000	72	11	5
38	48	280	68	0	8
40	42	400	58	0	6
41	25	600	39	15	4
42	24	800	65	11	4
43	26	540	48	7	3
44	20	1300	48	10	8

Appendix IV (continued)

Plot[a] No.	Avg. DBH (cm)	Stand Density number trees/ha	Total BA (m^2/ha)	Compositional Change Index [b]	No. Species
45	29	600	52	3	6
46	42	480	115	0	3
47	60	200	66	9	9
48	44	640	143	3	6
49	26	1020	88	29	11
50	19	1760	56	9	4
51	17	1100	58	35	4
52	34	480	56	26	4
53	22	1200	54	5	6
54	19	1860	56	4	4
55	27	820	61	15	6

[a] Plot numbers 4, 21, 22, and 39 were environmentally heterogeneous stands and were not analyzed.

[b] See Laboratory Methods for definition of terms.