

AN ABSTRACT OF THE THESIS OF

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Title: Morphological Variation and Habitat Relations of  
Intergradient Grand Fir (*Abies grandis*)/White Fir (*Abies concolor*)  
Populations in the Wallowa Mountains, Oregon

Abstract approved: \_\_\_\_\_

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Intergradients between *Abies grandis* and *A. concolor* were studied in a restricted area in the Wallowa Mountains, Wallowa-Whitman National Forest, Baker County, Oregon. The primary objective of this research is to clarify the characteristics and ecological relationships of this intergradient complex in a restricted area through examination of morphological variation, distribution, and habitat relationships of intergradient *A. grandis*/*A. concolor* populations. The intergradient populations, identified by selected morphological tree characteristics, are segregated by habitat and associated plant communities. Habitat segregation was assessed by sampling trees and vegetation in forty 500 m<sup>2</sup> reconnaissance plots. Plant community data includes cover classes of all vascular plants and basal area of conifer species; habitat information includes slope,

aspect, and elevation. Nine plots were chosen for pre-dawn xylem water potential measurements. A total of 431 trees, with at least 10 trees at each plot and 6 needles per tree were sampled for the number of adaxial stomatal rows, stomatal row length, needle length, and periderm color. A total of 3,208 additional trees were sampled for periderm color.

Three plant communities were identified using two-way indicator species analysis (TWINSpan): the Abies grandis/Clintonia uniflora Association, the Abies grandis/Spiraea betulifolia Association, and the Abies grandis/Symphoricarpos oreophilus Association. Sample plots were ordinated using detrended correspondence analysis (DECORANA). Plant associations were distributed along a complex topographic-moisture gradient defined principally by elevation and plant moisture stress. The Abies/Clintonia Association occupied the most mesic and the Abies/Symphoricarpos Association the most xeric and highest elevation sites.

Morphological characteristics of intergradient trees varied by habitat. The number of adaxial stomatal rows, stomatal length, and relative stomatal length were greater on sun-side needles than on shade-side needles. Stomatal length, relative stomatal length, and a stomatal index (number of rows x relative stomatal length) were individually and significantly weakly correlated with elevation. Stomatal index was better correlated with combined elevation and aspect. Shade-side stomatal indexes were greater for ridge-top populations than for nearby valley populations. On nine plots

sampled for pre-dawn xylem water potential, tree populations had stomatal index values that positively correlated with elevation and solar insolation, and were highly correlated with combined elevation and pre-dawn xylem water potential. Trees sampled for periderm color had three color classes: yellow, 65.8 %; red, 32.6 %; and pink, 2.6 %. Periderm color did not differentiate populations in different habitats or community groups.

Vegetation associations identified by classification formed the basis for grouping intergradient tree populations. The number of stomatal rows and stomatal length discriminate the Abies/Clintonia association, Abies/Spiraea Association, and Abies/Symphoricarpos Association. A hybrid index using stomatal rows, relative stomatal length, and periderm color further significantly differentiates tree population groups. The Abies/Clintonia Association had more A. grandis traits and the Abies/Symphoricarpos Association had more A. concolor traits.

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Morphological Variation and Habitat Relations of Intergradient Grand  
Fir (Abies grandis)/White Fir (Abies concolor) Populations in the  
Wallowa Mountains, Oregon

by

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MORPHOLOGICAL VARIATION AND HABITAT RELATIONS OF  
INTERGRADIENT GRAND FIR (Abies grandis)/WHITE FIR (Abies  
concolor) POPULATIONS IN THE WALLOWA MOUNTAINS, OREGON

INTRODUCTION

Today, there is urgent need for biogeographic studies to reflect that "...comprehensive view of the distribution of life on earth pioneered by Humboldt and established by Darwin" (Stoddart 1987:307). This research concerns the distribution of the Abies grandis complex reflecting a replicate pattern of distribution at a landscape and regional scale and aims to help satisfy this need.

Abies grandis (Dougl.) Lindl. and A. concolor (Gord. & Glend.) Lindl. are closely related conifer species widely distributed in western North America (Figure 1). Abies concolor is a polymorphic species divided into two varieties: A. concolor var. concolor, and A. concolor var. lowiana (Gord.) Lemmon. Where the ranges of A. grandis and A. concolor overlap there is a zone of intergradation in which species traits vary (Liu 1971). Individuals and populations in this zone have variable morphological traits that cause difficulties in identification of species and their distributions, and disagreement on taxonomic classification (Liu 1971). The primary objective of this research is to clarify the morphological characteristics and ecological relationships of this intergradient complex in a restricted area

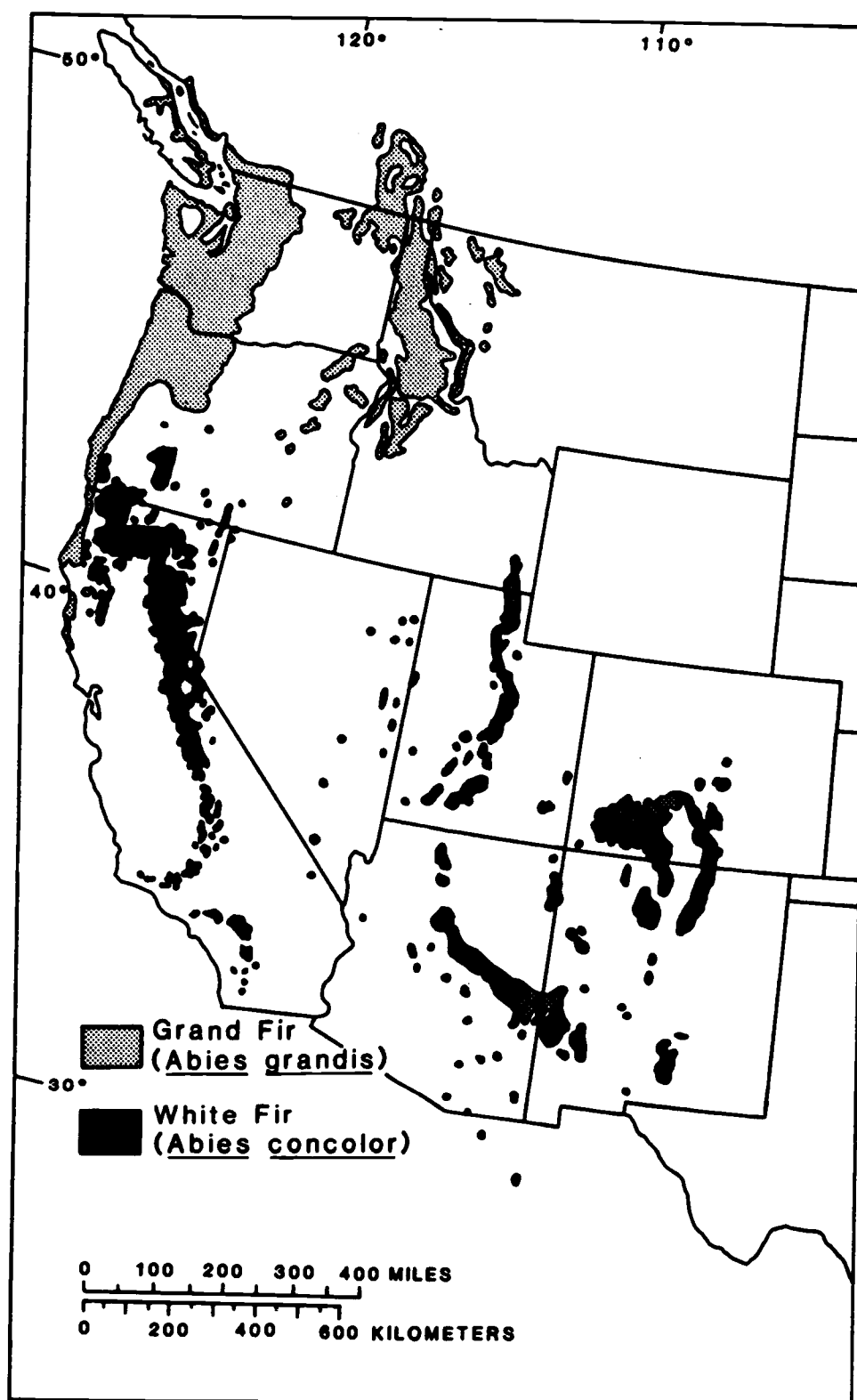


Figure 1. Distribution of *Abies grandis* and *A. concolor* in the western United States, after Little (1971).

through examination of morphological variation, distribution, and habitat relationships.

In this paper I refer to A. grandis and A. concolor as "grand fir" and "white fir" respectively, and to the specific variety A. concolor var. concolor as "concolor" and A. concolor var. lowiana as "lowiana". I refer to intergradient populations or trees from the zone of intergradation by the term "type" to indicate the phenotype (e.g., lowiana type).

### Taxonomy and Biogeography

Differentiation of grand fir from white fir can be made by the presence of adaxial stomata on the needles of non-reproductive branches (Liu 1971). Other important morphological characteristics distinguishing grand fir and white fir varieties are shown in Table 1. A brief description of their biogeography follows.

#### Grand fir

This species is large (100 m high x 1.5 m diam.), moderately shade tolerant, and usually found as a minor or codominant tree species in mixed coniferous forests in the Pacific Northwest (Liu 1971); however, in central Idaho grand fir forms extensive pure stands (Steinhoff 1978). Optimum habitats are moist sites with deep alluvial soils in valley and stream bottoms, or on gentle slopes. There are two forms, coastal and inland. The coastal form occurs from

Table 1. Major morphological characteristics differentiating Abies concolor from A. grandis (after Liu 1971).

	<u>Abies concolor</u>		<u>Abies grandis</u>
	var. <u>concolor</u>	var. <u>lowiana</u>	
Periderm color	yellow	yellow	red
Branchlet color	yellowish or olive-green	green, olive or yellowish green	olive-green to dark purplish red
Winter-bud	larger	smaller	smaller
Leaf apex	acute to rounded	rounded and emarginate	rounded and emarginate
adaxial surface	15-16 lines of stomata, slightly convex, glaucous	≥ 8 lines of stomata, grooved	may have apical stomatal spot, grooved
arrangement	irregular	2-ranked, pectinate	2-ranked, pectinate
Cone color	greenish or purple	chestnut-brown	bright green
Bract-scale shape	rectangular	roundish	quadrangular
upper margin	emarginate or truncate	emarginate	deeply emarginate

Sonoma County, California into British Columbia from elevations between near sea level to 900 m, and in the Cascade Mountains to 1,500 m. The general climatic classification of this distributional region is Mediterranean to Marine West-Coast (Strahler and Strahler 1978). The inland form occurs from eastern Washington to western Montana and south to the Blue Mountains, Oregon, at elevations between 900 and 1,500 m (1,800 m) (Liu 1971). The general climatic classification of the region is Highland within Dry Midlatitude climate (Strahler and Strahler 1978).

#### White fir

This species is large (80 m high x 2 m diam.), shade tolerant, and occurs in mixed coniferous forests in the southwest mountains and southern Rocky Mountains. Optimum habitats are moist to mesic in regionally dry areas (Franklin and Dyrness 1973) with deep loam soils or well drained sandy dry to coarse dry soils (Liu 1971). White fir ranges from latitude 30° to 45° N and longitude 105° to 124° W (Liu 1971). Concolor is found at elevations between 1,675 and 3,050 m in the Rocky Mountains, the Basin and Range Province in eastern Nevada; it is distributed from southern California to New Mexico and south to northern Mexico (Liu 1971). Climatic classification for this subregion is Highland within Dry Midlatitude and Dry Subtropical (Strahler and Strahler 1978). Lowiana occurs primarily in California on the western slope of the Sierra Nevada at elevations between 1,200 and 2,100 m, increasing in elevation to the

south and on eastern slopes (Liu 1971); in the San Bernardino Mountains at 3,000 m; in the northern Coast Ranges from 1,400 to 2,300 m; and from 600 to 2,400 m in mountain areas of southern Oregon, western Nevada, and northern Baja California (Liu 1971). Climatic classification for this region is Highland-influenced Mediterranean (Strahler and Strahler 1978).

### Paleobiogeography

Evidence suggests that a common ancestor for the genus Abies existed in either western North America or eastern Asia in the middle Eocene (Liu 1971). Ancestral Abies species developed in warm, humid climates and spread over the northern hemisphere. With increased cooling and aridity in the late Tertiary, grand fir, white fir, and other Abies species differentiated from a common ancestor (Liu 1971). Pliocene macrofossils of ancestral grand and white fir have been found in close proximity to each other in the Trapper Creek flora of eastern California (Axelrod 1976). Pleistocene glacial and interglacial periods caused shifts in the range of grand fir to mesic, coastal areas and white fir to dry, inland areas (Liu 1971, Zavarin et al. 1977). Concolor has been found as fossils in the mountains of the southern Great Basin and Mojave Desert dating to the last glacial maximum, 16,500 yr B.P., and it migrated north and east during the Holocene (Wells 1983). Lowiana macrofossils have been found dating 12,000 yr B.P. in the southern Sierra Nevada (Davis et al. 1985). Grand fir macrofossils are not recorded, and

Abies pollen is difficult to identify to species; however, it appears that grand fir was restricted to coastal areas during the last glacial period (Mack et al. 1983, Zavarin et al. 1977).

### Hybridization

Artificial hybridization in the genus Abies has been successful in 39 different crosses, including grand and white fir (Klaehn and Winieski 1962). Many of the parental species employed in the artificial hybridizations have been separated by oceans for millions of years (Liu 1971), suggesting that barriers to speciation are due to geographic isolation rather than genetic or physiological isolation (Klaehn and Winieski 1962, Liu 1971).

In areas where closely related species hybridize naturally, a zone of morphological intergradation can occur. It is widely believed that such a zone of intergradation exists between the ranges of grand and white fir (Liu 1971). Many stands in this zone exhibit a gamut of morphological phenotypes representing the total complex (Hitchcock et al. 1969). Intergradient populations have generated taxonomic controversy (Sudworth 1908), disagreements on species ranges (Daniels 1969), and conflicting autecological characteristics of species (Minore 1979, Yoder 1984).

### Morphology and Cortical Terpenoids

Morphological variation in the grand fir/white fir complex in western North America was studied by Daniels (1969) using foliage and bark characteristics. Stomatal pattern, needle twist angle, upper needle angle, needle notch depth, needle groove and bark color were used to construct hybrid indexes for populations at each site.

Populations of grand fir and the two varieties of white fir conformed well to their taxonomic classifications. In the zone of intergradation northern areas have individuals tending to resemble grand fir; in southern areas individuals tend to resemble white fir. In the Cascade Range of Oregon, populations showed a north-south cline between grand and white fir. Daniels (1969) supports the hypothesis that morphological variation in the zone of intergradation is caused by introgressive hybridization.

Variation in white fir morphology was evaluated by Hamrick and Libby (1972) using seedlings in a garden study at the Institute of Forest Genetics, Placerville, California. Seeds were collected throughout the range of lowiana and within the zone of intergradation. Thirteen characteristics were measured. From these data a hybrid index was constructed using two traits, number of adaxial stomatal rows and needle tip shape. Three major patterns of morphological variation were found: ecotypic variation; clinal variation with elevation (apparent mostly in seedling morphology), and clinal variation with elevation and latitude (evidenced by characteristics associated with growth). Hamrick and Libby (1972)

concluded that four major geographical divisions exist: central Oregon and northwestern California marked by intergrades of grand fir/white fir; south-central Oregon and central and northeastern California marked by lowiana; southern California and Arizona marked by concolor; and eastern Nevada and western Utah with concolor.

Local variation in intergradient grand fir and white fir populations in the central Oregon Cascades was studied by Zobel (1973) using periderm color, needle adaxial stomata, and needle tip type. West of the Cascade crest populations varied by elevation, with grand fir types at moist, lower elevations, and populations with some white fir traits at drier, higher elevations. East of the crest, populations varied by aspect, with grand fir types on north slopes. Periderm color and needle morphology varied together. Zobel (1973) concluded that introgressive hybridization between grand and white fir was responsible for the observed morphological variation.

Cortical terpenoids were used in a chemotaxonomic study of the grand fir complex by Zavarin et al. (1977), who distinguished three white fir groups: a Rocky Mountain race (concolor); a western race (lowiana); and a southern California race (Cuyamaca), which is more closely aligned with concolor than to lowiana. Grand fir differed chemically from all of these races but was more closely related to concolor than to lowiana. These chemotaxonomic results are in conflict with the hypothesis based on morphological traits that lowiana is intermediate between grand fir and concolor (Liu 1971). In the zone of intergradation in eastern Oregon and western Idaho, intergradient populations are chemically closer to lowiana than

predicted by morphologically based hybrid indices of Daniels (1969). Zavarin et al. (1977) support the hypothesis that variation in intergradient populations of grand fir and white fir is due to introgressive hybridization; their study also confirms the geographical divisions of white fir based on morphological characteristics by Hamrick and Libby (1972).

Morphology and chemotaxonomy of the grand fir complex in Idaho and Utah was examined by Houkal (1976). A fairly strong association was found between morphology and terpenoid data. Morphological and chemical variation in populations was correlated with elevation, grand fir types at low elevations and white fir types at high elevations. A north-south cline was identified with grand fir to the north and white fir to the south; highly variable intergradient populations occurred in between. Houkal (1976) concluded that introgressive hybridization was responsible for the observed variation.

### Research Objectives

Morphological variation in grand fir, white fir, and their intergrades has been the subject of many studies. These studies have focused on the extent of morphological variation encountered primarily between relatively distant populations, and have shown that morphological variation is related to the geographic location and local environment. However, populations within a restricted area have not been studied to see if there is a similar relationship between morphology and environment. The Summit Ridge study area on the

southern margin of the Wallowa Mountains, Oregon, has a heterogeneous topography and microclimate providing an opportunity to examine possible morphological variation between populations on contrasting environments within a restricted area.

The literature provides strong evidence for the existence of intergradient populations between grand fir and white fir. The degree to which these intergradient populations are segregated by habitat will be examined in this study. The following specific research tasks are addressed: 1) determine and describe selected plant communities and their environmental parameters; 2) classify plant communities using multivariate analysis; 3) describe selected morphological characteristics of grand fir/white fir populations associated with sampled plant communities; 4) correlate the stomatal index (number of stomatal rows multiplied by the relative stomatal row length) of sampled trees from selected sites with soil moisture stress and selected environmental characteristics; and 5) test the hypothesis that significant quantitative and qualitative morphological differences occur between tree populations grouped by their associated plant communities.

## SITE DESCRIPTION

### Location and Physiography

The Summit Ridge study area (Figure 2) is located in T.7 S., R.44 E. and T.7 S., R.45 E. Willamette Meridian (44° 59' N. latitude, 117° 15' W. longitude) on Summit Ridge in the Pine Ranger District, Wallowa-Whitman National Forest, Baker County, Oregon. The study area is 110 km<sup>2</sup> with an elevation range of 1,120 to 2,490 m.

Summit Ridge is situated in the heterogeneous central mountain unit of the Columbia Intermontane Geomorphic Province of northeastern Oregon and is typified by folded, faulted, and well-dissected mountains (Rosenfeld 1985). Summit Ridge is a long southeasterly trending ridge with broad plateaus and over-steepened (25-45°) concave slopes bounding U-shaped valleys that are the result of periodic glaciation. The overall aspect of the Summit Ridge area is southwesterly. Steep slopes are prone to severe localized mass movement resulting from a combination of logging, seasonally high precipitation, and volcanic ash deposits.

The study area is drained to the southeast by Summit Creek, Little Eagle Creek, Snow Fork Creek, and Holcomb Creek, which are tributaries of Eagle Creek. To the east, the area is drained by streams which flow into Pine Creek. Stream networks of the area are deeply incised with low drainage density. Many first and second

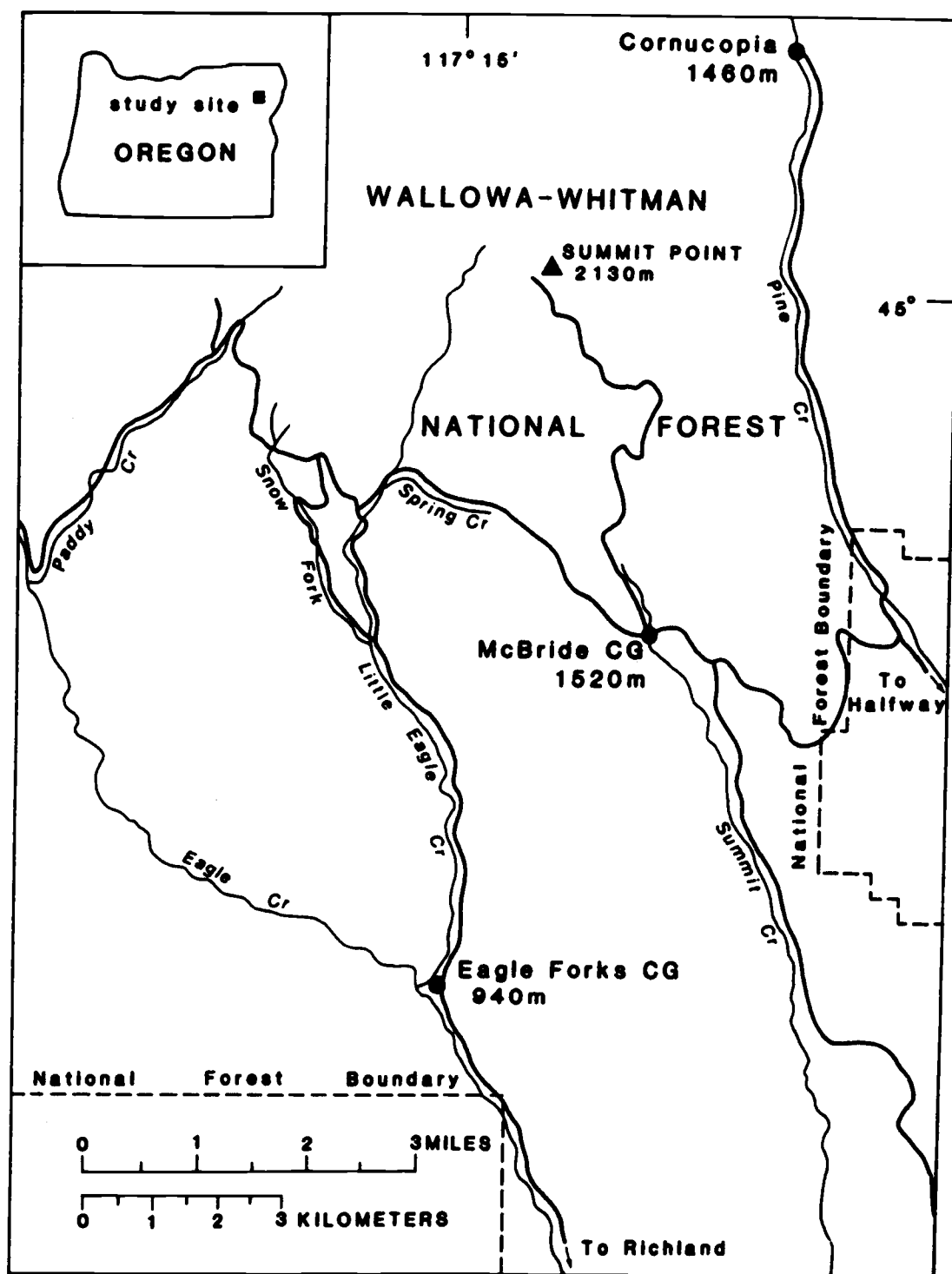


Figure 2. Location of the Summit Ridge study area, Wallowa Whitman National Forest, Baker County, Oregon.

order streams are dry in summer because of steep terrain and high infiltration rates of forest soils. Some streams that run through the summer are fed by subsurface flows. Infrequent, but destructive floods play a major role in stream morphology and sediment transport.

### Geology and Soils

The Wallowa Mountains are part of the Ochoco-Blue Mountains uplift (Rosenfeld 1985). Rocks of the Wallowa Mountains are divided into two main groups distinguished by their age (Brooks 1979). Rocks of the older group formed when northwest Oregon resembled the present Oregon Coast and Cascade Range in the Devonian to Late Jurassic periods. Typical rock types are metamorphosed volcanics (spilite, keratophyre and quartz keratophyre) and sedimentary rocks (conglomerate sandstones and argillite with smaller amounts of chert and limestone) (Brooks 1979). Compositionally similar volcanic arc terranes exist on the west coast of Canada and Alaska; it is believed that the rocks were members of the Wrangell Island Arc which were located at the equator during the Triassic (Brooks 1979). Since the late Triassic, these rocks have moved northward and were accreted to the northwestward-moving North American continent (Brooks 1979).

Rocks of the younger group are of Cenozoic age (Armstrong 1978). Sediments and volcanic materials were deposited on land and in lakes after the older group of rocks accreted to the continent

(Christiansen and McKee 1978). Except in higher areas of the Wallowa, Blue, and Ochoco Mountains, volcanic rocks and Yakima Flood Basalts covered most of northeastern Oregon (Smith and Eaton 1978). These basalts erupted during the Miocene from the Grand Ronde Volcano over a period of 10 million years (Armstrong 1978). Subsequently erosion has removed large amounts of the massive basalt flows, especially through glacial erosion.

During the Pleistocene epoch the Wallowa Mountains were extensively glaciated by a multiple glacial/ice field system rather than by an "ice cap" (Allen 1975). Nunataks were restricted to high peaks and narrow ridges. The area covered by ice is estimated at 873 km<sup>2</sup>, including nine large valley glaciers, numerous cirque glaciers and ice fields. The lower elevation limit of ice ranged from 790 to 900 m at the foot of canyon glaciers. Glacial thickness is estimated at between 300 and 750 m (Allen 1975).

The most recent major geologic event to affect the Wallowa Mountains was the eruption of Mount Mazama, ca. 6,800 B.P., in which the south flank of the Wallowa Mountains was covered by a fine ash fall. Prevailing southwest winds deposited air-fall tephra. High precipitation and subsequent runoff has since eroded the tephra from southern slopes and ash has accumulated in deep colluvial and alluvial deposits in flat areas and in deep ravines (pers. comm. W.H. Taubenecht 1985).

Soils in the study area have not been extensively studied or mapped. Forest Service soil scientists have conducted reconnaissance surveys of the area and have identified soil types

which are equivalent to the following local soil series: Tolo, Wolot, Kamela, and Klicker. The Tolo series is a medial over loamy, mixed, frigid typic vitrandept; the Wolot soil is a medial over loamy, mixed, mesic typic vitrandept; the Kamela soil is a loamy-skeletal, mixed, frigid dystic xerochrept; and the Klicker soil is a loamy-skeletal, mixed, frigid ultic argixeroll (Huddleston 1979).

### Climate

The macroclimate of the Wallowa Mountains is continental, modified by mid-latitude cyclonic storm patterns. Little research has been done on the upland climates of eastern Oregon. Trewartha (1968) places the Wallowa Mountains in the Highland Climates type. The Köppen classification for the study area is Dsb (continental snowy-forest climate, summer dry, with a warm summer)(Ackerman 1941). Loy (1976) places the Wallowa Mountains in the Northeastern Highlands Climatic Region which has a wide range of climates. Upland areas are cool and moist with an annual surplus of water, while lowlands are warmer and have an annual water deficit.

There are no weather stations within the study area. The nearest permanent station is Halfway, at elevation 810 m (810-1,750 m lower than the study area) and 5 km to the southeast. Table 2 presents climatic data from Halfway and Richland, 16 km south of the study area. The average annual temperature is 7.8° C. During 1982 the last spring freeze occurred 8 June and first freeze was 9 September (NOAA 1982). Average annual precipitation at this station

Table 2. Average temperature and precipitation data for selected stations near the Summit Ridge study area, Baker County, Oregon (NOAA 1982).

Weather Station <sup>a</sup>	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Ann.
Halfway													
Temperature (°C)	-5.1	-1.3	2.8	8.0	12.2	15.6	20.0	18.9	14.5	8.7	2.3	-2.3	7.8
Precipitation (cm)	8.0	5.8	3.9	3.8	4.5	4.4	0.9	1.3	2.1	3.4	6.5	8.2	52.8
Richland													
Temperature (°C)	m <sup>b</sup>	m	6.5	8.5	14.4	19.5	22.3	22.1	18.0	12.2	m	-0.1	m
Precipitation (cm)	m	m	2.6	3.3	3.9	2.9	9.3	0.7	0.9	5.1	1.1	3.5	m

<sup>a</sup>

Halfway has 36 years of record, elevation 810 m.

Richland has 38 years of record, elevation 675 m.

<sup>b</sup>

m=missing, Richland is a volunteer station with incomplete records.

is 53 cm with an average annual snowfall of 13 cm (precipitation equivalent). At Schneider Meadows, a similar forested area 5 km to the east at 1,649 m, the average annual precipitation is 120 cm (Forest Service records).

### Vegetation

The zonal vegetation classification system of Franklin and Dyrness (1973) is used to describe the general vegetation of the Summit Ridge study area. Depending on elevation, aspect and topographic position, vegetation can be placed in one of four zones. The Abies grandis Zone is the most prevalent type within the study area. Bounding the Abies grandis Zone at higher elevations is the poorly represented Abies lasiocarpa Zone. The Pseudotsuga menziesii and Pinus ponderosa Zones are found at lower elevations. The P. ponderosa Zone, the most warm and xeric, is sparsely represented in the study area. The two most prevalent zones are discussed.

#### Abies grandis Zone

The Abies grandis zone embraces two common plant communities. The Abies grandis/Vaccinium membranaceum Association (Franklin and Dyrness 1973) occupies cool, moist sites and has a well developed shrubby understory marked by V. membranaceum, Rosa gymnocarpa, Ribes lacustre, Sorbus sitchensis and Lonicera utahensis. The herb layer includes Bromus vulgaris.

Galium triflorum, Smilacina stellata, Carex geyeri, Calamagrostis rubescens, Thalictrum occidentale, Arnica cordifolia, Hieracium albiflorum, Linnaea borealis, Adenocaulon bicolor, Clintonia uniflora and Lupinus latifolia. Under very dense canopies, Chimaphila umbellata, Corallorhiza spp., and Pyrola secunda are found to the exclusion of other species. The overstory is dominated by A. grandis along with early seral Pseudotsuga menziesii, Pinus ponderosa, Larix occidentalis, and at higher elevations Picea engelmannii. The association and habitat type has been identified in the northern Wallowa-Whitman National Forest by Johnson (1982), and classified in the southern portion of the forest by Johnson (1959).

The Abies grandis/Calamagrostis rubescens Association is found in more xeric conditions and occupies gentle slopes and convex ridges. Rich in herbs, this community is marked by C. rubescens, Carex geyeri, C. concinnoides, Arnica cordifolia, Lupinus caudatus (or laxiflorus) and Hieracium albiflorum. The shrub layer is normally sparse, but Spiraea betulifolia var. lucida, Rosa spp., and Symphoricarpos albus may be present. Major seral tree species are Pinus ponderosa, P. contorta and Pseudotsuga menziesii. Hall (1973) identified the community as "mixed conifer-pinegrass." In the southern Wallowa Mountains Johnson (1959) has recognized the related habitat type as Abies grandis-Salix lasiolepis-Calamagrostis rubescens. Steele et al. (1981) has noted the habitat type as a minor one in central Idaho occasionally merging with the Pseudotsuga menziesii/Calamagrostis rubescens habitat type.

### Pseudotsuga menziesii Zone

Situated between the Abies grandis Zone and the xeric Pinus ponderosa Zone, the Pseudotsuga menziesii Zone embraces three dominant plant communities in the study area: Pseudotsuga menziesii/Calamagrostis rubescens, Pseudotsuga menziesii/Symphoricarpos albus and Pseudotsuga menziesii/Symphoricarpos oreophilus Associations.

The Pseudotsuga menziesii/Calamagrostis rubescens Association and habitat type has a broad distribution on cool and dry upper slopes and ridges at mid-elevations in which both Pinus ponderosa and Pseudotsuga menziesii occur. The shrub layer is sparse with occasional Amelanchier alnifolia, Prunus spp., Purshia tridentata, Ceanothus velutinus, and Symphoricarpos albus. The herb layer is dominated by Calamagrostis rubescens with occasional Carex geyeri, Arnica cordifolia, and other herbs. This habitat type has been identified by Daubenmire and Daubenmire (1968) in Washington and Idaho; Cooper et al. (1983) in northern Idaho; Steele et al. (1981) in central Idaho; Johnson (1982) in the northern Wallowa-Whitman National Forest; and Johnson (1959) in the southern Wallowa Mountains. Hall (1973) has recognized the type as a general "mixed conifer-pine grass" community of lower elevations.

The habitat type and related plant community, the Pseudotsuga menziesii/Symphoricarpos albus Association, is found on warm, dry slopes and benches. The shrub layer is well developed, typically including Symphoricarpos albus with Spiraea betulifolia, Rosa

woodsii, R. nutkana, Amelanchier alnifolia and Prunus spp.

Calamagrostis rubescens or Carex geyeri may form an herb layer below the shrubs. Daubenmire and Daubenmire (1968) identified this habitat type in northern Idaho and eastern Washington; Cooper et al. (1983) in northern Idaho; Steele et al. (1981) describe it in central Idaho; Johnson (1982) in the northern Wallowa-Whitman N. F.; and Johnson (1959) in the southern Wallowa-Whitman N. F. The habitat type seems to be similar to Hall's (1973) "ponderosa pine-Douglas fir-snowberry-ocean spray" community in the Blue Mountains.

The Pseudotsuga menziesii/Symphoricarpos oreophilus association and habitat type is found on ridges and steep slopes having a southerly-to-westerly aspect. Usually Pseudotsuga menziesii is the dominant tree with occasional Pinus ponderosa, P. albicaulis, P. flexilis, and P. contorta. The shrub layer is usually dominated by Symphoricarpos oreophilus and can be codominated by Artemesia tridentata var. vaseyana or Prunus virginiana; Ribes cereum may also be present. Agropyron spicatum and dry-site forbs may occupy shrub interspaces. The type has been identified by Steele et al. (1981) in central Idaho. Johnson (1959) described a Pseudotsuga menziesii/Symphoricarpos rotundifolius (= S. oreophilus) community in the southern Wallowa Mountains.

### History

The first Europeans to use the Halfway area were trappers. Sparse settlement of the area began in the mid-1870's prior to the discovery of gold at Cornucopia in 1884. The subsequent gold rush had a major impact on lower elevation forests, as lumber was cut for mines and buildings. As gold mining became less profitable, miners turned to ranching. Sheep grazing began in 1889 and, over the next four decades, can probably be considered the major cause of damage to the area (Johnson 1959). In 1906, the Forest Service started regulating grazing but regulation was not really effective until the 1950's, when tagging of cattle and reduction of sheep numbers began (Farr 1982).

Harvesting of timber and fire suppression have been practiced at lower elevations in the study area since mining began in the late 1800's. Although organized fire suppression was initiated in the 1930's, modern fire suppression techniques did not become effective until the 1960's. Prior to that time, the horse was still used for transportation to fires; suppression of small fires basically followed a let burn policy, or "herd the fire till it's out" (with horses) practice (pers. comm. Crow 1982). Major harvesting of upper elevation timbered areas began in the 1960's (U.S. Forest Service records). Timber harvesting was abetted by a comprehensive road system which, together with air support, has subsequently led to the effective suppression of all fires and the consequent development of a brush understory or dense conifer reproduction.

The Forest Service has continued to follow a multiple use management policy and within the study area, grazing and timber harvesting co-occur. The Summit Ridge study area has been logged at various times throughout the 1970's and presently is being harvested. Exact data on logging activities are not available. Range utilization has been estimated by the Forest Service to be at 20-45 percent of capacity, being fairly evenly distributed throughout the study area (pers. comm. Szymoniack 1983).

## METHODS

### Field Methods

#### Stand and plot selection

Potential grand fir stands were identified on natural color air photos provided by the U.S. Forest Service and then located on U.S.G.S. 15 minute topographic quadrangles. The first ten stands were systematically placed and sampled to identify areas of variability in grand fir populations. The data from these plots were then used to locate subsequent stands to be sampled. Forty stands were selected to represent a range of forested habitats where morphological variation had been identified. Some stands were selected in the field and were in close proximity to previously identified stands where sharply contrasting habitats were encountered. One stand was selected outside the study area at Cornucopia as a measure of variation over longer distances.

In each stand, a plot was subjectively placed to typify the structure and composition of the stand. However, each plot had to meet certain criteria, including: the presence of grand fir, a minimum lack of disturbance, homogeneous vegetation, and slope and aspect representative of the stand.

### Vegetation data collection

Vegetation was sampled with circular 12.6 m radius (500 m<sup>2</sup>) macroplots within which all trees, seedlings, shrubs and herbs were recorded by percent cover. Within each macroplot, four circular 2 m radius (12.5 m<sup>2</sup> each) subplots were placed 7.0 m from plot center at cardinal compass points to record seedlings and saplings less than 4 cm diameter at breast height (dbh) by species and percent cover. Tree basal area was measured by the Bitterlich method (Dilworth 1980) with a metric Relaskop read at plot center and at 3 to 5 points within the sampled stand at sufficient distance to avoid double counts. Tree species were also recorded by four diameter classes: 1, >60 cm; 2, 30-60 cm; 3, 15-30 cm ; and 4, <15 cm dbh. Collected plot data are shown in Appendix I, and a complete species list for all plots appears in Appendix II. Species nomenclature follows Hitchcock and Cronquist (1973).

### Environmental data collection

Elevation was interpolated from U.S.G.S. 15 minute topographic maps. Aspect, measured in degrees, was recorded by compass and slope measured in degrees with a Bitterlich Relaskop. Microtopography (local slope shape) and general position of the plot on the slope was also recorded. Ground cover estimates in percent were made for bedrock, loose rock, mineral soil, fine litter, moss, and lichen. A soil pit was dug at plot center to 20 cm depth where

depth of litter, and soil texture (proportions are <2.0 mm, gravel 2.0-7.5 mm, and cobbles >7.5 mm) was recorded.

### Tree selection

Trees selected for morphological sampling followed the criteria of Zobel (1973) and Daniels (1969). Sample trees had to be at least 70 m apart to diminish the possibility of sampling only one deme, and had to occur in the same stand. Between-tree age variation was minimized by sampling trees with developed periderm of the same height class (10 - 15 m tall). Sample trees had to be exposed to full sunlight for most of the day and have branches close to the ground on all sides. Sampled trees were chosen at a distance to avoid biasing the sample and all sampled trees had to appear disease free and be growing vigorously.

### Needle morphology

The primary aim in choosing where to sample needles was to minimize variability and maximize accessibility. Branches were collected from selected trees from the bottom one-third canopy. Foliage was sampled from non-reproductive branches on the shade-side and on the sun-side. Sun-side branches had to be in full light, while shade-side branches were in indirect light for most of the day. A selected branch cut from the tree included all of the previous year's growth. Three branch sections were taken from each side of

the tree, bundled, marked, and placed in a dark plastic bag for examination in the laboratory.

Measurement of needle morphological traits were made on the same day as needle sampling. Needles were removed from the middle section of the previous year's growth (1981) with the abaxial (lower leaf surface) side of the branch facing upward to avoid biasing the adaxial (upper leaf surface) stomata counts. Three needles were removed from each branch for a total of nine needles per side. The three longest needles were chosen for measurement from the nine needles selected from each side. A 10x Hastings triplex hand lens and a metal ruler were used for measurements. The following data were recorded: needle length to the nearest mm; length of the longest stomatal row to the nearest mm; number of stomatal rows at the midpoint along the longest stomatal row; and presence of a stomatal spot was recorded if there were no stomatal rows.

The use of needles from non-reproductive branches placed a limit on the interpretation of the data collected. Determination of species type is made based on the morphological characteristics of needles from mature, reproductive branches and cones (pers. comm. Chambers 1982). Interpretation of results will therefore be directed to the ecotype which most resembles the "parental" species type (e.g., grand fir type).

A number of morphological traits were measured on the first ten plots but were dropped from further measurement and consideration because I decided that these traits were not sufficiently diagnostic to warrant further recording. These included observations of

presence/absence of a needle notch, branch angle, branch xylem-to-periderm ratio, and needle color. I examined a number of other morphological traits but observations were too few to consider these traits for analysis. These additional traits included: cone color (purple), whether needles were glaucous or not, needle distribution with respect to branches (e.g., two ranked), and a presence/absence of a distal groove on needles.

#### Periderm color

Periderm color of the grand fir population was identified on thirty of the forty plots following the system of Zobel (1973). A Munsell color chart was used to characterize periderm color variation objectively (Munsell color chart for plant tissue 1971). Periderm color was found to consist of three color types: red with deep purplish colors (5R 4/4); yellow (7.5YR 7/4); and pink with no purplish-red color or yellow (5R 7/4). The Munsell color chart was dispensed with because consistent determinations could be made by eye. Periderm color determination was made by cutting the bark with a knife. On the first ten plots, periderm color was determined only on trees sampled for needle morphology. After the first ten plots, each population of the subsequent 30 plots was sampled for one hour or until one hundred trees were sampled, whichever came first. The periderm count of each population was recorded independently from the periderm color of trees sampled for needle morphology to eliminate double counting.

### Pre-dawn xylem water stress

Sites for pre-dawn xylem water stress measurements were chosen to represent a variety of habitats along an elevation gradient within an area small enough to complete sampling in a single night. The area chosen was the plateau area on Summit Ridge, from McBride Campground (plot 14) to Summit Ridge Lookout parking lot (plot 17). Seven sites were selected along the elevation gradient and two plots were located off the gradient; one, a warm forested site (plot 36), and the other a dry site with poor soil development (plot 4). At each moisture stress measurement site, six grand fir trees, 1.0 to 1.5 m high, were selected and marked the day before sampling. Variation in moisture stress was further reduced by selecting shaded branches from the north-side with current year's growth. Field measurement of xylem pressure stress followed Waring and Cleary (1967) and was conducted between the hours of 0015 and 0520 on 27 August 1982 using a PMS Model 600 pressure chamber (last measurable precipitation was 3 August 1982).

## Analytical Methods

### Vegetation classification

Vegetation was classified by M.O. Hill's (Hill 1979b) two-way indicator species analysis (TWINSpan) program, part of the Cornell University Ecology Program series. TWINSpan first ordinales the data by reciprocal averaging; then, species which characterize the axis extremes are emphasized to polarize the samples. Two clusters are then formed by breaking the ordination near the middle. Sample divisions are then refined and reclassified. The process is repeated until each cluster has no less than a minimum number of members (Gauch 1982). Prior to data entry, percent species cover data were transformed to midpoint percent cover values (Mueller-Dombois and Ellenberg 1974) and then converted to octave values after Gauch (1982) (Table 3). Percentage similarities between plant community groups were determined with the program AIDN (Overton et al. 1987). Plot 15 was an outlier plot and was dropped from analysis.

### Vegetation ordination

Ordination of samples and species was achieved by the Cornell Ecology Program DECORANA (Hill 1979a). DECORANA is a detrended form of reciprocal averaging which corrects the two main faults of polar ordination, an arch distortion of ordinated data and compression of the first axes ends relative to the axes' middle (Gauch

Table 3. Octave scale transformation conversion for species percent cover mid-point values for analytical purposes (after Gauch 1982).

Mid-point percent cover	Octave scale
0.25	1
0.75	2
1.50	3
3.00	4
6.00	5
12.00	6
24.00	7
48.00	8
82.00	9

1982). Ordination summarizes community field data having "high-dimensional" space from large numbers of samples and species into "low-dimensional" ordination space (Gauch 1982). The same floristic field data input into TWINSpan were used in DECORANA. Ordered data were displayed in an ordination graph where similar samples (species) were grouped together and floristically dissimilar samples were separated. Ordination graph axes can be considered to define conceptual ecological space within which sample floristic affinities are related to environmental gradients. Environmental gradients are expressed in standard deviation units of floristic change.

#### Tree population analysis

Needle morphology data were grouped by community types previously arrived at through classification by TWINSpan. Shade-side needles were used in analysis to minimize variation. All shade-side needle morphological characteristics were included in the analysis. The number stomatal rows and maximum stomatal length were used to differentiate tree community groups. A stomatal index  $[100 \times (\text{number of stomatal rows}) \times (\text{length of the longest stomatal rows} + \text{length of needle})]$  was computed as a single, composite measure; in cases where there was a stomatal spot with no rows, a nominal number of 0.125 was used following Daniels (1969).

Community-grouped needle data were analyzed with SPSS (Statistical Package for the Social Sciences) on a CYBER 3084 computer using the subprograms t-test and nonpar; and with Stats View on a

Macintosh Plus for regression analysis. Where data were normally distributed, paired t-tests were used to test significant differences between sides of trees within community groups. Differences were tested at 0.01 and 0.05 significance levels. Nonparametric statistics were used to test the difference between trees grouped by community types where data were not normally distributed and where group sizes were not equal (Norusis 1982). In the nonparametric analysis, I used the Mann-Whitney U test to examine differences between groups because it is distribution-free in its assumptions, and rejection of the null-hypothesis implies that one population has a higher median (Snedecor and Cochran 1980). As used here, the Mann-Whitney U test will stipulate that one group is higher ranked than the other; the test of significance will therefore be one tailed (Shaw and Wheeler 1985).

### Hybrid index

Comparison of tree population characteristics was accomplished by employing a hybrid index calculated for each tree population group (Anderson 1949). Hybrid indexes employed in other studies were not used for two reasons: there has been no consistent morphological hybrid indexes used; and this study was designed to compare tree populations within a restricted study area, not to compare taxonomically the study area populations with other areas.

The hybrid index I employed considered needle characteristics sampled from the shade-side of trees. Based on the taxonomic literature, I considered morphological characteristics that differentiate grand fir from white fir. Three morphological characteristics were used: number of stomatal rows, relative stomatal row length (ratio of the length occupied by stomatal lines to the needle length expressed as a percent), and periderm color (Appendix IV). Each characteristic was assigned a rating number of 1, 2, or 3 depending on the magnitude of the characteristic. A hybrid index value was determined based on the range of morphological values (Table 4); thus, a tree with 2.7 stomatal rows, 37.5 relative stomatal length, and red periderm would have an index of  $1 + 2 + 1 = 4$ .

Of the five needle morphological characteristics, stomatal index, stomatal length and needle length were not employed. Stomatal index was abandoned because it incorporates, and therefore confounds, two other important traits (number of stomatal rows and relative stomatal row length). Stomatal row length was not used as it is not standardized due to variations in needle length. On the other hand, relative stomatal row length is independent of needle length. Needle length was not employed as it is not sufficiently variable in the study area to be a good discriminator. A low index value corresponds to trees with grand fir characteristics, while a high value corresponds to white fir characteristics.

Table 4. Definition of hybrid index values based on ranges of morphological characteristics and periderm color taken from the shade-side of Abies grandis trees in the Summit Ridge study area, Baker County, Oregon.

Range of Morphological Characteristics			
Rating number intervals	Number stomatal rows	Relative stomatal length	Periderm color
1	0-3.3	0-31.7	red
2	3.4-6.6	31.8-63.4	pink
3	6.7-10.0	63.5-95.1	yellow

### Pre-dawn xylem water stress

Of the six xylem pressure stress measurements at each site, the highest and lowest readings were eliminated from analysis to remove outliers. The average score of the remaining measurements for each site was then employed for analysis. The dependent variable was the shade-side stomatal index (number of stomatal rows multiplied by the length of the longest stomatal rows), a composite measure of needle characteristics. Three independent variables were assessed: 1) a direct variable expressed by the average pre-dawn xylem water stress measured in pounds per square inch (psi); 2) an indirect variable based on the solar index for April-August growing season expressed in Langleys ( $\text{gm}/\text{cm}^2$ ) (Frank and Lee 1966); and 3) another direct variable, elevation in meters. These variables were associated with plots from which pre-dawn xylem water stress measurements were taken. Data were analyzed by forward selection multiple linear regression in SPSS.

## RESULTS

### Vegetation Classification

Floristic vegetation data from 39 macroplots were classified by TWINSpan into four clusters ranging in size from 4 to 19 plots (Table 5). Because the 10 and 11 clusters were only represented by four and five plots respectively, I decided to combine these clusters into a single cluster, 1. Three clusters are shown at the bottom of the TWINSpan classification as the 00, 01, and 1 clusters. The 39 plots are therefore aggregated into 3 clusters or community groups, herein referred to as associations. The clusters were respectively named the Abies grandis/Clintonia uniflora Association consisting of 11 plots, the A. grandis/Spiraea betulifolia Association consisting of 19 plots, and the A. grandis/Symphoricarpos oreophilus Association consisting of 9 plots. Percentage similarities between the three associations were determined with the program AIDN. The Spiraea group was most similar to the Symphoricarpos group (58.8% similarity); on the other hand, the Symphoricarpos group was least similar to the Clintonia group (45.3% similarity). Environmental characteristics of sample plots are given in Appendix I.

Table 5. TWINSpan two way classification table of 39 plots by species in the Summit Ridge study area, Baker County, Oregon. Species acronyms are identified in Appendix III. Values are cover classes.

		Association <sup>a</sup>											
		<u>Clintonia</u>				<u>Spiraea</u>				<u>Symphoricarpos</u>			
Plot		24122212	33	3333		1123	1233	11221123					
Species		40325749701	2345132689013652889	680679174									
GAAP		2-211211-12	-1	-----	-11112--	-1111-11--							
LAPA 2		-----2-1--2	-----	-1--1--	-----11-1--								
POPU		---2-1-----	-----	-----	-----1-								
ANMA		-----11--	-----	-----	-----1								
CLUN		213-212-1-1	-----	-----	-----								
CYMO		-----2-1--1	-----	-----	-----								
DITR		2---21-1-11	--1	-----	-----								
GOOB		--111111-22	-----	-----	-----								
LIBO L		-1----551--	-----	-----	-----								
LOUT 2		-2312432--	-2	-----	-----								
MIST 2		---1--2--2	-----	-----	-----1								
PIEN		-----4-2--	-----	-----	-----2								
PYSE		-1211111--1	-1	-----	-----2								
RILA		23-1-251-24	-----	-----	-----2								
SOSI		--21-12-1--	-----	-----	-----								
VAME		555555545--	-5	-----	-----44								
ADBI		2-42342-222	12--3	-----	-----1211								
CHUM O		41-22221111	11-1-1	-----	-----2--12								
THOC		2-42322122	-1--32	-----	-----11-1								
VIAD		---22-1122	---1	-----	-----11--3--1								
FEOC		121--2-2-22	-22	-----	-----22--22								
PTAQ P		-2-----11	-----	-----	-----221								
RIVI		5-1233-3--	-2322	-----	-----1--4--								
AMAL C		222-11-1222	-212	-----	-----1								
SMST		22112--1-2	-11--11	-----	-----1-1-12-1								
CIVU		21--11-1--1	-----	-----	-----1111-1								
HIAL		1-1--112112	1111--2	-----	-----11--1--1								
ROGY		412322-2-2	-1-232	-----	-----221-2								
SPBE L		312-23-3312	22235522233121	-432	-4-21----	-1							
ASCO		---21-----	-1--1-1-1	-----	-----2--								
FRVI P		52214453222	2222455224212145	-11	-----	-1							
PRVU		-----11	-----1	-----	-----2-1								
SYAL		2---2224455	2155532525-2-513555		-----								
VIAM		1-2---11-11	-112	-----	-----11								

Table 5 (continued)

Association a			
	<u>Clintonia</u>	<u>Spiraea</u>	<u>Symphoricarpos</u>
APAN	-----2-	-----11-22-2---2-	-----
ARCO	-1221112-1-	1-1-554-3442--31---	--1-----
CAGE	-1-11111322-	21-4344532115--1---	--1-----
HAEL	-----1-	1-1--2-----	-----
PHPR	-----1-	-----11-----111-	-----
ASOC	-----	1-2-2-----	-----
CAMI 2	-----	2---1-1-----	-----
DAGL	-----	1---22-----	-----
EPAN	-----	1--11--11-----	-----
HIAL 2	-----	21--22211--121-----	-----
CARU	-1---2--422	52-255554525422-2--	22-----
CEVU	-----	11---22--1--11-----	1-1-----
POKE	-----	11-1-----	-----1
SALI X	225---11--	2322-5-24224-----	2122-----
CAEU 2	-----	1-----1---	1-----
PIPO	12-----	33234-21-5---4---2-3--	2---3
CYOF	-1--1-----1	121-1--1--1--1--1--	11-----
LANE C	11-----	2-1---11-----	1-----
LIHA	-----	111-----1-1-----	1-----
VETH	2---1--1---	111-1-112-1--1--2---	-----
ABGR	42553554454	4244531444452355422	233334243
LAOC	22--2-----	1-223-----	-----2--
OSCH	--1---11111	111-111-1-1111-1--1	1111-----
RUAC	2-----	111-----1-----	-----1
BERE	--1-1111122	--2---221--2-3--33-3-	3-31-----
SIME	1--122-1-12	1211-----1-11-1-11-	212-1---
ELGL	-----	11---1--1--1--1212-	1-----1
TRDU	-----	1-1--1-1-1--1--1111-	1-----
ACMI	2-1--1111-	1111222221112111111	112212211
GADI	1-----1-	11-----111-211--1--	1--111-2
POGL	2--11--1-1-	111-2222-2-121111111	11-211111
PSME G	132-1---244-	341443-4---23---2-3	242442-2
ASPE	-----	21-----	1--2--
COPA	-----	1--1-1-----11111--	111111111
COGR 2	-----	1-1--2-----11-----	1--11-111
COLI 2	-----11-	11--1-111--111-----	1-1111111
MAGL	1-----	1-----1--11--1--	1--11-1
NAIN P	-----	1-----1-1--	1-1-1
PHHE	-----	1111-11--1--	11-111-1
PRVI M	-----	-----2-3--	21--1--
ANLU	1-----	2--11-----	11-----4
ERIN 2	-----	2-----	1--1-----
LULA	-----	1111-2-2-1121-----	11-11-211
BRVU	1-1111--1-	-----1-1--1-----	121-1-1311

Table 5 (continued)

Association <sup>a</sup>			
	<u>Clintonia</u>	<u>Spiraea</u>	<u>Symphoricarpos</u>
CRAF	1-----11--	-----1-----1--1--	1-1-----1-
DERI V	1-----	-----1-----	-----1-----
POMA 2	1-----1--	1-----1--1111111	13-21112-
ARHO	-----	-----1-----	11--1-----1
AGUR	-----	-----2--	2-5--22--
BRIN	1-----	-----	--2-11---
CAHO	1-----	-----1--	-----2--
CHFR	1-----	-----	1-1-11---
HAMI	-----	-----2--	11-112--
OSOC	---1-----	-----	1---11-1-
PABR	-----	-----1--	111-1111-
ALAC	-----	-----1--	1--11--1
ARTR V	-----	-----	44--4444-
ASIN	-----	-----	-----231-
ORLI	-----	-----	1---1--11
RICE	-----	-----2--	-----322
SYOR	-----	123-----11--	335554554
PEBO	-----	-----	1--111-1-
STJA	-----	-----	111-1111-
ERHE	-----	-----	11-413-22
SEAL 2	-----	-----	2-----12
TWINSpan	000000000000	0000000000000000000000	1111111111
clusters	000000000000	11111111111111111111	

<sup>a</sup> Associations are:Abies grandis/Clintonia uniflora AssociationA. grandis/Spiraea betulifolia AssociationA. grandis/Symphoricarpos oreophilus Association

The three plant associations are the basis for the subsequent analysis of Abies grandis needle morphology and periderm color patterns, but first I describe these associations and their relationships to other regional vegetation classifications.

#### Abies grandis/Clintonia uniflora Association

The Abies grandis/Clintonia uniflora Association is a cool, moist forest type established on northerly aspects with slight to moderate slopes at mid-elevations in the study area. The association also occurs at lower elevations in shaded riparian areas affected by cold air drainage. The forest canopy is dominated by Abies grandis. A two-tier shrub layer is generally present. The herb layer is well represented. There is much litter, a well-developed humus layer and cryptogams are generally present. Soils are deep, containing high amounts of volcanic ash and are similar to the Tolo series.

Although stands are dominated by Abies grandis, Pseudotsuga menziesii is usually present and there are occasional individuals of Picea engelmannii, Larix occidentalis, and Pinus ponderosa. Conifer cover is often biased toward non-commercial species because of logging. The understory is dominated by Vaccinium membranaceum. Other tall shrubs with high constancy are Amelanchier alnifolia, Symphoricarpos albus, Rosa gymnocarpa, and Lonicera utahensis. Herbaceous species with high constancy are

Fragaria spp., Adenocaulon bicolor, Galium spp., and Thalictrum occidentale.

Abies grandis has 100 percent constancy, 16 percent average cover and 10.6 m<sup>2</sup>/ha average stand basal area. The other major species is Pseudotsuga menziesii with 64 percent constancy, average cover of 3 percent and average stand basal area of 1.7 m<sup>2</sup>/ha. Old-growth trees are only Abies grandis. Regeneration is predominantly A. grandis, with 82 percent constancy, P. menziesii 18 percent constancy, and Picea englemannii 9 percent constancy in the macroplots. The average stand tree basal area is 13.4 m<sup>2</sup>/ha. The forest floor has 20-70 percent litter cover and 0-20 percent cryptogam cover.

Although this association appears to be equivalent to W. Johnson's (1959) Abies grandis/Vaccinium membranaceum community, Johnson did not identify indicator species. Johnson and Simon's (1986) Abies grandis/Clintonia uniflora Association, for which full floristic information is available, is also similar. Membership of these stands in the Abies grandis/Clintonia uniflora Association is especially based on the constancy of Clintonia uniflora and other floristic and topographic similarities. Of 12 indicator species given by Johnson and Simon (1986), 10 were encountered in study area plots. Based on constancy values of indicator species alone, it appears that my study plots are in an early to mid-seral stage (Johnson and Simon 1986).

Abies grandis/Spiraea betulifolia Association

The Abies grandis/Spiraea betulifolia Association is a warm, moist forest type located on moderate to flat slopes with various aspects at lower elevations in the study area. The overstory is open and park-like with abundant Abies grandis reproduction in the understory. Understory vegetation is well developed with much low shrub and herbaceous cover. The forest floor has exposed rocks.

The shrub layer is dominated by Symphoricarpos albus. Other shrubs with high constancy are Spiraea betulifolia, Salix spp. and Berberis repens. Herbaceous species with high constancy are Achillea millefolium, Calamagrostis rubescens, Fragaria spp., Potentilla glandulosa, Hieracium albiflorum, and Carex geyeri.

The overstory is dominated by Abies grandis with 100 percent constancy, 13 percent average cover and 7.2 m<sup>2</sup>/ha average stand basal area. Pinus ponderosa has 53 percent constancy, 4 percent cover and 2.5 m<sup>2</sup>/ha average stand basal area; and Pseudotsuga menziesii has 53 percent constancy, 4 percent cover and 1.8 m<sup>2</sup>/ha stand basal area. Larix occidentalis and Picea engelmannii did not occur on any plots but are found occasionally within the stands. Regeneration is predominantly by Abies grandis with 74 percent constancy in subplots. Pseudotsuga menziesii has 32 percent constancy, Pinus ponderosa 16 percent constancy, and Larix occidentalis 11 percent constancy in subplots. The average stand basal area is 12.7 m<sup>2</sup>/ha. The forest floor had 2-50 percent average

rock cover, 15-50 percent average forest litter cover and few cryptogams.

The Abies grandis/Spiraea betulifolia Association has also been recognized in northeastern Oregon and adjacent Idaho by a number of researchers. W. Johnson (1959) identified an Abies grandis/Calamagrostis rubescens community in the Pine Valley allotment, south Wallowa Mountains; this type is similar to the Abies grandis/Spiraea betulifolia Association described in this study. My association is also similar to Hall's (1973) mixed conifer-pine grass community in the Blue Mountains, Oregon, and, Johnson and Simon's (1986) Abies grandis/Spiraea betulifolia Association in the south Wallowas.

#### Abies grandis/Symphoricarpos oreophilus Association

The Abies grandis/Symphoricarpos oreophilus Association is a cool, dry forest/shrub type with southwesterly aspects and moderate slopes, typically occupying the brow of ridges at higher elevations in the study area. Forest vegetation tends to be sparse and consists of isolated stands of conifers amid shrub fields. Forbs are abundant but small. Soils are poorly developed, mainly consisting of coarse rock fragments, and similar to the Klicker series.

This shrubby forest community is codominated in the overstory by Abies grandis and Pseudotsuga menziesii and in the understory by Symphoricarpos oreophilus and Artemisia tridentata var. vaseyana. Symphoricarpos has a 100 percent constancy and 22 percent average

cover; Artemisia has a 67 percent constancy, and 8 percent average cover. Other shrub species which may occur are Prunus virginiana and Ribes cereum. The herbaceous layer has a high proportion of annual plants. Species with high constancy are Achillea millefolium, Collinsia parviflora, Potentilla glandulosa, Polygonum majus, Lupinus laxiflorus, Paeonia brownii, Collomia linearis, and Stellaria jamesiana.

Conifers are short with an open growth form. Abies grandis has 100 percent constancy, 7 average percent cover and 3.5 m<sup>2</sup>/ha average basal area; Pseudotsuga menziesii has 89 percent constancy, 6 percent average cover and 3.1 m<sup>2</sup>/ha average basal area. Occasional associated species are Pinus ponderosa and Larix occidentalis at lower elevations, and Abies lasiocarpa at higher elevations. Where trees occur, regeneration by A. grandis and Pseudotsuga menziesii is poor at 33 percent and 11 percent constancy, respectively, in subplots. In brushy areas, regeneration is very poor. The average stand basal area is 8.0 m<sup>2</sup>/ha. The forest floor has an average 30-65 percent bare rock, 1-35 percent average litter and few cryptogams.

The Abies grandis/Symphoricarpos oreophilus Association has not been recognized in northeastern Oregon. W. Johnson (1959) described an Artemisia tridentata var. vaseyana/S. rotundifolius (= S. oreophilus) community in the spruce-fir zone of the Pine Valley allotment, south Wallowa Mountains. No trees were recorded on Johnson's plots; however, scattered trees are just off and adjacent to the plots in photos. Steele et al. (1981) identified a Pseudotsuga menziesii/Symphoricarpos oreophilus habitat type in east-central Idaho where Artemisia tridentata var. vaseyana is co-dominant on

more than 50 percent of the plots. Mauk and Henderson (1984) described a Pseudotsuga menziesii/Symphoricarpos oreophilus habitat type in northeast Utah and Johnson and Simon (1986) described a Pseudotsuga menziesii/Symphoricarpos oreophilus community type in the south Wallowa Mountains.

The Abies grandis/Symphoricarpos oreophilus Association is most similar to Johnson and Simon's (1986) Pseudotsuga menziesii/Symphoricarpos oreophilus community type; although Johnson and Simon do not report the presence of A. grandis. The main environmental difference is that Johnson and Simon's community plot elevation range is 1,300-1,620 m (1,480 m average) compared to my community plot elevations of 1,440-2,080 m (1,800 m average). Johnson and Simon's plots have a high occurrence of Pinus ponderosa and absence of Abies grandis in the overstory, while my plots have a low occurrence of Pinus ponderosa and a co-dominance of A. grandis in the overstory in an area with limited logging activity. Johnson and Simon's plots have a shrub layer with high occurrences of Amelanchier alnifolia and high cover of S. oreophilus and lack Artemisia tridentata, while my plots have S. oreophilus with a co-dominance of A. tridentata var. vaseyana and lack Amelanchier alnifolia. Herbaceous species are very different. Johnson and Simon's principal indicator species are Fragaria vesca, Osmorhiza chilensis, Galium aparine, Cynoglossum officinale, Calamagrostis rubescens, Carex geyeri, and C. hoodii. In my study area plots, F. vesca is very rare, while all other indicator species have much lower constancy values than were reported by Johnson and Simon (1986).

### Vegetation Ordination

Detrended correspondence analysis (DCA) ordination was used to display different plant communities with respect to indirect environmental gradients. Thirty-nine plots are ordinated by detrended correspondence analysis (Figure 3). The first three ordination axes have eigenvalues and percent variability accounted for of 0.462 (66.7%), 0.139 (20.1%), and 0.089 (12.9%) respectively, suggesting that most (87%) of the floristic variation is accounted for by the first two axes.

Although the DCA ordination does not classify vegetation, it can be used to display different plant communities. Figure 3 shows the three final associations superimposed on the ordination. The Abies grandis/Clintonia uniflora Association with high shrub dominance and diversity can be seen, on the left of the ordination, to be the most homogeneous community, i.e., plots are more-or-less packed together. This community corresponds to the TWINSPAN 00 cluster. The Abies grandis/Spiraea betulifolia Association is the most heterogeneous of the types and is identified as the TWINSPAN 01 cluster. The Abies grandis/Symphoricarpos oreophilus Association is the most open of the communities and has low forb composition. This type corresponds to the TWINSPAN 1 cluster.

The ordination x-axis suggests a moderately strong environmental gradient representing 4.4 standard deviation units of floristic change. The cluster of nine samples to the extreme right of the diagram represents samples from sites at higher elevation, exposed ridges

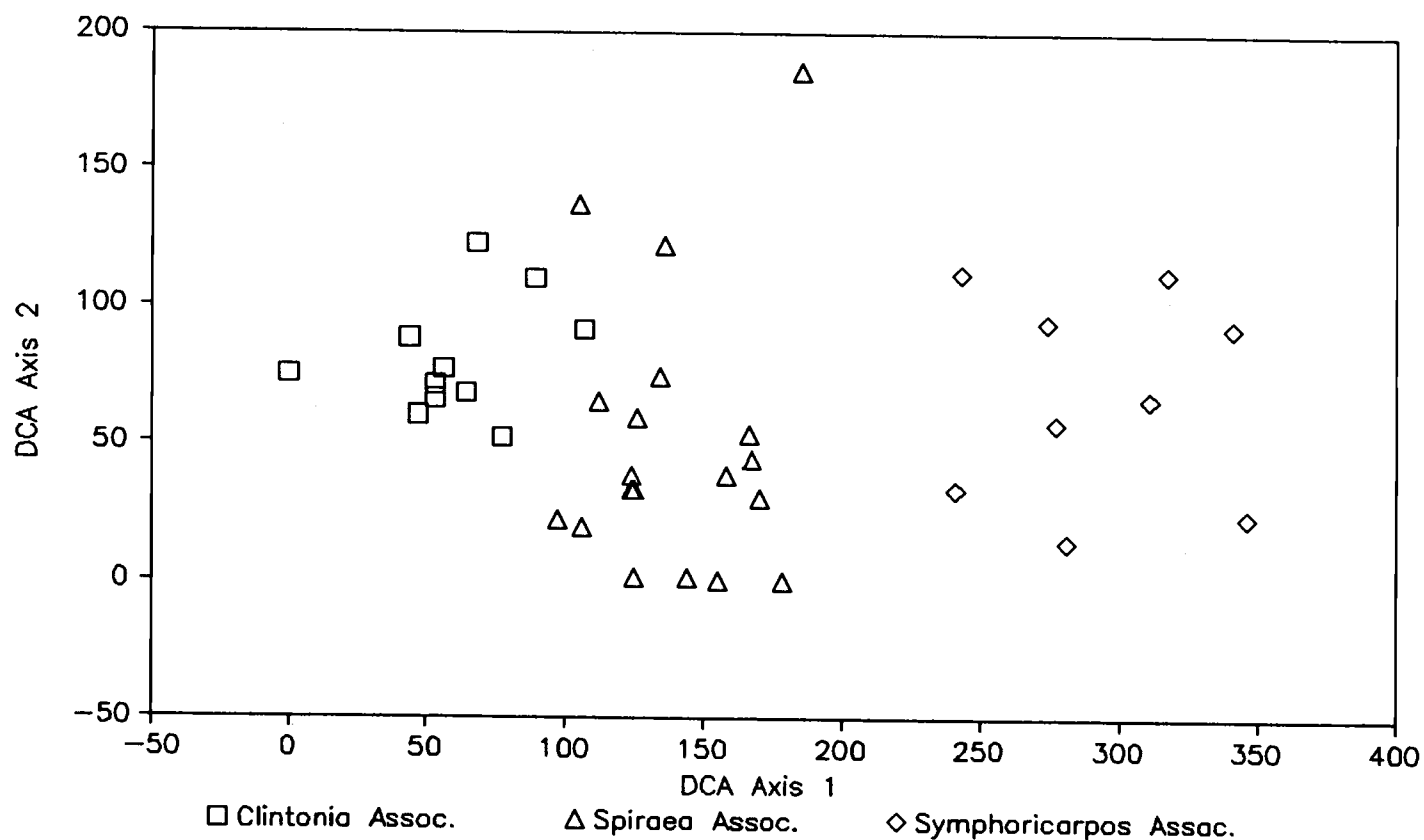


Figure 3. Detrended correspondence analysis ordination of 39 sample plots in the Summit Ridge study area, Baker County, Oregon. Species groups correspond to the Abies grandis/Clintonia uniflora Association, A. grandis/Spiraea betulifolia Association, and the A. grandis/Symphoricarpos oreophilus Association.

and/or with poor soil development derived from residual basaltic parent material, moderate slopes (average 8.9 degrees), and a general southwest aspect. The more-or-less tight cluster of eleven samples on the extreme left represents samples from moderately disturbed sites at intermediate elevations with well-developed deep colluvial soils (derived from volcanic ash), low slopes (average 5.6 degrees), and generally east to north aspects. The centrally located loose cluster of samples represents ecologically intermediate sites with respect to the other associations. These sites have varied slopes with low angles; however, these intermediate sites tend to be geographically more closely associated with the group on the left, but their elevation range is not as great.

The DCA x-axis is interpreted as a complex topographic, moisture gradient, expressing diminished effective moisture. Evidence for this interpretation comes from significant relations between selected environmental characteristics from 39 plots and the DCA ordination x-axis position (Table 6). Weak but significant correlations were found respectively between the x-axis position and elevation and solar insolation index. Somewhat stronger significant correlations were gained between the x-axis position and combined elevation and the solar insolation and between the x-axis position and combined elevation and aspect. Correlation between the x-axis position and aspect, alone, was not significant.

Table 6. Single and multiple regression relationships between the DECORANA x-axis position and selected environmental measurements at 39 sample plots in the Summit Range study area, Baker County, Oregon.

Environmental measurement	r	Relationship
Elevation	0.652 **	$y = 0.075x - 216.2$
Solar insolation	0.534 **	$y = 0.759x - 483.8$
Elevation and solar insolation	0.727 **	$y = 0.061x_1 + 0.495x_2 - 559.2$
Elevation and aspect	0.669 **	$y = 0.070x_1 + 0.201x_2 - 225.9$
** significance, $p \leq 0.01$		

Still further support for this environmental interpretation of the ordination comes from the positive correlation between pre-dawn xylem water stress and the x-axis position, (even though pre-dawn xylem water stress values could not be considered stressful) (Figure 4). Positive correlations were found between the x-axis as the dependent variable and the independent variables of pre-dawn xylem water stress, elevation, and solar insolation (Table 7). Elevation and solar insolation individually are again both significantly correlated to the x-axis position. Elevation and pre-dawn xylem water stress together regressed against the x-axis position have a very strong and significant correlation. Pre-dawn xylem water stress combined with solar insolation regressed against the x-axis position are well correlated. Finally, elevation, pre-dawn xylem water stress, and solar insolation combined are strongly correlated to the x-axis position; however, solar insolation does not add much information to the multiple regression model. Elevation and solar insolation together are not significantly correlated to the x-axis position, leading to the conclusion that solar insolation should be dropped from the model.

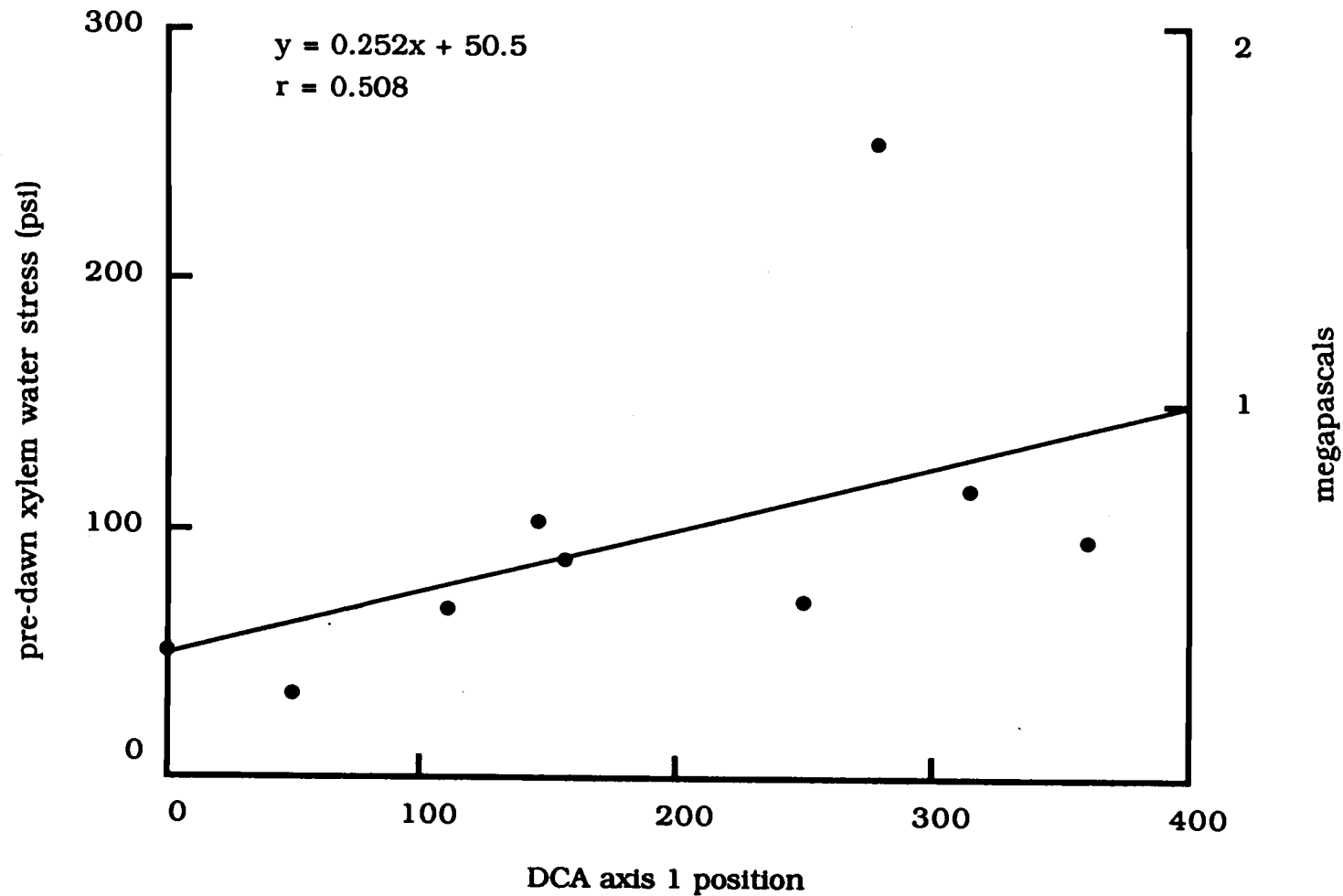


Figure 4. Relation between the plot position along the detrended correspondence analysis ordination axis-1 and pre-dawn xylem water potential from nine selected plots in the Summit Ridge study area, Baker County, Oregon.

Table 7. Single and multiple regression relationships between the DECORANA x-axis position and selected environmental characteristics for nine plot samples selected for pre-dawn xylem water stress measurements in the Summit Ridge study area, Baker County.

Environmental measurement	r	Relationship
Elevation	0.700 *	$y = 0.106x - 371.4$
Pre-dawn xylem water stress	0.508	$y = 1.024x + 86.4$
Solar insolation	0.701 *	$y = 2.346x - 1,859.7$
Elevation and pre-dawn xylem water stress	0.932 **	$y = 0.124x_1 + 1.320x_2 - 594.6$
Elevation solar insolation	0.701	$y = 0.067x_1 + 1.499x_2 - 1473.7$
Pre-dawn xylem water stress and solar insolation	0.719 *	$y = 0.784x_1 + 2.099x_2 - 1720.7$
Elevation, pre-dawn xylem water stress, and solar insolation	0.934 **	$y = 0.106x_1 + .207x_2 + 0.623x_3 - 1033.1$

\*\* significance,  $p \leq 0.01$

\* significance,  $p \leq 0.05$

## Needle Morphological Characteristics and Environment

### Shade-side vs. sun-side

The shade-side and sun-side of Abies grandis trees differ in their needle characteristics. Trees were placed into three groups based on the pattern of adaxial stomata among shade and sun-side of trees: 1) trees with more adaxial stomata on the sun-side than shade-side; 2) trees with more adaxial stomata on the shade-side than sun-side; and 3) trees with no adaxial stomata on either the sun-side or shade-side. Ninety-four percent of the 431 sampled trees show more adaxial stomata on the sun-side than shade-side; 5.3 percent of the trees show the reverse pattern of more adaxial stomata on the shade-side than the sun-side. Only 1.2 percent of the trees lack adaxial stomata on both sides of the tree.

Distinction between the sun-side and shade-side of trees is further exhibited by the five needle morphological characteristics measured on 431 trees (Table 8). Each morphological characteristic taken individually distinguishes the sun from the shade side. The sun-side needles have a significantly more stomatal rows than the shade-side needles (3.8 vs. 2.4 rows). Stomatal length was also significantly greater on the sun-side than shade-side of trees (1.4 vs. 1.0 cm). There was a significantly greater relative stomatal length on the sun-side than shade-side of trees (31.6 vs. 24.0 percent). The stomatal index (number of stomatal rows x relative stomatal length)

Table 8. Paired t-test on mean needle characteristics sampled from the sun-side and shade-side of Abies grandis trees (n=431) in the Summit Ridge study area, Baker County, Oregon.

Needle characteristic	Sun-side	Shade-side	Difference	t-score	
Stomatal rows (no)	3.8	2.4	1.4	21.8	**
Stomatal length (cm)	1.4	1.0	0.4	12.8	**
Needle length (cm)	4.5	4.2	0.3	11.1	**
Relative stomatal length (%)	31.6	24.0	7.6	11.8	**
Stomatal index <sup>a</sup>	178.4	97.2	81.2	13.2	**

\*\* significant,  $p \leq 0.01$

<sup>a</sup> number of stomatal rows x relative stomatal length

was about twice as great on the sun-side than on the shade-side of trees (178.4 vs. 97.2), a significant difference.

#### Topography and environmental relations of leaf characteristics

Shade-side adaxial stomata from grand fir populations varied with topography. The number of stomatal rows, stomatal length, relative stomatal length, and stomatal index (number of stomatal rows x relative stomatal length) from tree populations associated with 39 plots were regressed against selected environmental characteristics to find the best descriptor. Simple and multiple regressions of morphological characteristic were run with elevation, solar insolation, slope, and aspect. Table 9 shows the significant relationships from these regressions. Elevation was weakly correlated with stomatal index, stomatal length, and relative stomatal length. Multiple regression revealed a weak but somewhat higher correlation between the stomatal index as the dependent variable, and combined elevation and aspect as the independent variable.

In further support of the environmental relations of needle morphology, grand fir tree populations located on ridge-top sites have higher shade-side stomatal index values than populations on nearby valley sites. Four paired plots were chosen such that one of each pair was from a ridge site and the other from a valley site within 250 m of each other (Table 10). Plot 7 is a valley site and has a stomatal index of 18.5. Plot 6, the paired ridge site, has a steeper, exposed slope with trees having a stomatal index of 179.3. Plot 15, a

Table 9. Correlation coefficients and significant regression relationships between Abies grandis shade-side needle characteristics and selected environmental characteristics from 39 plots in the Summit Range study area, Baker County, Oregon.

	Elevation	Elevation and aspect
Stomatal rows (no)	0.262 ---	0.389 ** $y = 0.0004x_1 + 0.004x_2 - 0.3$
Stomatal length (cm)	0.509 ** $y = 0.0004x - 0.906$	0.505 * $y = 0.0004x_1 + 0.001x_2 - 1.0$
Relative stomatal length (cm)	0.520 ** $y = 0.009x - 20.997$	0.507 ** $y = 0.009x_1 + 0.024x_2 - 22.0$
Stomatal index <sup>a</sup>	0.538 ** $y = 0.059x - 160.032$	0.558 ** $y = 0.047x_1 + 0.207x_2 - 169.1$

\*\* significance,  $p \leq 0.01$

\* significance,  $p \leq 0.05$

a number of stomatal rows x relative stomatal length

Table 10. Morphological needle characteristics and periderm color of *Abies grandis* and stand environmental characteristics for eight paired plots from proximate ridge and valley positions in the Summit Ridge study area, Baker County, Oregon.

Plot (n)	6 (10)	7 (10)	16 (10)	15 (10)	21 (10)	22 (10)	26 (11)	27 (10)
Topographic position	ridge	valley	ridge	valley	ridge	valley	ridge	valley
Stomatal index <sup>a</sup> mean (shade)	179.3	18.5	180.2	37.5	277.5	52.4	134.6	3.6
Stomatal index <sup>a</sup> range (shade)	0.0- 423.6	0.0- 151.5	0.1- 609.2	1.3- 162.2	8.7- 840.0	0.9- 257.1	3.7- 484.2	0.0- 8.4
Slope (%)	19	2	45	18	21	62	18	18
Aspect (degrees)	222	200	240	326	240	68	180	80
Elevation (m)	1340	1290	1550	1560	1930	1860	1580	1510
Periderm color (% of trees)								
yellow	--	--	68	71	68	68	72	72
red	--	--	29	27	29	31	23	26
pink	--	--	3	2	3	1	4	2

<sup>a</sup> number of stomatal rows x relative stomatal length

valley site with a northerly aspect, has a stomatal index of 37.5. Plot 16, the paired ridge site, has a more southerly aspect and steeper slope with a stomatal index of 180.2. Plot 22, a valley site with a northeasterly aspect and a steep slope has a stomatal index of 52.4. Plot 21, the paired ridge site, has a more southerly aspect and a stomatal index of 227.5. Plot 27 is a valley site with a northerly aspect and has a stomatal index of 3.6. Plot 26, the paired ridge site with a southerly aspect has a stomatal index of 134.6.

A relationship between needle morphology and environment is shown by shade-side stomatal index values from nine selected plots from which pre-dawn xylem water stress data was collected. Needle morphology correlates with moisture stress as well as other site characteristics (Table 11). As with the other relationships of the 39 plot data, simple regression revealed correlations between stomatal index and elevation, and stomatal index and solar insolation. There was no significant relationship between pre-dawn xylem water stress and stomatal index, although the two were positively correlated. Multiple regression was used to correlate stomatal index values as the dependent variable against the independent variables of solar insolation, pre-dawn xylem water stress, and elevation. Elevation and pre-dawn xylem water stress together are strongly correlated to the stomatal index. Pre-dawn xylem water stress combined with solar insolation are well correlated to the stomatal index. Pre-dawn xylem water stress, solar insolation, and elevation have the highest correlation to the stomatal index of the combined environmental measures. Addition of solar insolation as an independent variable

Table 11. Single and multiple regression relationships between shade-side stomatal index (number of stomatal rows x relative stomatal length) and selected environmental characteristics for nine plot samples selected for pre-dawn xylem water potential measurements in the Summit Ridge study area, Baker County.

Environmental measurement	r	Relationship
Elevation	0.696 *	$y = 0.106x - 371.4$
Pre-dawn xylem water potential	0.516	$y = 0.767x + 38.7$
Solar insolation	0.694 *	$y = 2.346x - 1859.7$
Elevation and pre-dawn xylem water potential	0.938 **	$y = 0.091x_1 + 0.958x_2 - 463.1$
Elevation and solar insolation	0.696	$y = 0.050x_1 + 1.083x_2 - 1092.6$
Pre-dawn xylem water potential and solar insolation	0.716 *	$y = 0.592x_1 + 1.524x_2 - 1247.2$
Elevation, pre-dawn xylem water potential, and solar insolation	0.940 **	$y = 0.079x_1 + 0.907x_2 + 0.423x_3 - 716.3$

\*\* significance,  $p \leq 0.01$

\* significance,  $p \leq 0.05$

apparently does not improve the relationship between shade-side stomatal index and elevation and pre-dawn xylem water stress. Stomatal index and the x-axis position have similar correlations with these independent variables because stomatal index is strongly correlated with the x-axis position.

#### Needle characteristics of trees grouped by association

Three floristic associations are identified in the study area:

Clintonia Association = Abies grandis/Clintonia uniflora Association;

Spiraea Association = Abies grandis/Spiraea betulifolia Association;

Symphoricarpos Association = Abies grandis/Symphoricarpos

oreophilus Association. Five shade-side needle morphological characteristics were used to describe and differentiate trees grouped by association: maximum number of stomatal rows, stomatal length, needle length, relative stomatal length (percent of needle length), and stomatal index (number of stomatal rows x relative stomatal length).

All associations have highly variable needle characteristics (Appendix V and VII). In the Clintonia Association, the number of stomatal rows varied from 0 to 7 and stomatal length from 0 to 3.1 cm; relative stomatal length ranged from 0 to 93 % and stomatal index from 0 to 648. In the Spiraea Association, the number of stomatal rows varied from 0 to 10 and stomatal length from 0 to 5.4 cm; relative stomatal length ranged from 0 to 94 % and stomatal index from 0 to 2,106. In the Symphoricarpos Association, the

number of stomatal rows varied from 0 to 9 and stomatal length from 0 to 5.5 cm; relative stomatal length ranged from 0 to 95 %, and stomatal index from 0 to 847. Needle length range was not as great in the Spiraea and Symphoricarpos Associations (ranging from 2.5 to 6.3 cm and 2.6 to 6.2 cm respectively) than the Clintonia Association where it ranged from 1.8 to 6.2 cm.

Despite the variability within each association, associations are significantly differentiated by mean needle characteristics in almost all cases. While the composite stomatal index is a good single measure for relating plant communities to environment, the simple measures of the number of stomatal rows and/or stomatal length are better at discriminating between associations (Table 12). In differentiating between associations, the number of stomatal rows and stomatal length will be used; other needle characteristics and their significance levels are in Appendix V.

The Clintonia and Symphoricarpos associations have the largest, highly significant difference in the number of stomatal rows (1.8 vs 3.4) and mean stomatal length (0.6 vs 1.8 cm); however, there is no significant difference in needle length. The Spiraea and Symphoricarpos associations are also distinguished by highly significant differences in the number of stomatal rows (2.3 vs 3.4) and stomatal length (0.9 vs 1.8 cm). The Clintonia and Spiraea associations are differentiated by highly significant differences in the number of stomatal rows (1.8 vs 2.3) and stomatal length (0.6 vs 0.9 cm); however, there is no significant difference between these two associations in relative stomatal length.

Table 12. Differentiation of associations by the means of selected Abies grandis shade-side needle characteristics in the Summit Ridge study area, Baker County, Oregon. Significant differences tested by the Mann-Whitney U test.

Association <sup>a</sup> (n)	<u>Clintonia</u> (117)		<u>Symphoricarpos</u> (93)	
	Mean	sd	Mean	sd
Stomatal rows (no)	1.77	1.42**	3.41	2.11**
Stomatal length (cm)	0.64	1.09**	1.75	1.59**
Association <sup>a</sup> (n)	<u>Spiraea</u> (199)		<u>Symphoricarpos</u> (93)	
	Mean	sd	Mean	sd
Stomatal rows (no)	2.27	1.65**	3.41	2.11**
Stomatal length (cm)	0.92	1.32**	1.75	1.59**
Association <sup>a</sup> (n)	<u>Clintonia</u> (117)		<u>Spiraea</u> (199)	
	Mean	sd	Mean	sd
Stomatal rows (no)	1.77	1.42**	2.27	1.65**
Stomatal length (cm)	0.64	1.09**	0.92	1.32**

\*\* significant,  $p \leq 0.01$

<sup>a</sup> groups are:

Abies grandis/Clintonia uniflora Association

A. grandis/Spiraea betulifolia Association

A. grandis/Symphoricarpos oreophilus Association

### Periderm color

Bark color has traditionally been associated with and used to distinguish grand fir from white fir. Table 13 shows percent occurrence of the three periderm color classes with respect to all trees sampled (3,208), and to trees associated with associations (3,108 trees sampled). Three periderm color classes were recorded: yellow, red, and pink. All periderm samples had intermixed layers of brown (2.5 YR 3/6) dead phloem interspersed with the color class type. Yellow is the dominant periderm color in the study area, exhibited by 65.8 percent of the trees sampled. Between associations, no periderm color class varied more than 2.6 percent. It appears that periderm color does not significantly differentiate the associations.

Periderm color was also sampled to differentiate between tree populations located on paired plots (Table 10). Periderm color samples were taken on six paired plots (15, 16; 21, 22; and 26, 27) located less than 250 m apart in contrasting habitats. Although there is a significant difference in shade-side stomatal indexes between these plots, there is no significant difference in periderm color. Periderm color, although found useful in distinguishing species types outside of the study area, does not distinguish between associations within the study area.

Table 13. Percent periderm color from 3,208 Abies grandis trees sampled in the Summit Ridge study area, Baker County, Oregon.

	Community Group			All trees sampled <sup>a</sup>
	<u>Clintonia</u>	<u>Spiraea</u>	<u>Symphoricarpos</u>	
Trees (n)	969	1292	848	
Plots (n)	11	19	9	
Yellow periderm	64.3	66.2	63.6	65.8
Red periderm	34.0	31.6	32.4	32.6
Pink periderm	1.7	2.2	4.0	2.6

<sup>a</sup> 40 plots, 3,209 trees sampled

### Hybrid index

A hybrid index was used to further distinguish associations. A low index value corresponds to trees with grand fir characteristics and a high value corresponds to trees with white fir characteristics. Figure 5 shows the percent frequency distribution of hybrid index values with respect to the three associations based on data collected from 421 trees sampled for needle characteristics. In all cases, the mode of distribution in all associations is index number 5. The Clintonia and Spiraea associations have a predominance of low index values and tend toward grand fir types. The Clintonia Association can be differentiated from the Spiraea Association by a slight shift in index values to the left of the mode (88 and 75 percent respectively as seen in Figure 5). The Symphoricarpos Association approaches a more normal distribution of hybrid index values with a shift more towards the white fir type, 48 percent of the trees occurring to the right of the mode. While grand fir-like needle characteristics appear to dominate the study area, the Symphoricarpos association shows relatively more white fir traits.

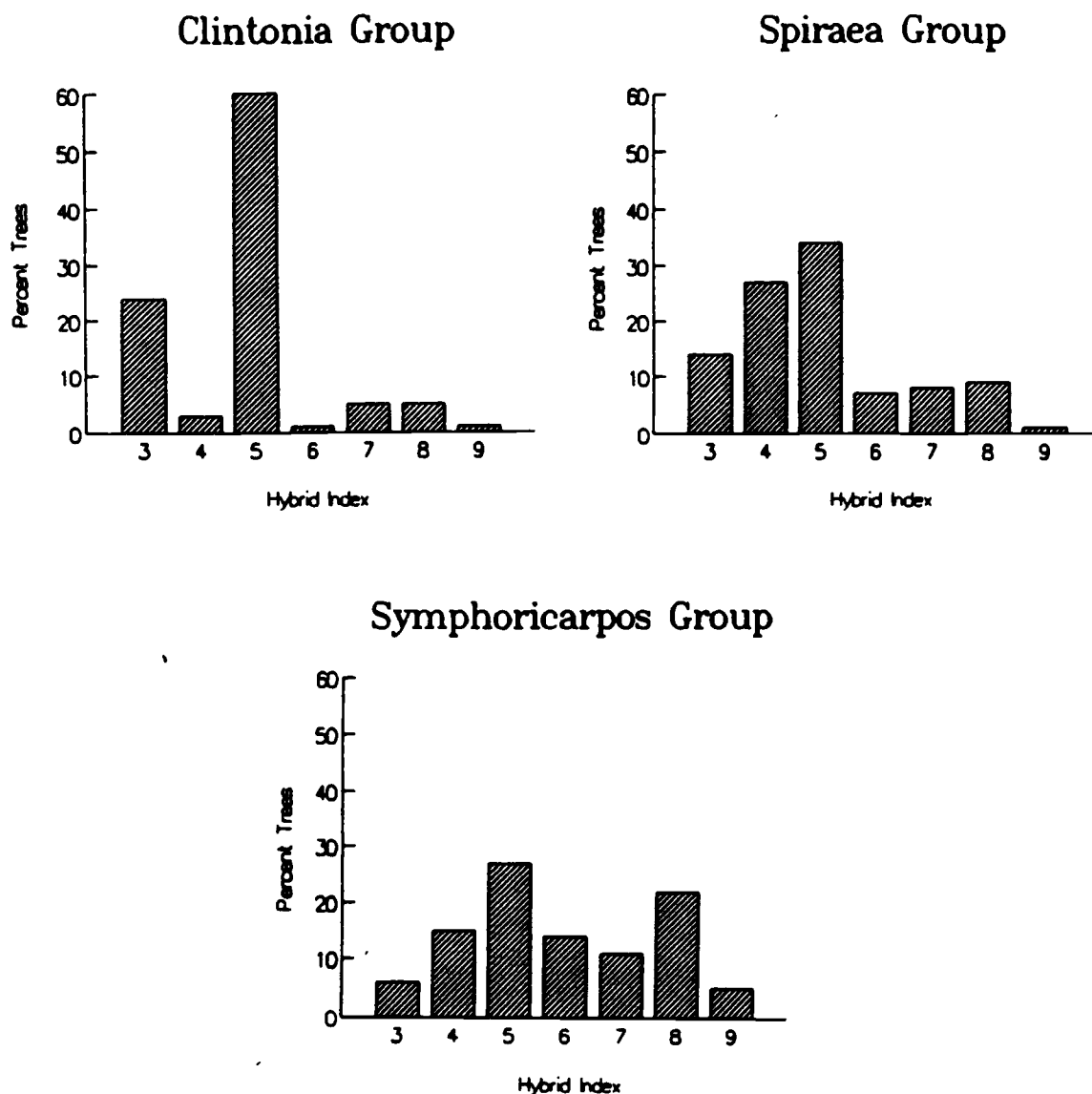


Figure 5. Distribution of hybrid index values among Abies grandis trees in three community groups in the Summit Ridge study area, Baker County, Oregon. Low hybrid index values indicate grand fir traits, high hybrid indexes white fir traits. Community groups correspond to the Abies grandis/Clintonia uniflora Association, A. grandis/Spiraea betulifolia Association, and the A. grandis/Symphoricarpos oreophilus Association.

## DISCUSSION

### Morphological Variation and Habitat Segregation

Morphological data collected from the Summit Ridge study area, within the zone of intergradation between grand fir and white fir, reveal variation in selected morphological traits between grand and white fir. With respect to selected environmental measurements, intergradient populations of grand fir/white fir in the study area vary in the number of rows and relative length of adaxial stomata between the sun and shade sides of individual trees, between stands on contrasting proximate environments, and between tree populations grouped by vegetation associations. Furthermore, adaxial stomatal characteristics varied continuously within Summit Ridge study area stands and between the stomatal characteristics typical of grand fir and white fir. The characteristics and distribution of needle adaxial stomata have been shown to be genotypic (Hamrick and Libby 1972) but there is also a phenotypic response to environmental differences (Hamrick and Libby 1972, Zobel 1973). These highly variable intergradient populations in the Summit Ridge study area are probably derived from historic hybrid swarms undergoing evolutionary sorting and environmental selection.

Identification of plant communities in the study area provide the foundation for an analysis of grand fir populations. Three plant associations are identified by multivariate analysis of the total vegetative composition: the Abies grandis/Clintonia uniflora Association; the Abies grandis/Spiraea betulifolia Association; and Abies grandis/Symphoricarpos oreophilus Association. Ordination of the vegetative composition data with DECORANA and regression of the principal ordination axis with selected environmental measurements indicates that the sample plots span a complex topographic/moisture gradient.

There was considerable variation in needle morphology associated with environmental characteristics of the 39 study plots. Stomatal index gave the highest correlation of the measured stomatal characteristics when regressed against elevation and against combined elevation and aspect. A limited data set of nine plots chosen for sampling pre-dawn xylem water stress revealed that elevation was weakly correlated with stomatal index; however, elevation and pre-dawn xylem water stress together are highly correlated with shade-side stomatal index. I feel that the stomatal index (number of stomatal rows x relative stomatal length) is an easier and faster method of computing a stomatal index than that of Daniels (1968), who used the number of stomatal rows in each quarter of the needle length, summed the number of rows in each quarter, and then divided by four.

Variation in needle morphology, as defined by the shade-side adaxial stomata, was also found on trees growing over short distances in contrasting habitats. Four sets of paired plots were chosen such that one plot of each pair was an exposed ridge site and the other plot was a proximate sheltered valley site. Exposed ridge stands have high mean stomatal indexes, a white fir trait, while shaded valley stands have low mean stomatal indexes, a grand fir trait. Differences in stomatal patterns were accompanied by differences in their physiological activity in the Oregon Cascades (Zobel 1974). Variation between populations over short distances therefore implies that that seed stock selected for silvicultural regeneration programs should be as site specific as possible.

Local variation in morphological traits between habitats within the zone of intergradation has not often been studied. Zobel (1973) reported that needle morphology of tree populations at Black Butte, east of the central Oregon Cascade Range, varied locally with aspect; grand fir growing mostly on north slopes and white fir types mostly on south slopes, but needle morphology did not vary with elevation.

In the Summit Ridge study area, white fir types with more adaxial stomata were associated with increased elevation and decreased available soil moisture; however, available moisture usually increases with elevation due to an increase in precipitation and diminished temperature. An explanation for this apparently anomalous relationship is found with pre-dawn xylem water stress measurements in the study area. Although pre-dawn xylem water stress was not high, plot four, an edaphically dry low elevation site,

had the highest value. Moreover, study populations at higher elevations have southwest exposures, and coarse well drained soils with low available soil moisture. From these site factors and water stress measurements, I conclude that decreased available soil moisture, rather than elevation per se, best explains the distribution of white fir traits at high elevations in the study area.

My findings, that white fir traits are found in areas with increased moisture stress, support the findings of Zobel (1975), who demonstrated that needles had more adaxial stomata in sites with high moisture stress, when the ranges of both grand and white fir were considered. In trying to explain this paradox, Zobel hypothesized that more adaxial stomata permit higher assimilation rates, and will have an adaptive advantage in areas with short growing seasons associated with lengthy summer drought.

In the Summit Ridge study area, periderm color is a poor discriminator of grand fir and white fir types and associations. The most common color type at all sites is yellow, often considered a white fir trait (Liu 1971). Tree populations in different environmental settings differed only slightly in percentage of periderm color, and these differences were not significant. Proximal stands in contrasting environments show distinct differences in needle morphology, but show no differences in periderm color. Similarly, associations with significant differences in needle morphology have no differences in periderm color. These results confirm the findings of Zavarin et al. (1977) that periderm color tends to vary independently between terpene species types within

the zone of intergradation. In contrast, Zobel (1973) reported from Black Butte that local variation in both periderm color and needle morphology conformed to aspect differences.

I originally hypothesized that significant quantitative and qualitative morphological differences occur between intergradient Abies grandis/A. concolor populations grouped by their associated plant communities. The three grand fir populations grouped by associations; i.e., the Clintonia, Spiraea, and Symphoricarpos associations, were all quantitatively discriminated by the shade-side needle characteristics of the number of stomatal rows and stomatal length, and to a lesser degree, by stomatal index. A hybrid index for each association, combining stomatal rows, relative stomatal length, and the periderm color, qualitatively discriminated the three associations. The index also revealed dominance of grand fir traits in the Clintonia and Spiraea associations, which are more similar to each other, and less dominance of these traits in the Symphoricarpos association where a more intergradient distribution between grand fir and white fir is seen. These results confirm, in most respects, Zobel's (1973) observation that variation in needle morphology can be inferred from the vegetation matrix within which tree populations grow.

Grand fir populations within the study area have been shown to be morphologically variable. This variation has been correlated to local environment and plant community type and was ascribed to hybridization between grand and white fir (Liu 1971, Zobel 1973, Zavarin et al. 1977). I also hypothesized that hybridization between

grand and white fir is responsible for this variation. This hypothesis cannot be confirmed by this study, for only phenotypes of field-grown, non-reproductive needles were sampled. A common garden study (Hamrick and Libby 1972) or use of needles that more clearly differentiate the species (pers. comm. K. Chambers 1988), could be used to clarify the genetic pattern. Hybridization and paleobiogeography are discussed below in support of the hypothesis.

#### Hybridization/Introgressive Hybridization

A zone of intergradation between pure grand fir populations and pure var. lowiana populations exists in northern California, Oregon, Idaho, and Washington (Daniels 1969, Lacaze and Tomassone 1967). Within this zone there is considerable morphological variation (Hitchcock et al. 1969). Such morphological variation can occur when the two distinct populations are sympatric/parapatric (Endler 1977). Hybridization (secondary intergradation) may occur when two distinct populations are separated allopatrically and subsequently become sympatric (Endler 1977, Heiser 1973). Secondary intergradation may also occur at various taxonomic levels (Anderson 1949). Secondary intergradation of grand fir/white fir at the species level is widely supported (Klaehn and Winieski 1962, Daniels 1969, Liu 1971, Hamrick and Libby 1972, Zobel 1973, Houkal 1976, Zavarin et al. 1977, Steinhoff 1978).

A north-south cline in morphological traits in the zone of intergradation between grand and white fir has been widely reported (Daniels 1969, Houkal 1976, Lacaze and Tomassone 1967). In a garden study, Lacaze and Tomassone (1967) identified a north-south cline in occurrence of adaxial stomata between 45° and 41° latitude. On the other hand, Hamrick and Libby (1972) found that amount of adaxial stomata has an "ecotypic pattern of variation" rather than clinal. Since my research was localized, correlation with latitude was not possible; however, within the study area which is just south of 45° latitude, amount of adaxial stomata varies continuously between grand and white fir within sites and varies significantly between habitats. My results show that the amount of adaxial stomata have local phenotypic patterns consistent with ecotypic variation and can not confirm Lacaze and Tomassone's (1967) findings with respect to latitude, but appear to confirm the findings of Hamrick and Libby (1972).

The most prevalent needle type in tree populations within the study area is the grand fir trait of few adaxial stomata. In contrast, most trees had the white fir characteristic, yellow periderm. Zavarin's et al. (1977) chemotaxonomic study of grand and white fir sheds light on the taxonomy of populations in which there is a dominance of grand fir needle characteristics but in which white fir periderm characteristics prevail. They found trees and populations within the zone of intergradation which have grand fir needle characteristics yet did not always have grand fir cortical terpenes as indicated by yellow periderm. They concluded that the highly

variable nature of grand fir/white fir trees in the zone of intergradation is derived from introgressive hybridization (introgression).

Introgression has been cited as the source of morphological variation within the zone of intergradation (Daniels 1969, Zavarin et al. 1977). Heiser (1973) states that morphological variation is the most obvious characteristic of hybridization and is used as evidence of introgression; however, repeated backcrossing between hybrids and the parental population is needed to produce introgressed populations (Anderson 1949), and "with repeated backcrossing it becomes increasingly difficult to recognize any effects of the hybridization" (Heiser 1973). My study area populations are morphologically variable, and are out of genetic contact with parental populations. The nearest parental lowiana populations are perhaps in northern California, 500 km away, and the nearest parental grand fir populations are perhaps 200 km to the northeast in Idaho. I conclude that study populations are not undergoing introgression, although they probably originated from hybridization, possibly involving some introgression.

Chemotaxonomic, morphological, physiological, and ecological data all support the hypothesis that hybridization is the source of variation within the zone of intergradation. In order to further confirm the possibility of natural hybridization and help explain the source of parental populations, paleobiogeographical considerations are discussed.

### Paleobiogeography

Three possible migration scenarios are presented to help explain the presence of grand fir/white fir populations in the Wallowa Mountains. The first scenario is that hybrid progeny from the contact of grand fir and var. lowiana, originating in northern California, migrated across central Oregon to the Wallowa mountains. A second scenario is that hybrids from northern California contacted grand fir from the Columbia Basin in the Blue Mountains where multiple contacts occurred. And third, Abies species were present in the Wallowas during the glacial period surviving on nunataks.

It seems unlikely that arboreal species were present in the Wallowa Mountains during the Fraser glaciation (20,000-12,500 B.P.). Wells (1983) studied the paleobiogeography of the Great Basin since the last glaciopluvial using pollen and Neotoma middens. Near the Owyhee River, Oregon, periglacial species have been identified together with patterned ground, stone stripes, and other periglacial features. Present-day vegetation types of southeast Oregon were found farther south, characterizing a cold desert. Cold deserts, dominated by Artemisia tridentata, prevailed in the Mojave Desert and pinyon-juniper woodland occurred north of the Mojave Desert. Under full-glacial conditions, var. concolor was located in southern California and in the southern Basin and Range of Nevada and Arizona (Wells 1983). Given such environmental conditions, I conclude that present day arboreal species migrated to the Wallowa Mountains

some time at the very end of, or after, the late/glacial Holocene (12,500-20,000 B.P.)(Wells 1983).

The most likely scenario is that hybrid progeny migrated from northern California into the Blue Mountains to the Wallows. Hamrick and Libby (1972) postulate that secondary contact between grand and white fir is of recent origin. Zavarin et al. (1977) found var. lowiana terpenes in coastal populations of grand fir near Eureka, California; the terpenes of white fir decrease both to the south and north in coastal California. Farther north, coastal grand fir populations have no white fir terpenes. The occurrence of var. lowiana terpenes in grand fir populations is good evidence that natural grand fir/white fir intergrades are derived from hybridization that occurred in northern California.

Secondary contact in the Blue Mountains between pure grand fir from the Columbia Basin, and white fir hybrids from northern California could also have occurred. In Montana, Zavarin et al. (1977) found grand fir populations with no white fir terpenes. Furthermore, they reported less terpene variation between coastal grand fir and inland grand fir than in other species of Pinaceae with a similar, large distributional range, and they concluded that a historical range restriction occurred along the Pacific Coast during the last glacial period. Based on climatic reconstruction and pollen occurrence with associated species, Mack et al. (1983) report that grand fir arrived in the Kootenai River Valley, Montana, no earlier than 4000 B.P. Grand fir near Wenatchee, Washington have traces of white fir terpenes (Zavarin et al. 1977). The northern range extension of white fir

probably occurred during the Thermal Maximum (= Hypsithermal). Grand fir would have had to migrate through and past the Columbia River Gorge before the Hypsithermal to arrive in the northern Montana without the presence of white fir terpenes. The same climatic changes of regional warming, leading to the northward and eastward migration of grand fir by the end of the Hypsithermal, could have also allowed grand fir to move southward into the Blue Mountains.

The first and second scenarios vary only with respect to recontact of pure grand fir with white fir hybrids. Grand fir-like trees in the Summit Ridge study area dominate the Clintonia association where the habitat is similar to the cool, moist habitat associated with the parental type. In the study area riparian zones, some individuals closely resemble pure grand fir, with two-ranked needles and thin periderm. The question of whether the habitat is selecting for grand fir traits (species reconstitution), or whether contact is more recent and is preserving species types, cannot be answered.

While neither the geographic history nor the nature of hybridization in the Summit Ridge study populations is certain, it is apparent that habitat selection within intergradient populations is occurring, and that selection is for traits that resemble parental types on associated habitats. My research on Abies hybrids agrees with the generalization by Benson et al. (1967) that hybrid swarms (e.g., Quercus) show sensitivity to the environment through morphological segregation in a relatively small range of

environmental variation. The ability to adapt rapidly to new environments, rather than by hybrid vigor alone, may have aided the colonization of intergradient grand fir/white fir trees in the Blue Mountains.

## CONCLUSIONS

From this research on intergradient populations of grand fir and white fir in the Summit Ridge study area, the following conclusions are drawn:

1) Populations intergradient between grand and white fir occur among three plant associations: the Abies grandis/Clintonia uniflora Association; the Abies grandis/Spiraea betulifolia Association; and Abies grandis/Symphoricarpos oreophilus Association.

2) Populations vary in the number of stomatal rows and relative length of adaxial stomata between the sun and shade sides of individual trees.

3) Populations vary in these same morphological traits between stands on contrasting proximate environments.

4) Populations from different vegetation associations vary in these traits.

5) Adaxial stomatal characteristics in the study area vary continuously between those typical of grand fir and those of typical white fir.

6) Populations with more adaxial stomata are most common on sites with low soil moisture availability and at higher well-drained and exposed sites where periods of assimilation are short, an observation supporting Zobel's (1975) hypothesis.

7) Periderm color in the study area is a poor discriminator between grand fir and white fir types.

8) Grand fir populations vary in their morphological and probably also in related physiological characteristics over short distances, confirming that seed stock selected for silvicultural regeneration programs should be as site specific as possible.

9) Study populations are not undergoing introgression because the populations are out of genetic contact with parental populations.

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## APPENDICES

Appendix I. Environmental characteristics and site locations of 40 plots in the Summit Ridge study area, Baker County, Oregon.

Plot	Slope	Aspect	Elevation	Solar <sup>a</sup>	Stomatal <sup>b</sup>	Basal	DCA	Comm. <sup>c</sup>	Pre-dawn	Location
(no)	(%)	(deg.)	(m)	insol. (ly)	index shade- side	area (m <sup>2</sup> )	x-axis pos.	group	xylem water stress (psi)	
1	9	350	1,190	790	87	8.7	156	Spir.	---	T7S R44E Sec. 36 NWNW
2	23	60	1,340	799	36	10.8	174	Spir.	---	T7S R44E Sec. 26 NWNW
3	25	90	1,420	829	48	14.0	141	Spir.	---	T7S R44E Sec. 13 SWSE
4	14	141	1,440	870	213	9.3	372	Symp.	242	T7S R45E Sec. 28 SENE
5	7	264	1,440	834	185	14.0	134	Spir.	---	T7S R45E Sec. 28 NWNW
6	19	222	1,340	880	179	7.6	183	Spir.	---	T7S R44E Sec. 13 SWSE
7	2	200	1,290	864	19	14.8	49	Clin.	---	T7S R44E Sec. 13 SESW
8	29	270	1,390	826	227	10.8	180	Spir.	---	T7S R44E Sec. 13 SENE
9	3	210	1,460	826	34	7.7	146	Spir.	---	T7S R44E Sec. 11 NESE
10	27	235	1,730	895	75	14.0	140	Spir.	---	T7S R44E Sec. 1 NENE
11	42	201	1,440	921	30	13.0	198	Spir.	---	T7S R45E Sec. 21 NESW
12	19	225	1,390	881	27	16.0	114	Spir.	---	T7S R45E Sec. 27 SWSW
13	36	360	1,460	668	144	17.4	24	Clin.	---	T7S R45E Sec. 29 NENE
14	2	40	1,410	835	43	15.0	0	Clin.	51	T7S R45E Sec. 28 NWNW
15	18	362	1,440	750	38	12.0	---	---	---	T7S R45E Sec. 8 SESW
16	45	180	1,550	924	180	5.6	256	Symp.	---	T7S R45E Sec. 17 NENW
17	45	200	2,080	924	244	7.5	343	Symp.	82	T7S R45E Sec. 5 SWSW
18	27	240	1,900	864	249	9.0	444	Symp.	---	T7S R45E Sec. 8 SWNE
19	23	212	1,830	861	166	6.4	356	Symp.	107	T7S R45E Sec. 9 SWSW
20	25	220	1,730	910	173	6.7	418	Symp.	70	T7S R45E Sec. 16 NENW
21	21	240	1,930	910	277	9.3	370	Symp.	---	T7S R45E Sec. 7 NWNW
22	62	68	1,860	714	52	15.0	427	Clin.	---	T7S R45E Sec. 7 NENE
23	25	170	1,630	897	101	14.0	39	Spir.	94	T7S R45E Sec. 17 NENE
24	21	84	1,460	831	25	10.8	194	Clin.	68	T7S R45E Sec. 21 NWSW
25	7	108	1,490	847	26	11.0	54	Clin.	---	T7S R45E Sec. 21 SWNE

# Appendix I: (continued)

Plot (no)	Slope (%)	Aspect (deg.)	Elevation (m)	Solar insol. (ly)	<sup>a</sup> Stomatal index shade- side	<sup>b</sup> Basal area (m <sup>2</sup> )	DCA x-axis pos.	Comm. <sup>c</sup> group	Pre-dawn xylem water stress (psi)	Location
26	18	180	1,900	808	135	7.3	22	Symp.	---	T7S R45E Sec. 20 NWNE
27	18	80	1,510	830	4	15.0	41	Clin.	46	T7S R45E Sec. 20 NWNE
28	14	144	1,460	870	73	12.7	199	Spir.	---	T6S R45E Sec. 34 SENW
29	47	60	1,290	740	83	11.2	63	Clin.	---	T8S R45E Sec. 3 SENW
30	29	90	940	697	12	13.3	63	Clin.	---	T8S R45E Sec. 6 NENW
31	7	88	1,100	834	8	11.7	143	Clin.	---	T7S R45E Sec. 31 SENW
32	21	260	1,520	831	99	15.0	129	Spir.	---	T7S R45E Sec. 7 SWSW
33	14	320	1,510	785	59	13.0	133	Spir.	---	T7S R45E Sec. 28 NWSW
34	16	70	1,390	808	101	11.0	31	Spir.	---	T8S R45E Sec. 3 NWNW
35	12	38	1,490	800	8	13.2	169	Spir.	---	T7S R45E Sec. 28 SESW
36	21	210	1,340	894	52	13.2	172	Spir.	118	T7S R45E Sec. 27 NWSE
37	36	258	1,950	870	129	11.5	193	Symp.	---	T7S R45E Sec. 8 NWNE
38	31	210	1,200	911	49	15.0	438	Spir.	---	T7S R45E Sec. 22 NESW
39	7	180	1,160	871	107	19.3	176	Spir.	---	T7S R44E Sec. 24 SWSE
40	29	58	1,370	697	145	12.8	171	Clin.	---	T7S R44E Sec. 14 NWSE

<sup>a</sup> langleys for 19 April - 25 August

<sup>b</sup> (stomatal rows x relative stomatal length)

<sup>c</sup> associations are:

Abies grandis/Clintonia uniflora Association.

A. grandis/Spiraea betulifolia Association.

A. grandis/Symphoricarpos oreophilus Association.

Appendix II: All vascular plant species encountered in 40 plots in the Summit Ridge study area, Baker County, Oregon. Nomenclature follows Hitchcock and Cronquist (1973).

Species	Common Name
<u>Abies concolor</u> (Gord. & Glend.) Lindl.	white fir
<u>Abies grandis</u> (Doug.) Lindl.	grand fir
<u>Abies lasiocarpa</u> (Hook.) Nutt.	subalpine fir
<u>Acer glabrum</u> var. <u>douglasii</u> (Hook.) Dippel	Douglas' maple
<u>Achillea millefolium</u> ssp. <u>lanulosa</u> (Nutt.) Piper	yarrow
<u>Adenocaulon bicolor</u> Hook.	trail-plant
<u>Agastache urticifolia</u> (Benth.) Kuntze	horse-mint
<u>Agropyron repens</u> (L.) Beauv.	wheat grass
<u>Allium acuminatum</u> Hook.	tapertip onion
<u>Amelanchier alnifolia</u> var. <u>cusickii</u> (Fern.) Hitchc.	serviceberry
<u>Anaphalis margaritacea</u> (L.) B. & H.	pearly-everlasting
<u>Antennaria anaphaloides</u> Rydb.	tall pussy-toes
<u>Antennaria luzuloides</u> T. & G.	woodrush pussy-toes
<u>Apocynum androsaemifolium</u> L.	spreading dogbane
<u>Arabis holboellii</u> Hornem.	Holboell's rockcress
<u>Arnica cordifolia</u> Hook.	arnica
<u>Arnica longifolia</u> D. C. Eat.	seep-spring arnica
<u>Artemisia tridentata</u> var. <u>vaseyana</u> (Rydb.) Boivin	mountain sagebrush
<u>Aster conspicuus</u> Lindl.	showy aster
<u>Aster integrifolius</u> Nutt.	thick-stemmed aster
<u>Aster occidentalis</u> var. <u>intermedius</u> Gray	western mountain aster
<u>Aster perelegans</u> Nels. & Macbr.	elegant aster
<u>Berberis repens</u> Lindl.	creeping Oregongrape
<u>Brodiaea douglasii</u> Wats.	Douglas' brodiaea
<u>Bromus carinatus</u> H. & A.	California brome
<u>Bromus inermis</u> Leys.	smooth brome
<u>Bromus tectorum</u> L.	cheat grasss
<u>Bromus vulgaris</u> (Hook) Shear	Columbia brome
<u>Calamagrostis rubescens</u> Buckl.	pine grass
<u>Calochortus eurycarpus</u> Wats.	big-pod Mariposa lily
<u>Carex geyeri</u> Boott	elk sedge
<u>Carex hoodii</u> Boott	Hood's sedge
<u>Castilleja miniata</u> Dougl.	scarlet paintbrush
<u>Ceanothus velutinus</u> Dougl.	buckbrush
<u>Cerastium arvense</u> L.	field chickweed
<u>Chenopodium fremontii</u> Wats.	Fremont's goosefoot
<u>Chimaphila umbellata</u> (L.) Bart.	prince's-pine
<u>Cirsium arvense</u> (L.) Scop.	Canadian thistle
<u>Cirsium vulgare</u> (Savi) Tenore	common thistle
<u>Clarkia rhomboidea</u> Dougl.	common clarkia
<u>Clematis ligusticifolia</u> Nutt.	western clematis
<u>Clintonia uniflora</u> (Schult.) Kunth.	beadlily
<u>Collinsia parviflora</u> Lindl.	blue-eyed Mary
<u>Collomia grandiflora</u> Dougl.	large-flower collomia
<u>Collomia linearis</u> Nutt.	narrow-leaf collomia
<u>Corallorhiza striata</u> Lindl.	striped coral-root
<u>Cornus stolonifera</u> var. <u>occidentalis</u> (T.&G.) Hitchc.	dogwood
<u>Cryptantha affinis</u> (Gray) Greene	slender cryptantha
<u>Cynoglossum officinale</u> L.	common hounds-tongue

## Appendix II: (continued)

Species	Common Name
<u>Cypripedium montanum</u> Dougl.	mountain lady's-slipper
<u>Dactylis glomerata</u> L.	orchard-grass
<u>Delphinium nuttallianum</u> Pritz.	larkspur
<u>Descurainia richardsonii</u> var. <u>viscosa</u> (Rydb.) Peck	tansymustard
<u>Disporum trachycarpum</u> (Wats.) B. & H.	wartberry fairy-bell
<u>Elymus glaucus</u> Buckl.	blue wildrye
<u>Epilobium angustifolium</u> L.	fireweed
<u>Epilobium minutum</u> Lindl.	small-flowered willow-weed
<u>Epilobium paniculatum</u> Nutt.	tall willow-weed
<u>Epilobium watsonii</u> var. <u>occidentale</u> (Trel.) Hitchc.	willow-weed
<u>Equisetum arvense</u> L.	common horsetail
<u>Erigeron inornatus</u> Gray	daisy
<u>Eriogonum heracleoides</u> Nutt.	buckwheat
<u>Festuca idahoensis</u> Elmer	Idaho fescue
<u>Festuca occidentalis</u> Hook.	western fescue
<u>Fragaria vesca</u> L.	woods strawberry
<u>Fragaria virginiana</u> var. <u>platypetala</u> (Rydb.) Hall	broadpetal strawberry
<u>Galium aparine</u> L.	cleavers
<u>Galium asperifolium</u> Gray	rough bedstraw
<u>Galium triflorum</u> Michx.	fragrant bedstraw
<u>Gayophytum diffusum</u> T. & G.	groundsmoke
<u>Gilia aggregata</u> (Pursh) Spreng.	skyrocket
<u>Goodyera oblongifolia</u> Raf.	rattlesnake-plantain
<u>Habenaria elegans</u> (Lindl.) Boland.	bog-orchid
<u>Habenaria unalascensis</u> (Spreng.) Wats.	rein-orchid
<u>Hackelia micrantha</u> (Eastw.) J. L. Gentry	stickseed
<u>Helianthella uniflora</u> var. <u>douglasii</u> (T. & G.) Weber	little-sunflower
<u>Heuchera micrantha</u> Dougl.	alumroot
<u>Hieracium albertinum</u> Farr	western hawkweed
<u>Hieracium albiflorum</u> Hook.	white-flowered hawkweed
<u>Hydrophyllum fendleri</u> (Gray) Heller	waterleaf
<u>Iliamna rivularis</u> (Dougl.) Greene	globemallow
<u>Kelloggia galioides</u> Torr.	kelloggia
<u>Larix occidentalis</u> Nutt.	western larch
<u>Lathyrus nevadensis</u> Wats.	sweet-pea
<u>Lathyrus pauciflorus</u> Fern.	sweet-pea
<u>Lathyrus pauciflorus</u> var. <u>utahensis</u> (Jones) Peck	sweet-pea
<u>Linanthus harknessii</u> (Curran) Greene	linanthus
<u>Linnaea borealis</u> L.	twinflower
<u>Lomatium gravei</u> Coult. & Rose	desert parsley
<u>Lonicera utahensis</u> Wats.	honeysuckle
<u>Lupinus laxiflorus</u> Dougl.	lupine
<u>Madia glomerata</u> Hook.	tarweed
<u>Microseris</u> spp.	microseris
<u>Mitella stauropetala</u> Piper	mitrewort
<u>Navarretia intertexta</u> var. <u>propinqua</u> (Suksd.) Brand	needle-leaf navarretia
<u>Orogenia linearifolia</u> Wats.	turkey-peas
<u>Osmorhiza chilensis</u> H. & A.	mountain sweet-root
<u>Osmorhiza occidentalis</u> (Nutt.) Torr.	western sweet-root
<u>Paeonia brownii</u> Dougl.	peony
<u>Penstemon spatulatus</u> Pennell	Wallowa penstemon

## Appendix II: (continued)

Species	Common Name
<u>Penstemon payettensis</u> Nels. & Macbr.	Payette penstemon
<u>Penstemon venustus</u> Dougl.	hotrock penstemon
<u>Perideridia bolanderi</u> (Gray) Nels. & Macbr.	yampah
<u>Phacelia heterophylla</u> Pursh	virgate phacelia
<u>Phleum pratense</u> L.	timothy
<u>Picea engelmannii</u> Parry	silver spruce
<u>Pinus ponderosa</u> Dougl.	ponderosa pine
<u>Plantago lanceolata</u> L.	plantain
<u>Poa pratensis</u> L.	Kentucky bluegrass
<u>Poa</u> spp.	bluegrass
<u>Polemonium pulcherrimum</u> Hook.	sky-pilot
<u>Polygonum kelloggii</u> Greene	knotweed
<u>Polygonum majus</u> (Meisn.) Piper	Palouse knotweed
<u>Populus trichocarpa</u> T. & G.	poplar
<u>Potentilla glandulosa</u> Lindl.	sticky cinquefoil
<u>Prunella vulgaris</u> L.	self-heal
<u>Prunus emarginata</u> (Dougl.) Walp.	bittercherry
<u>Prunus virginiana</u> var. <u>melanocarpa</u> (Nels.) Sarg.	chokecherry
<u>Pseudotsuga menziesii</u> var. <u>glauca</u> (Beissn.) Franco	Rocky Mountain Douglas-fir
<u>Pteridium aquilinum</u> (L.) Kuhn.	bracken
<u>Pterospora andromedea</u> Nutt.	pinedrops
<u>Pyrola asarifolia</u> Michx.	leafless pyrola
<u>Pyrola picta</u> Smith	white vein pyrola
<u>Pyrola secunda</u> L.	sidebells pyrola
<u>Ranunculus</u> spp.	buttercup
<u>Ribes cereum</u> Dougl.	squaw currant
<u>Ribes lacustre</u> (Pers.) Poir.	prickly currant
<u>Ribes viscosissimum</u> Pursh	sticky currant
<u>Rosa gymnocarpa</u> Nutt.	baldhip rose
<u>Rosa woodsii</u> var. <u>ultramontana</u> (Wats.) Jeps.	pearhip rose
<u>Rumex acetosella</u> L.	sour weed
<u>Salix</u> spp.	willow
<u>Sambucus cerulea</u> Raf.	elderberry
<u>Scrophularia lanceolata</u> Pursh	figwort
<u>Sedum lanceolatum</u> Torr.	stonecrop
<u>Sidalcea oregana</u> (Nutt.) Gray	checker-mallow
<u>Silene menziesii</u> Hook.	campion
<u>Smilacina racemosa</u> (L.) Desf.	western solomon-plume
<u>Smilacina stellata</u> (L.) Desf.	starry solomon-seal
<u>Sorbus sitchensis</u> Roemer	mountain-ash
<u>Spiraea betulifolia</u> Pall.	shiny-leaf spiraea
<u>Stellaria jamesiana</u> Torr.	starwort
<u>Stipa occidentalis</u> Thurb.	needlegrass
<u>Symphoricarpos albus</u> (L.) Blake	common snowberry
<u>Symphoricarpos oreophilus</u> Gray	mountain snowberry
<u>Taraxacum officinale</u> Weber	dandelion
<u>Thalictrum occidentale</u> Gray	meadowrue
<u>Tragopogon dubius</u> Scop.	yellow salsify
<u>Trillium ovatum</u> Pursh	wake-robin
<u>Urtica dioica</u> ssp. <u>gracilis</u> (Ait.) Seland.	slender nettle
<u>Vaccinium membranaceum</u> Dougl.	big huckleberry

## Appendix II: (continued)

Species	Common Name
<u>Veratrum californicum</u> Durand	skunk-cabbage
<u>Verbascum thapsus</u> L.	mullein
<u>Vicia americana</u> Muhl.	vetch
<u>Viola adunca</u> Sm.	early blue violet
<u>Viola orbiculata</u> Geyer	round-leaved violet
<u>Viola purpurea</u> Kell.	goosefoot violet
<u>Viola</u> spp.	violet

Appendix III: Species acronyms for vascular plants in 39 plots included in TWINSpan analysis of vegetation in the Summit Ridge study area, Baker County, Oregon (Garrison et al. 1976).

Species	Acronym
<u>Abies grandis</u>	ABGR
<u>Acer glabrum</u> var. <u>douglasii</u>	ACGLD
<u>Achillea millefolium</u> ssp. <u>lanulosa</u>	ACMI
<u>Adenocaulon bicolor</u>	ADBI
<u>Agastache urticifolia</u>	AGUR
<u>Allium acuminatum</u>	ALAC
<u>Amelanchier alnifolia</u> var. <u>cusickii</u>	AMALC
<u>Anaphalis margaritacea</u>	ANMA
<u>Antennaria luzuloides</u>	ANLU
<u>Apocynum androsaemifolium</u>	APAN
<u>Arabis holboellii</u>	ARHO
<u>Arnica cordifolia</u>	ARCO
<u>Artemisia tridentata</u> var. <u>vaseyana</u>	ARTRV
<u>Aster conspicuus</u>	ASCO
<u>Aster integrifolius</u>	ASIN
<u>Aster occidentalis</u> var. <u>intermedius</u>	ASOC
<u>Aster perelegans</u>	ASPE
<u>Berberis repens</u>	BERE
<u>Bromus inermis</u>	BRIN
<u>Bromus vulgaris</u>	BRVU
<u>Calamagrostis rubescens</u>	CARU
<u>Calochortus eurycarpus</u>	CAEU2
<u>Carex geyeri</u>	CAGE
<u>Carex hoodii</u>	CAHO
<u>Castilleja miniata</u>	CAMI2
<u>Ceanothus velutinus</u>	CEVU
<u>Chenopodium fremontii</u>	CHFR
<u>Chimaphila umbellata</u>	CHMUO
<u>Clintonia uniflora</u>	CLUN
<u>Collinsia parviflora</u>	COPA
<u>Collomia grandiflora</u>	COGR2
<u>Collomia linearis</u>	COLI2
<u>Cryptantha affinis</u>	CRAF
<u>Cynoglossum officinale</u>	CYOF
<u>Cypripedium montanum</u>	CYMO
<u>Dactylis glomerata</u>	DAGL
<u>Descurainia richardsonii</u> var. <u>viscosa</u>	DERIV
<u>Disporum trachycarpum</u>	DITR
<u>Elymus glaucus</u>	ELGL
<u>Epilobium angustifolium</u>	EPAN
<u>Erigeron inornatus</u>	ERIN2
<u>Eriogonum heracleoides</u>	ERHE
<u>Festuca occidentalis</u>	FEOC
<u>Fragaria virginiana</u> var. <u>platypetala</u>	FRVIP
<u>Galium aparine</u>	GAAP
<u>Gavophytum diffusum</u>	GADI
<u>Goodyera oblongifolia</u>	GOOB
<u>Habenaria elegans</u>	HAEL

## Appendix III: (continued)

Species	Acronym
<u>Hackelia micrantha</u>	HAMI
<u>Hieracium albertinum</u>	HIAL
<u>Hieracium albiflorum</u>	HIAL2
<u>Larix occidentalis</u>	LAOC
<u>Lathyrus nevadensis</u>	LANEC
<u>Lathyrus pauciflorus</u>	LAPA2
<u>Linanthus harknessii</u>	LIHA
<u>Linnaea borealis</u>	LIBOL
<u>Lonicera utahensis</u>	LOUT2
<u>Lupinus laxiflorus</u>	LULA
<u>Madia glomerata</u>	MAGL
<u>Mitella stauropetala</u>	MIST2
<u>Navarretia intertexta</u> var. <u>propinqua</u>	NAINP
<u>Orogenia linearifolia</u>	ORLI
<u>Osmorhiza chilensis</u>	OSCH
<u>Osmorhiza occidentalis</u>	OSOC
<u>Paeonia brownii</u>	PABR
<u>Perideridia bolanderi</u>	PEBO
<u>Phacelia heterophylla</u>	PHHE
<u>Phleum pratense</u>	PHPR
<u>Picea engelmannii</u>	PIEN
<u>Pinus ponderosa</u>	PIPO
<u>Polemonium pulcherrimum</u>	POPU
<u>Polygonum kelloggii</u>	POKE
<u>Polygonum majus</u>	POMA2
<u>Potentilla glandulosa</u>	POGL
<u>Prunella vulgaris</u>	PRVU
<u>Prunus virginiana</u> var. <u>melanocarpa</u>	PRVIM
<u>Pseudotsuga menziesii</u> var. <u>glauca</u>	PSMEG
<u>Pteridium aquilinum</u>	PTAQP
<u>Pyrola secunda</u>	PYSE
<u>Ribes cereum</u>	RICE
<u>Ribes lacustre</u>	RILA
<u>Ribes viscosissimum</u>	RIVI
<u>Rosa gymnocarpa</u>	ROGY
<u>Rumex acetosella</u>	RUAC
<u>Salix</u> spp.	SALIX
<u>Sedum lanceolatum</u>	SEAL2
<u>Silene menziesii</u>	SIME
<u>Smilacina stellata</u>	SMST
<u>Sorbus sitchensis</u>	SOSI
<u>Spiraea betulifolia</u>	SPBEL
<u>Stellaria jamesiana</u>	STJA
<u>Symphoricarpos albus</u>	SYAL
<u>Symphoricarpos oreophilus</u>	SYOR
<u>Tragopogon dubius</u>	TRDU
<u>Vaccinium membranaceum</u>	VAME
<u>Verbascum thapsus</u>	VETH
<u>Vicia americana</u>	VIAM
<u>Viola adunca</u>	VIAD

Appendix IV: Correlation matrix of shade-side needle morphological characteristics from 421 Abies grandis trees in the Summit Ridge study area, Baker County, Oregon.

	Stomatal rows	Stomatal length	Needle length	Relative stomatal length	Stomatal index
Stomatal rows (no)	---				
Stomatal length (cm)	0.71	---			
Needle length (cm)	0.10	0.15	---		
Relative stomatal length (%)	0.71	0.98	0.02	---	
Stomatal index <sup>a</sup>	0.80	0.84	0.04	0.87	---

<sup>a</sup> number of stomatal rows x relative stomatal length

Appendix V: Mean shade-side needle characteristics and differences between three Abies grandis associations in the Summit Ridge study area, Baker County, Oregon, by the Mann-Whitney U test.

Association (n)	<u>Clintonia</u> (117)			<u>Spiraea</u> (199)	
	Mean	Sd		Mean	Sd
Stomatal rows (no.)	1.77	1.42	**	2.27	1.65
Stomatal length (cm)	0.64	1.09	**	.92	1.32
Needle length (cm)	3.90	0.65	**	4.28	0.73
Relative stomatal length	16.17	27.17		21.21	30.03
Stomatal index <sup>a</sup>	55.92	127.11	*	83.54	170.20

Association (n)	<u>Clintonia</u> (117)			<u>Symphoricarpos</u> (93)	
	Mean	Sd		Mean	Sd
Stomatal rows (no.)	1.77	1.42	**	3.41	2.12
Stomatal length (cm)	0.64	1.09	**	1.75	1.59
Needle length (cm)	3.90	0.65	**	4.23	0.04
Relative stomatal length	16.17	27.17	**	41.45	36.53
Stomatal index <sup>a</sup>	55.92	127.11	**	195.14	238.38

Association (n)	<u>Symphoricarpos</u> (93)			<u>Spiraea</u> (199)	
	Mean	Sd		Mean	Sd
Stomatal rows (no.)	3.41	2.12	**	2.27	1.65
Stomatal length (no.)	1.75	1.59	**	.92	1.32
Needle length (no.)	4.23	0.04	**	4.28	0.73
Relative stomatal length	41.45	36.53		21.21	30.03
Stomatal index <sup>a</sup>	195.38	128.38	**	83.54	170.20

\*\* significant,  $p \leq 0.01$

\* significant,  $p \leq 0.05$

<sup>a</sup> number of stomatal rows x relative stomatal length

Appendix VI: Single and multiple correlation relationships between shade-side needle morphological characteristics and selected environmental measure for nine plots selected for pre-dawn xylem water stress in the Summit Ridge study area, Baker County, Oregon.

	Stomatal rows	Stomatal length	Relative stomatal length	Stomatal index <sup>a</sup>	Stomatal rows and stomatal length	Stomatal rows and relative stomatal length	stomatal rows x stomatal length
	(no)	(cm)	(%)				
Elevation	0.700 *	0.693	0.767 *	0.696 *	0.683 *	0.680 *	0.697 *
Pre-dawn xylem water stress	0.470	0.491	0.460	0.516	0.482	0.462	0.448
Solar insolation	0.724	0.690	0.625	0.694 *	0.717 *	0.634	0.617
Elevation and pre-dawn xylem water stress	0.900 **	0.847 **	0.862 **	0.938 **	0.890 **	0.870 **	0.876 **
Pre-dawn xylem water stress and solar insolation	0.720 **	0.693	0.591	0.716 *	0.720 *	0.603	0.570

\*\* significance,  $p \leq 0.01$

\* significance,  $p \leq 0.05$

a number of stomatal rows x relative stomatal length

Appendix VII. Descriptive statistics for shade-side needle characteristics from Abies grandis associations and all trees sampled in the Summit Ridge study area, Baker County, Oregon.

Association	Mean	sd <sup>a</sup>	CV <sup>b</sup>	Range
<u>Clintonia</u> (n=129)				
Stomatal rows (no)	1.77	1.42	80.64	0-7
Stomatal length (cm)	0.64	1.09	171.41	0-5
Needle length (cm)	3.90	0.65	16.76	1.8-6.2
Relative stomatal length (%)	16.17	27.19	168.20	0-92.6
Stomatal index <sup>c</sup>	55.92	127.11	227.31	0-648.2
<u>Spiraea</u> (n=199)				
Stomatal rows (no)	2.27	1.65	72.53	0-10
Stomatal length (cm)	0.92	1.32	144.07	0-5.4
Needle length (cm)	4.28	0.73	17.06	2.5-6.4
Relative stomatal length (%)	21.21	30.03	141.62	0-94.2
Stomatal index <sup>c</sup>	83.54	170.20	203.73	0-2,106
<u>Symphoricarpos</u> (n=93)				
Stomatal rows (no)	3.41	2.11	61.85	0-9
Stomatal length (cm)	1.75	1.59	90.79	0-5.5
Needle length (cm)	4.23	0.70	16.65	2.6-6.2
Relative stomatal length (%)	41.45	36.53	88.12	0-95.1
Stomatal index <sup>c</sup>	195.14	238.38	122.16	0-847.8
All trees sampled (n=431)				
Stomatal rows (no)	2.36	1.79	75.71	0-10
Stomatal length (cm)	1.01	1.37	136.43	0-5.5
Needle length (cm)	4.16	0.73	17.52	1.8-6.4
Relative stomatal length (%)	23.95	31.97	133.50	0-95.1
Stomatal index <sup>c</sup>	98.36	182.33	185.38	0-2,106

<sup>a</sup> standard deviation

<sup>b</sup> coefficient of variation

<sup>c</sup> number of stomatal rows x relative stomatal length