BOT. GAZ. **134**(3):209–220. 1973.

LOCAL VARIATION IN INTERGRADING ABIES GRANDIS–ABIES CONCOLOR POPULATIONS IN THE CENTRAL OREGON CASCADES: NEEDLE MORPHOLOGY AND PERIDERM COLOR

DONALD B. ZOBEL

Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331

ABSTRACT

In the central Oregon Cascades, grand fir morphology varies from that of typical *Abies grandis* to that of populations with a variety of morphological types, some closely resembling *A. concolor*. Low-elevation populations west of the Cascade crest, mostly on river terraces, resemble *A. grandis*. High-elevation west-side populations, disjunct from those at low elevations and occupying ridge tops and steep, dry slopes, include trees with some traits of *A. concolor*. Populations on the east flank of the Cascades show a greater but widely variable influence of *A. concolor*. East-side populations vary locally with aspect, being most like *A. grandis* on north slopes, but they do not clearly vary with elevation. Incidence of characteristics resembling *A. concolor* increases from north to south within the study area, although this pattern shows deviations not associated with obvious changes in topography. Periderm color and needle morphology show the same general relationships between the populations sampled. Either "maximum number of adaxial stomatal rows" or "percentage of length of needle with adaxial stomata" can be used to describe the extent of adaxial stomata. Needle notch depth is not consistently correlated with stomatal characteristics on a tree-to-tree basis, but shows a similar, less distinct, geographic and habitat pattern. The variation within populations is greater in the intermediate populations than in those of "typical" *A. grandis*. This is consistent with the origin of the intermediate populations being introgression, as proposed by earlier workers. The described patterns of morphological variation provide a basis from which ecological and physiological variation in these intergrading populations may be studied.

Introduction

Genetic variability within a group of populations can increase as a result of hybridization and backcrossing between two previously allopatric species. Such introgressive hybridization (introgression) should result in formation of populations adapted to environmental conditions outside the range of either parent species. Thus, if an environment suitable for intermediates exists, the complex of the two parent species and the intergrading hybrids should occupy a wider range of environments than the parental populations did before introgression occurred (ANDERSON 1949).

Several instances of apparent introgression between forest tree species have been documented. Populations of *Picea,* intermediate between recognized taxa, which occupy large areas in British Columbia and occur in habitats intermediate between those of the parent taxa, have been attributed to introgression. This pattern is evident in both cone morphology of native trees and the more clearly adaptive trait of date of growth cessation of seedlings (ROCHE 1969). Farther south, however, no morphological evidence of introgression was found in mixed stands of *P. engelmannii* and *P. pungens* (DAUBENMIRE 1972). In eastern North America, introgression between *P. rubens* and *P. mariana* has produced considerable intermediacy of individual trees, even though most populations resemble one species or the other (MORGENSTERN and FARRAR 1964). That there is a clearly adaptive difference associated with morphology has been shown by the fact that the degree of spruce-budworm defoliation is correlated with the morphological hybrid index of intermediate trees (MANLEY and FOWLER 1969). In southern California, natural selection on hybrid populations of *Quercus* has resulted in widely differing populations in local areas. Population characteristics are correlated with slope aspect, the plants on northeast-facing slopes closely resembling one parent and those on southwest-facing slopes resembling the other, with intermediates between (BENSON, PHILLIPS, WILDER et al. 1967).

Another apparent example of range extension through introgression is the existence of widespread populations morphologically intermediate between *Abies grandis* and *A. concolor*. Grand fir (*A. grandis* [Dougl. ex D. Don] Lindl.) occurs primarily in the Pacific Northwest and in the Rocky Mountains from central Idaho to southern British Columbia. White fir (*A. concolor* [Gordon and Glend.] Lindl. ex Hildebr.) grows in the southern Cascade, Sierra Nevada, and Rocky mountains, south of the range of grand fir (LITTLE 1971). The Sierran populations of white fir are often referred to *A. concolor* var. *lowiana* (Gord.) Lemmon and those of the southern Rocky Mountains to *A. concolor* var. *concolor*. Between the ranges of undisputed grand and white fir is a large area where individual trees and populations are not easily assigned to either species.

General patterns of morphological variation in this species complex have been described. Spontaneous hybrids between the species occur in cultivation and result in a variety of combinations of morphological characteristics in the offspring (SCHEPLITZ 1956). Studies of phenotypic variability have determined the composition and general extent of the intermediate populations. DANIELS (1969) found, within a more complex rangewide variation pattern, that populations of fir in the Oregon Cascades show a clinal north-south variation in several needle characteristics and in bark color. The more southerly populations resemble *A. concolor* var. *lowiana*. Populations to the north become steadily more like *A. grandis*. His results generally confirm those of HAMRICK (1966), who sampled needle characteristics in northern California and Oregon, and also correspond to patterns of intermediacy in cortical terpene chemistry. Low percentages of camphene in cortical terpenes are characteristic of populations of the Sierra, Siskiyou, and of the extreme southern Cascade mountains. The percentage of trees with high camphene levels, characteristic of *A. grandis,* increases northward, and becomes 100% in central Washington (W. B. CRITCHFIELD, personal communication, 1969).

Seedlings from several native seed sources of *A. grandis* (LACAZE and TOMASSONE 1967), of intermediate populations, and of Sierran *A. concolor* var. *lowiana* (HAMRICK and LIBBY 1972) have been grown together. These common-garden studies confirm a genetic basis for the phenotypic variation patterns described above. Morphological and growth-related characteristics of Cascade populations were intermediate between those of seedlings from coastal *A. grandis* and those of Sierran *A. concolor*. LACAZE and TOMASSONE (1967) differentiate a coastal type of grand fir from that found in the Cascades and the interior. They emphasize that the boundary between these types is west of the crest of the Cascades in Oregon. North-south variation was also described. A suggested zone of introgression between *A. grandis* and Sierran *A. concolor* at 43°–44° N (LACAZE and TOMASSONE 1967) corresponds with a region of abrupt change in bark characteristics and with a zone of morphological intergradation defined by hybrid index and stomatal distribution (DANIELS 1969). Thus, a zone of transition between typical *A. grandis* and mixed populations including trees resembling *A. concolor* var. *lowiana* apparently exists in the central Oregon Cascade Range.

The origin of these intermediate Cascade populations, along with others of eastern Oregon and Idaho, is attributed to hybridization and introgression between *A. grandis* and *A. concolor* var. *lowiana* (DANIELS 1969; HAMRICK and LIBBY 1972), although DANIELS admits that conclusive evidence for introgression is lacking.

Sampling in studies cited above was designed primarily to determine large-scale geographic patterns of variation in morphology and phenology of growth, and little information about local variation is available. Local variation in morphology was not detected in two transects spanning 300 m of elevation in southern Oregon (DANIELS 1969). No correlation of morphology with elevation was found in the intermediate populations sampled by HAMRICK (1966).

This paper reports the geographic and habitat distribution and patterns of local variation in morphology of populations in the *A. grandis–A. concolor* species complex in the central Oregon Cascade Range. These patterns of distribution and morphology should serve as a basis for the study of variation in physiology and of the environmental influence on population characteristics in these populations.

In this paper, "grand fir" will refer to any extant population in the species complex occurring in the area studied. Specific names will be used for populations or characteristics typical of one of the species.

Geographic and habitat distribution

Physiography, soils, climate, and regional vegetation of the central Oregon Cascades are described by FRANKLIN and DYRNESS (1969). In the Western Cascades Province (see fig. 1), the mountains are deeply dissected and have fairly well-developed soils. Precipitation is high—166 cm at McKenzie Bridge and up to 350 cm on the adjacent ridges. The High Cascades Province, paralleling the Western Cascades to the east, has relatively gentle topography (except for recent volcanic peaks) and soil materials of much more recent origin than the Western Cascades. Precipitation is somewhat lower and temperature extremes are greater, as the maritime influence is weaker than in the Western Cascades. A marked decrease in precipitation occurs down the east slope of the High Cascades (from 230 cm to 130 cm in 12 km) and continues east of the base of the range. Precipitation at Sisters (see fig. 1) is 43 cm.

WESTERN CASCADES

Sampling was primarily limited to the area from 44°7′ to 44°27′ N latitude and was concentrated around the H. J. Andrews Experimental Forest (see fig. 1). Data from 300 reconnaissance samples of vegetation from the H. J. Andrews Forest and vicinity (DYRNESS, FRANKLIN, and MOIR 1973) suggest that grand fir is limited primarily to low-

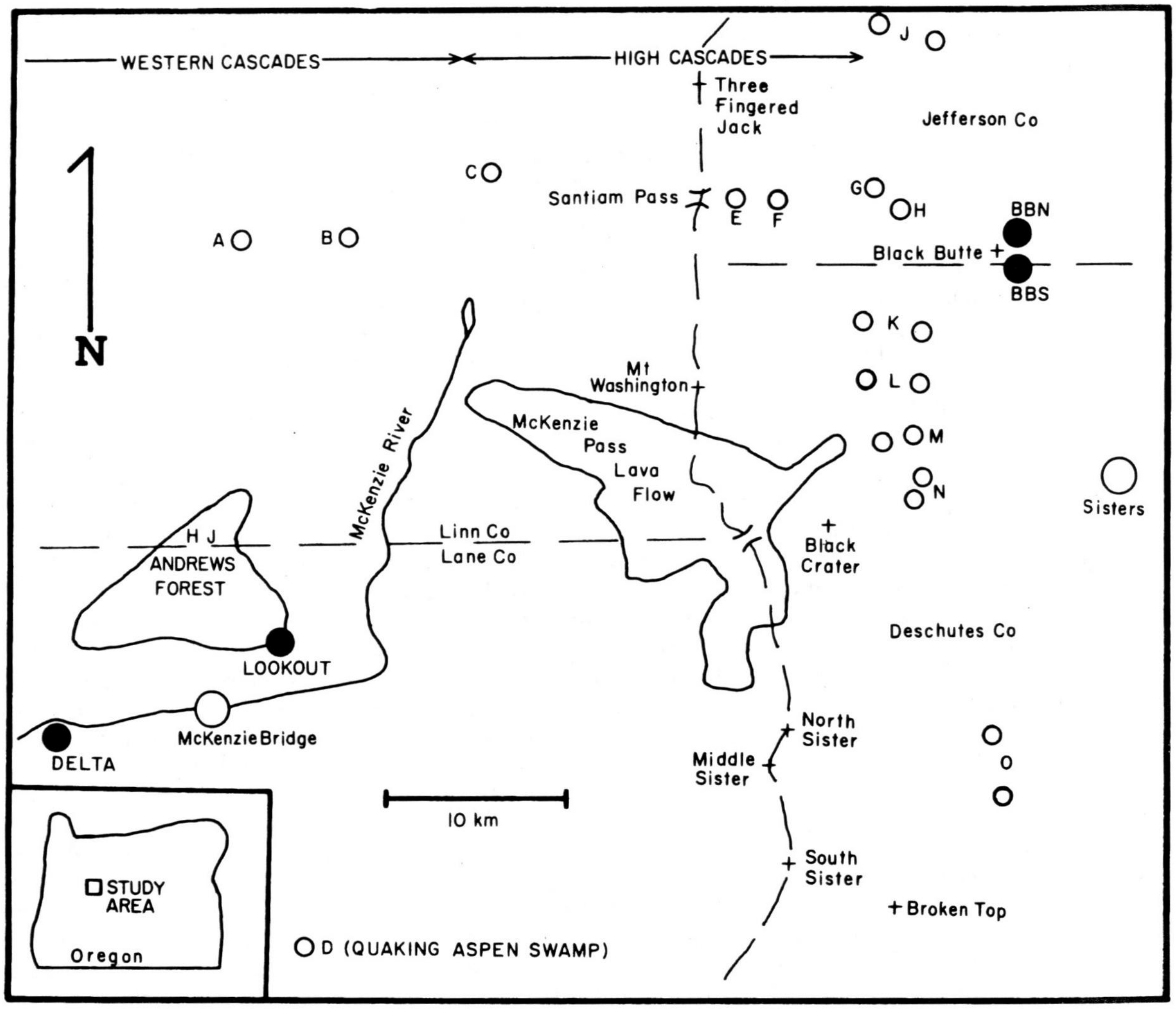

FIG. 1.—Map of the study area. Solid circles are plots for intensive sampling of needle morphology. Small open circles are sites where periderm color was determined. Large open circles are towns. The area shown as McKenzie Pass Lava Flow is mostly without vegetation or has only scattered trees. Broken lines are county boundaries. The crest of the High Cascades coincides with the north-south county line shown.

elevation stream terraces and to areas above 980 m on slopes of south to southeast aspect.

Considerable ground survey work confirmed the existence of an elevational disjunction of grand fir populations in the area of the H. J. Andrews Forest. Grand fir is rare, if not absent, between 610 and 980 m (ZOBEL 1969). At elevations below 610 m, in the *Tsuga heterophylla* zone (FRANKLIN and DYRNESS 1969), grand fir is confined primarily to major stream terraces and floodplains such as those along the McKenzie River. It is abundant in some local areas. However, many stands including mature trees have little or no reproduction, and many areas with considerable reproduction have few mature trees. The second concentration of populations in the H. J. Andrews Forest is at 980–1,460 m, within the *Abies amabilis* zone. Mature trees grow primarily on rocky ridge tops and steep southerly slopes with very open forest. Seedlings are more widely distributed, but still limited to southerly slopes.

Distribution north of the H. J. Andrews Forest appears to follow a similar pattern, with grand fir occurring on nonzonal habitats (including a frost pocket and lava flow) at high elevations, and on low-elevation stream terraces. South of the McKenzie River, grand fir becomes more abundant in a wider variety of high-elevation habitats.

HIGH CASCADES

In the High Cascades Province, grand fir is apparently rare or absent on the gentle western slopes, but it becomes common at middle and lower elevations on the eastern flank of the mountains (SWEDBERG 1961). In the area of relatively level topography but rapidly decreasing precipitation to the east, it extends to approximately the 84 cm isohyet (estimated from maps in WEST 1964) at 44° 25′ N latitude. Throughout most of this region it is the major climax species and is presently the most important dominant at the wetter end of the precipitation gradient (FRANKLIN and DYRNESS 1969). At the drier end of this gradient, grand fir has become established in *Pinus ponderosa* forests only in this century, since exclusion of periodic fires (WEST 1969). The limit of the area with considerable grand fir is approximated by the eastern or northern samples of the sample pairs G-H through 0 (fig. 1). Grand fir extends farther east along higher elevations at the southern end of the study area.

Grand fir is a dominant on Black Butte, a symmetrical volcanic cone rising to 1,963 m about 7.5 km east of the base of the High Cascades. Here it occurs at all elevations on the north side, and is a major dominant on the northwest to southeast slopes. It is the apparent climax tree on a larger area, with seedlings established on slopes with somewhat more southern aspect and at lower elevations than where it presently dominates (SHERMAN 1969). The Black Butte populations are separated from those to the west by a narrow zone (1–2 km) in which grand fir is rare and is present only as seedlings or saplings.

About 100 km farther east, grand fir is common to abundant over large areas of the Ochoco Mountains (a portion of its range sampled in studies of HAMRICK [1966] and DANIELS [1969] but not shown in LITTLE [1971, maps 5-W and 6-W]).

Periderm color of population samples

A cut across mature outer bark of *Abies grandis* exposes alternating layers of reddish periderm and brownish nonfunctional phloem. In *A. concolor,* however, the periderm is yellowish (CHANG 1954). (Weathered peripheral layers of bark do not show coloration of the periderm.) This red-yellow contrast occurs in the "sequent" periderm, which develops after a number of years, not the "first" periderm formed early in the life of the tree, as recently described by MULLICK (1971). A population of trees may be sampled to determine the percentage of trees with a given periderm color. DANIELS (1969) found that rangewide variation patterns in periderm color were similar to those of needle characteristics. DANIELS's periderm color pattern in the Sierra-Cascade ranges closely parallels that of terpene chemistry of bark resins (W. B. CRITCHFIELD, personal communication, 1969). Within local population samples, periderm color does not appear to be associated with microhabitat factors, as DANIELS (1969) also concluded. Because of its independence of microhabitat, correlation with other characteristics, and rapidity of determination, periderm color was the most widely used character in this investigation.

METHODS

In practice, the periderm color difference is not entirely distinct, as DANIELS (1969) also found. The convention used in my sampling was: (*a*) any reddish color (slight pink to deep reddish purple) was scored as "red"; (*b*) yellow was scored as "yellow"; and (*c*) a neutral color, neither "red" nor "yellow," was scored as "intermediate." "Intermediate" trees did not exceed 5% in any population, and were usually only 0–2%. Interpretations reported here are based primarily on "percentage yellow," since yellow is the more homogeneous color class.

In each population, trees were sampled for 1 hour or until a minimum sample size of 100 was reached. Occasional samples were of less than 100 trees used where tree density was low. All trees large enough to have periderm that could be sampled easily were used. In recently thinned or selectively logged areas, cut stumps were included in the sample. On smaller trees, sampling was possible at the base, around limb bases, or over healed wounds. Trees in habitats where growth is slow develop periderm while they are relatively small. All color determinations were made in the field from axe or knife cuts in the outer bark. One caution necessary in sampling was to avoid *Pseudotsuga,* which has yellow periderm. Outer bark of young trees of the two species is similar. When both species were present, foliage was examined on all "yellow" trees and cut stumps were avoided.

Results are presented as: (*a*) the geographic and habitat pattern within the region; (*b*) aspect gradients on Black Butte; (*c*) elevational gradients east of the Cascades; and (*d*) local east-side variation not associated with topography.

RESULTS

REGIONAL PATTERNS.—All trees sampled in low-elevation west-side populations along the McKenzie River and a major tributary, Horse Creek, had red periderm (table 1, Delta sample and McKenzie Bridge areas). The periderm was uniformly dark reddish purple, and the bark was hard compared with east-side samples. One tree in a sample of 42 near the upper limit of low-elevation grand fir in the H. J. Andrews Forest had yellow periderm. High-

TABLE 1

PERCENTAGE OF SAMPLE TREES WITH YELLOW PERIDERM AT SAMPLE AREAS SHOWN ON FIGURE 1

A. WEST OF THE CASCADE CREST

Sample and location	Elevation (m)	*N*	% Yellow
A: Iron Mountain	1,460	100	4
B: Lost Prairie	1,080	100	4
C: Nash Crater Lava Flow	1,180	130	9
Lookout	1,370	99	10
Delta, McKenzie Bridge areas	340–440	232	0
D: Quaking Aspen Swamp area	1,360–1,700	387	12

B. EAST OF THE CASCADE CREST (EXCEPT BLACK BUTTE)

Sample	Kilometers south of J	Elevation (m)	Closed forest		Open forest	
			N	% Yellow	*N*	% Yellow
J	0	975, 910	316	18	82	24
E	. . .	1,380	242	17	. . .	. . .
F	. . .	1,250	245	24	. . .	. . .
G	9.8	1,040	175	19	. . .	. . .
H	10.5	1,010	. . .	. . .	127	8
K	16.7	1,160, 1,070	391	23	105	21
L	19.4	1,280, 1,160	427	36	138	47
M	22.2	1,230, 1,160	456	47	238	47
N	25.3, 24.1	1,220, 1,160	466	34	164	40
O	41.6, 37.6	1,860, 1,560	422	52	152	52

NOTE.—N = number of trees in sample. Kilometers south of J = how far south of site J each site in the N-S transect is.

elevation samples in the Western Cascades showed small percentages of yellow periderm. The percentage increased somewhat from north to south (table 1).

Along the east flank of the Cascades, higher proportions of yellow (8%–52%) were found in most samples. On Black Butte, 15%–38% of trees were yellow. The detailed patterns will be outlined below.

The only sample taken farther east was on the north slope of the Ochoco Mountains, where grand fir was the major reproducing tree as well as sharing overstory dominance. Here 67% of 302 trees had yellow periderm.

ASPECT GRADIENTS ON BLACK BUTTE.—Populations were sampled at elevations of 1,410–1,640 m at all aspects where grand fir grows on Black Butte. Samples were taken every 0.56 km along a forest road from the west to the north to the southeast slope of the butte. A few supplementary samples were taken. In general, incidence of yellow periderm increases as the aspect changes from north toward south (fig. 2). The single major exception, 29% yellow in the middle of the gradient, is on an area apparently no different from other nearby areas sampled. The difference between the aspect of sample areas and north was correlated ($<.01$ probability) with periderm color distribution of the population ($r = .74$ with arcsin $\sqrt{\text{percentage yellow}}$.)

ELEVATIONAL GRADIENTS EAST OF THE CASCADES.—Series of samples were taken along the lower north slope of Black Butte (fig. 2) and along the Santiam Pass Highway (fig. 1, samples H, G, F, E: 1,000–1,380 m) to determine whether a clear elevational gradient in periderm color could be demonstrated. The Santiam transect showed no particular pattern with elevation (table 1). A number of habitat characteristics varied from sample to sample along with elevation, the unknown effect of which could obscure any effect of elevation. Sample H is exceptional among east-side populations for the low incidence of yellow periderm. The Black Butte elevational transect (fig. 2) showed some decrease in "yellow" periderm with elevation, but not a unidirectional change. Scattered trees ($N = 146$) on the lower east side of the butte did show more yellow periderm than the populations above.

EAST-SIDE VARIATION NOT ASSOCIATED WITH TOPOGRAPHY.—In general, a north-south increase in frequency of "yellow" periderm is obvious in this latitudinal zone. Much of the change is across a

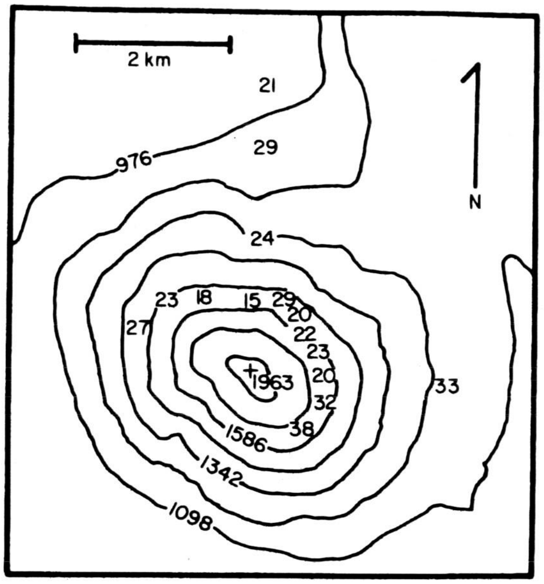

FIG. 2.—Periderm color on Black Butte. Three- and four-digit numbers are elevations in meters. Two-digit numbers represent the percentage of trees with yellow periderm at each location. Sample size varies from 80 to 398, averaging 240 on the horizontal transect and 128 at the four lower elevation areas.

region of relatively uniform soils and topography. A north-south transect of seven pairs of samples was taken along the base of the east flank of the High Cascades, from 44° 31′ to 44° 08′ N latitude (fig. 1, samples G, H; sample pairs J–O). Each pair consisted of: (*a*) a stand near the edge of the grand fir range, where fir trees were scattered individually or in small clumps in relatively open *Pinus ponderosa* forest and (*b*) a stand well into closed forest, where grand fir formed a dense understory, often occurring also as old-growth trees. The northern three sample pairs (J, G–H, K) show no particular gradient and are interpreted as representing variation within a general population similar to that on most of Black Butte (table 1). The 8% yellow value (sample H) is certainly not characteristic of most east-side populations and may be related to a local soil situation; a 40 cm layer of coarse pumice overlies finer material similar to that found in the top 75 cm at the other sites checked.

In the 6 km from samples K to M, there is a rapid north-south change from about 22% to 47% yellow periderm, not associated with any readily apparent general change in topography or substrate. Immediately to the south (sample N), percentage yellow decreases somewhat.

The southernmost samples (O) are located at higher elevations (as is the range of grand fir) on the north slope of an eastward extension of the High Cascades Province. The further increase in these samples in frequency of yellow periderm occurs across much more uneven topography than the change from K to M.

DISCUSSION OF PERIDERM COLOR RESULTS

The general patterns of bark color variation and species distribution can be interpreted as showing low-elevation west-side populations of (according to periderm color) almost pure *Abies grandis*. A small proportion of trees in the disjunct upper elevation populations have yellow periderm, a trait of *A. concolor,* and the incidence of this trait increases slightly from north to south. The upper-elevation west-side populations are apparently disjunct also from those on the east flank of the High Cascades, most of which show a much larger but widely variable influence of *A. concolor*. This influence also increases from north to south. This general pattern fits the pattern of variation expected in this area from previous wider ranging but much less intensive sampling (DANIELS 1969; HAMRICK 1966; LACAZE and TOMASSONE 1967). These authors interpret this pattern as having formed following introgression between *A. grandis* and *A. concolor*.

Local variability with slope aspect is demonstrated on Black Butte. Soils vary little on the butte (SHERMAN 1969), and the populations are continuous between sampling points. It appears that such a pattern would have developed in response to selection by microclimatic factors that vary with slope aspect, shading by the butte itself, and perhaps local precipitation patterns around the butte.

Any clear pattern of variability with elevation has been hard to define in this study, even on the mid-to-lower slope of Black Butte, with uniform aspect and apparently uniform soils. Earlier workers were not able to find morphological variability with elevation within intermediate populations, although growth-related characters in Sierran *A. concolor* did vary clinally with elevation as well as latitude (HAMRICK and LIBBY 1972).

The local north-south change of bark color along the eastern base of the Cascades may simply be a result of regional change due to introgression. It seems more likely that at least some features of it are the result of local selective pressures. Aspect pattern on Black Butte shows that periderm color may change markedly with apparent changes in environment. The location of an extreme value (8% yellow) on substrate unlike any seen elsewhere also points to the probability of local perturbation of the rangewide introgression pattern by local selective pressures.

Local effects may also explain the rapid change in bark color and its reversal, which occurs near the McKenzie Highway (table 1, sites K–N). There seem to be at least two possible environmental differences that may be responsible for this latter morphological change. One is a substrate difference not visible in exploratory observations. The other, which I consider more likely and more interesting, might be associated with the presence, directly to the west, of a large expanse of the relatively unvegetated McKenzie Pass lava flow (see fig. 1). This extends to within 2.5 km of sample M. From its extreme eastern point it extends, largely uninterrupted, over 21 km to the west (as shown on U.S. Geological Survey Quadrangle Maps). Air moving from the west to the zone where the change in periderm color occurs would probably pass south of Mt. Washington (2,377 m) and be forced north of Black Crater (2,212 m), and thus certainly cross a large expanse of lava. Air passing north of Black Crater would pass over sites M and L unobstructed, whereas site N is sheltered by the northern slopes of Black Crater. Marine air masses crossing the lava flows would probably experience greater heating or cooling, depending on prevailing conditions, than those crossing the more heavily forested parts of the High Cascades. If there is, for this reason, a mesoclimate with greater temperature extremes (and accompanying changes in moisture conditions), one might expect selection to favor *A. concolor*-type trees here more than either to the north or immediately to the south (shielded somewhat by Black Crater).

Whether any characteristic that contributes to periderm color has adaptive value has not been demonstrated. The chemical basis of periderm color is at least partially known, since one anthocyanidin and two other pigments, probably anthocyanins, were isolated from *A. grandis* (presumably from coastal British Columbia) (MULLICK 1969). MULLICK suggests that the presence of anthocyanidins, toxic to fungi and bacteria, in conifer bark "may be significant" (p. 1,421). Even if periderm color has no adaptive value, it is known from studies of other species that inheritance of morphological characters and of those governing growth and survival is strongly correlated (HIESEY, NOBS, and BJORKMAN 1971).

Needle morphology

Needle characteristics of *Abies grandis* and *A. concolor* differ considerably and have been used in taxonomy and previous studies of variation. Their quantification is more time-consuming than that of periderm color. Samples from selected areas were collected to allow comparison of patterns shown by periderm color with those of other morphological characteristics.

METHODS

Needle characters used were:

1. Stomata on adaxial surface: *Abies grandis* usually has either no stomata on the upper needle surface or only a few around the notch at the end of the needle. In contrast, *A. concolor* has a large number of stomata on the upper leaf surface. This characteristic was examined on fresh needles, and was quantified as: (*a*) maximum number of adaxial stomatal rows and (*b*) the percentage of length of the needle bearing any adaxial stomata (scored as 0, "<5%," or estimated to the nearest 5%). In some cases, stomatal row counts, necessary to compute the "stomatal index" of DANIELS (1969), were made.

2. Shape of needle apex: *A. grandis* has a conspicuous notch at the needle tip, whereas *A. concolor* needles are not notched. Shape of the apex was quantified by: (*a*) assigning each needle to one of HAMRICK's (1966) "needle tip types" or (*b*) measuring the depth of the notch of needles dried at room temperature. For method (*b*) the two longest needles on each twig were used, and the perpendicular distance was measured from the deepest point of the notch to a line tangent to both points of the bifid needle apex, using an ocular micrometer and a dissecting microscope.

Needle morphology may vary between "sun" and "shade" branches on the same tree. This variation is rather large for adaxial stomata, since there are more on "sun" leaves. Sun-shade variation in needle-notch depth was found in only a few cases (DANIELS 1969). Occurrence of sun-shade variation requires that caution be used in interpretation of the stomatal data presented here. Trees sampled in this investigation of needle morphology were almost all small (1–3 m tall) and thus tended to have all "shade" or all "sun" branches, and at most locations they tended to be either all "sun" or all "shade" trees. Therefore, phenotypic patterns will depend in considerable part on the local environment.

Sampling of needle characteristics was at two levels: (*a*) intensive sampling of a few trees in four populations in contrasting habitats and (*b*) extensive sampling on more trees over a larger area. In all cases, needles of the previous growing season were sampled.

RESULTS

INTENSIVE SAMPLING.—Intensive needle sampling was done at four sites (see fig. 1). Delta is at 350 m on a terrace along the McKenzie River. Here seedlings and saplings occur under a closed canopy. All mature grand fir sampled along this terrace had red periderm.

Lookout is at 1,370 m on a steep southeast-facing rocky slope. Grand fir occurs singly or in scattered clumps as seedlings to pole-sized trees with *Pseudotsuga menziesii*. Grand fir regeneration is mostly on the uphill side of Douglas-fir or in clumps of shrubby *Quercus garryana*. Of the grand fir, 10% had yellow periderm.

"Black Butte North" (BBN) is at 1,570 m on a north-facing slope along a gully on the northeast face of the butte. Grand fir seedlings, saplings, and poles are dense under a closed overstory of *Pinus ponderosa, Pseudotsuga,* grand fir, *Pinus monticola,* and recently dead *Larix occidentalis* snags. Bark of 22% of the sample had yellow periderm.

"Black Butte South" (BBS) is at 1,640 m on the southeast face of Black Butte. A clump of grand fir seedlings and saplings occupies a slight depression under an open canopy of *P. ponderosa.* Grand fir grows no farther south at this elevation on Black Butte. Yellow periderm occurs on 37.5% of trees in the area.

At each site five or six trees were sampled for (*a*) maximum number of adaxial stomatal rows in each quarter of the needle (ROWS) and (*b*) percentage of length of needle having adaxial stomata (LENGTH). The six longest needles from the previous year were sampled on 4–11 twigs per tree. "Stomatal Index" (SI) of DANIELS (1969) was computed as the sum of maximum number of rows of stomata in each of the four quarters of the needle divided by four. Following DANIELS's convention, needles with adaxial stomata only in a small spot around the apical notch were assigned SI = 0.125.

At each site, 9–12 trees were sampled for notch depth (DEPTH). On each tree, needles from 30 to 32 twigs were sampled.

The characteristics SI, ROWS, and LENGTH are lowest at Delta, highest at BBS, and intermediate at BBN and Lookout, with Lookout being slightly higher in all cases (table 2). In all cases a marked difference occurs between Delta and the other sites, and between BBS and the other sites.

Notch depth shows a slightly different pattern. It is higher at Delta than at other sites, then decreases slightly from Lookout to BBN to BBS (table 2).

A rather close relationship exists among SI, ROWS, and LENGTH, as might be expected (table 3A). It appears that SI, ROWS, or LENGTH would well represent the extent of adaxial stomata. The SI and DEPTH of individual trees are not well correlated (table 3A). At Delta and Lookout, rather large variation in DEPTH occurs with little change in SI, while at BBS large tree-to-tree variation in SI is not correlated with DEPTH. Thus, it appears that DEPTH and the stomatal characteristics may vary from tree to tree at least somewhat independently of each other.

Conclusions drawn from this sampling generally support those drawn from periderm color. Delta has needles characteristic of *Abies grandis.* The other sites are somewhat intermediate between *A. grandis* and *A. concolor,* with BBS showing the greatest *A. concolor* influence. The difference between Lookout and BBN, evident in bark color, did not appear in needle morphology. Relative lack of shading at Lookout may have allowed full expression of genetic tendencies toward having adaxial stomata, whereas deeper shade at BBN perhaps suppressed their development.

QUAKING ASPEN SWAMP SAMPLE.—Needles were collected from 26 trees in and around a meadow at about 1,700 m elevation on a ridge above Quaking Aspen Swamp in the Western Cascades (fig. 1, sample D). Needles were collected as in extensive sampling (see following section) but were analyzed as in intensive samples. Averages are similar to those of Lookout and BBN (table 4), although the standard deviations are somewhat larger. The sampled trees were mostly similar to *A. grandis* in

TABLE 2

INTENSIVE SAMPLING SITE MEANS OF NEEDLE CHARACTERISTICS ± STANDARD DEVIATION (BASED ON TREE MEANS)

CHARACTERISTIC	SAMPLING SITE Delta	 Lookout	 BBN	 BBS
SI	0.031 ± 0.016 (6)	0.797 ± 0.287 (6)	0.668 ± 0.304 (5)	2.665 ± 2.459 (5)
ROWS	0.38 ± 0.20 (6)	3.14 ± 0.63 (6)	2.68 ± 0.67 (5)	5.09 ± 2.27 (5)
LENGTH	All < 5% (6)	11.2 ± 8.3 (6)	10.9 ± 11.3 (5)	53.1 ± 39.2 (5)
DEPTH	5.83 ± 1.36 (12)	3.51 ± 1.15 (9)	3.38 ± 0.72 (9)	3.10 ± 0.81 (9)

NOTE.—Number of trees sampled is given in parentheses. For site locations see fig. 1. SI = adaxial stomatal index; ROWS = maximum number of rows of stomata on the adaxial needle surface; LENGTH = percentage of length of adaxial needle surface with stomata; and DEPTH = depth of apical notch in micrometer units (1 unit = 0.025 mm).

TABLE 3

CORRELATION COEFFICIENTS BETWEEN TREE MEANS OF NEEDLE CHARACTERISTICS, INTENSIVE AND QUAKING ASPEN SWAMP AREA SAMPLES

A. INTENSIVE SAMPLES ($N = 22$ TREES)

	ROWS	Arcsin$\sqrt{\text{LENGTH}}$	DEPTH
SI	.89	.90	—.26
ROWS	...	.84	—.52
Arcsin$\sqrt{\text{LENGTH}}$ ...	...	...	—.41

B. QUAKING ASPEN SWAMP AREA ($N = 26$ TREES)

	ROWS	Arcsin$\sqrt{\text{LENGTH}}$	DEPTH
SI	.92	.98	.55
ROWS	...	.90	.45
Arcsin$\sqrt{\text{LENGTH}}$ ...	...	...	.51

NOTE.—Character abbreviations identified in table 2.

TABLE 4

NEEDLE CHARACTERISTICS NEAR QUAKING ASPEN SWAMP

	SI	ROWS	LENGTH	DEPTH
Mean	0.683	2.28	11.6	3.68
Standard deviation ...	0.960	2.10	22.0	1.24

NOTE.—Twenty-six trees were sampled with six needles per tree. Character abbreviations are identified in table 2.

stomatal characteristics, but there were a few trees with extensive adaxial bands of stomata. In general, needle morphology here shows the same relationship to other sites as does periderm color (12% yellow).

The characteristic ROWS and the transformation of LENGTH again were well-correlated with SI (table 3B), while stomatal characteristics were less well, but significantly, correlated with notch depth. Note that the latter correlation coefficients are positive. Here, those trees with the most adaxial stomata had the deepest needle notch. In the four intensively sampled sites (22 trees), a shallower notch was found with more extensive stomata (table 3A).

EXTENSIVE SAMPLING.—Sample sites were distributed as follows in four contrasting areas: (*a*) four sites at low elevations on the west side, near Delta; (*b*) 10 sites at high elevations in the H. J. Andrews Experimental Forest; (*c*) eight sites around BBS, and extending at 200 m intervals for about 1 km to the north around the contour of Black Butte; and (*d*) five sites around BBN and extending 400 m to the south around the contour.

Five trees (1–3 m tall) were sampled at each site. Six needles per tree were sampled—the longest needle of the previous year's growth on three twigs each on the north and south sides of the crown.

Needles were checked for maximum number of adaxial stomatal rows (ROWS), percentage of adaxial surface with stomata (LENGTH), "tip type" of HAMRICK (1966) (TIP), and angle of the two ranks of the present year's needles above the horizontal (ANGLE). The characteristic TIP was quantified by comparison with HAMRICK's illustration and either placed in one of his classes (3,4, or 5) or considered intermediate (3.5 or 4.5). Values of TIP for needles within a tree and site were arithmetically averaged.

Abundance of adaxial stomata (ROWS, LENGTH) increases from the Delta region to the high elevations of the H. J. Andrews Forest to the BBN area to the BBS area (table 5). The TIP shows little variation, although BBS is significantly lower (statistically) than the other areas (i.e., less like *A. grandis*). This is a different pattern from that shown by intensive sampling of notch depth, where Delta differed considerably from all the other sites. The ANGLE increases similarly to stomatal abundance, except that in the high H. J. Andrews populations (mostly in open forest) it is slightly greater than at BBN (closed forest). Tree-to-tree

TABLE 5

EXTENSIVE SITE MEANS OF NEEDLE CHARACTERISTICS ± STANDARD DEVIATION

	SAMPLING AREA			
CHARACTERISTICS	Low West	High West	Near BBN	Near BBS
N	20	49	25	40
ROWS	0.51 ±0.49	2.78 ± 1.49	3.37 ± 1.45	4.69 ± 1.65
LENGTH	4.2 ± 2.2	10.8 ± 18.0	15.4 ± 21.6	41.0 ± 33.2
TIP	4.40 ± 0.28	4.53 ± 0.30	4.42 ± 0.28	4.25 ± 0.25
ANGLE	8.1 ± 6.0	24.4 ± 21.7	19.6 ± 16.4	42.0 ± 21.0

NOTE.—Six needles were sampled per tree. TIP = "tip type" (HAMRICK 1966). ANGLE = angle of needles above a horizontal plane through the twig. Other character abbreviations are given in table 2.

variation of ANGLE is large. DANIELS (1969) found little significant geographic variation in this character.

The ROWS and LENGTH vary together ($r = .81$), as do ROWS and ANGLE, to a lesser degree ($r = .45$). However, ROWS and TIP are seemingly not related ($r = .01$).

Hybrid indices

To allow an overall comparison of tree characteristics, a hybrid index (ANDERSON 1949) (HI) was computed for all trees, as follows. Within each study (intensive and extensive), the range of all characters was divided into 10 equal parts. The extreme level of expression of each character most similar to *Abies grandis* was assigned a value of one, and that most unlike it, a value of 10. "Values" for each character of each tree were summed to give the tree HI.

In the intensive needle sampling and the Quaking Aspen Swamp area studies, SI and DEPTH were the characteristics used. To each tree mean was added a value, computed for each stand, reflecting the bark color in the stand (1 = 0% yellow, 10 = 52% yellow). Tree HI's (possible range = 3–30) were averaged for each site; site averages are shown in table 6A and B.

Hybrid indices for "extensive" areas were computed on ROWS, LENGTH, TIP, and ANGLE, giving a possible range of 4–40. Area means are shown in table 6C.

TABLE 6

AVERAGE HYBRID INDEX (HI) AT EACH SITE ± STANDARD DEVIATION

A. INTENSIVE SAMPLE SITES

	Delta	Lookout	BBN	BBS
N	6	6	5	5
HI	6.5 ± 2.1	11.0 ± 2.2	14.8 ± 1.3	21.0 ± 3.2

B. QUAKING ASPEN SWAMP

$N = 26$ HI = 12.6 ± 1.5

C. EXTENSIVE SAMPLE AREAS

	Low West	High West	Near BBN	Near BBS
N	20	49	25	40
HI	9.4 ± 2.7	13.6 ± 5.7	14.5 ± 4.5	23.2 ± 6.0

NOTE.—For A and B, SI, DEPTH, and percentage yellow periderm were used (possible HI range = 3–30). For C, ROWS, LENGTH, TIP, and ANGLE were used (possible HI range = 4–40).

The conclusions drawn from hybrid indices calculated for both intensive and extensive study sites are similar to each other and to conclusions from periderm sampling alone. The low-elevation west-side stands are most similar to typical *A. grandis*. They show little or no difference from the "pure" species. Populations from west-side high elevations, the northeast slope of Black Butte and the southeast slope of Black Butte, show increasingly more variation toward *A. concolor*. The largest difference in hybrid index, more obvious than in the periderm color results, is between the Black Butte populations.

Hybrid indices of intensive sampling sites are strongly correlated with those of their corresponding extensive sampling areas ($r = .97$) and with the five-tree extensive samples taken at the same sites ($r = .94$). The nature of the variability in the extensively sampled areas is perhaps best seen in histograms of percentage of trees with each HI value (fig. 3). Trees as similar to *A. grandis* as some of those at Delta occur in all areas. The variability of individual trees within areas is evident. Those in the upper HI range have needle characters very similar to descriptions of Sierran *A. concolor,* except for the presence of at least some needle notch on almost all trees studied. The increased degree of variability in the intermediate populations, as one might expect in an apparent case of introgression (ANDERSON 1949), is obvious from both figure 3 and the standard deviations in table 6C. The symbols indicating the HI of intensive study trees (fig. 3) are placed at 1.33 of their true HI value to give them the correct relative position to the histograms. (Maximum HI value for intensive study trees was 30 compared with 40 for extensive study trees.)

The HIs computed in this study are useful only for comparison between trees and populations within the study areas, not for their comparison with pure populations of grand and white fir. However, the Delta population probably represents—or is at least very similar to—"pure" *A. grandis*.

General discussion

The needle characteristics used in this study have been demonstrated to vary with environment (DANIELS 1969). Studies of progeny in cultivation and field studies of sun and shade foliage have shown, however, that genetically based variation in needle characters does occur (DANIELS 1969; HAMRICK and LIBBY 1972; LACAZE and TOMASSONE 1967). Shading at BBN and lack of it at Lookout have probably minimized needle differences between these sites. These differences are much smaller than, or the reverse of, differences in periderm color. Ob-

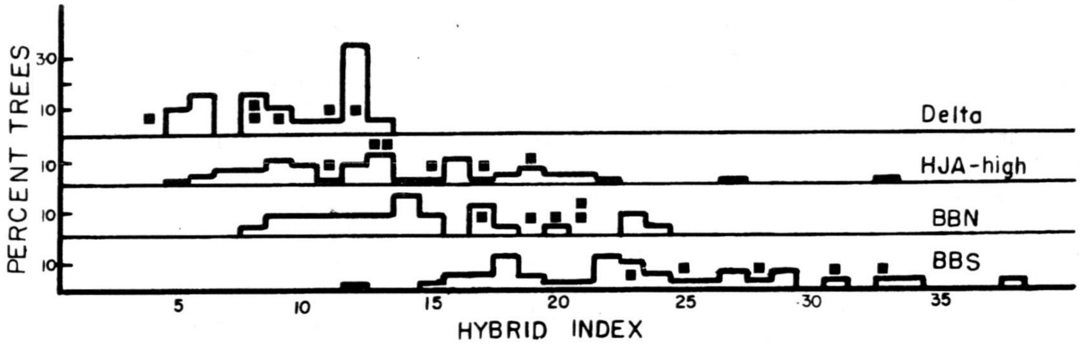

FIG. 3.—Distribution of trees by hybrid index (HI) value for extensive sampling areas. Each square indicates the HI (×1.33) for one intensively sampled tree for comparison. (Maximum possible HI for trees from intensively sampled areas was 30.)

vious differences in needle characteristics occur between equally shaded habitats (ZOBEL, unpublished data) on the east and west sides (Delta vs. BBN, Lookout vs. BBS), indicating that differences observed are not completely due to shading.

Of the needle characteristics used, either maximum number of adaxial stomatal rows or percentage of needle length with adaxial stomata would seem to give the most information for the effort expended, and these are easily determined in the field. If a second needle character is desired, depth of the needle notch varies somewhat independently of stomatal characters on a tree-to-tree basis but gives a similar but less distinct geographic pattern. It requires collection and microscopic study of needles for quantification. HAMRICK's "tip type" was not very useful in this region, where most trees were between his types 4 and 5.

If a population is to be characterized by needle morphology, use of the extensive sampling method (only six needles per tree, from contrasting sides of the crown) seems to be better than the intensive sampling method. For populations, the results of extensive sampling appear to be similar to results of more intensive sampling, and the former method allows a look at many more trees for the same work expended, which is a very important consideration in the variable populations considered here. For characterization of a single tree, a more intensive sampling technique would be desirable.

Periderm color patterns generally reflect those shown by needle morphology as DANIELS (1969) found on a rangewide basis. Sampling of periderm color appears to give a good estimate of the morphologic character of the population (not of an individual tree). It has the added advantages of showing no apparent variation with shading and being easy to determine.

Morphology of trees in the study area fits the rangewide pattern within the *A. grandis–A. concolor* complex described and attributed to introgressive hybridization by earlier investigators (DANIELS 1969; HAMRICK 1966; LACAZE AND TOMASSONE 1967). Characteristics change over relatively small distances in both an east-west and north-south direction. Within this overall pattern, even smaller-scale variations occur in the general patterns of both periderm color and needle morphology. These small-scale variations are correlated in some cases with environmental differences which can be inferred from elevation, aspect, slope, substrate, and especially the vegetational matrix in which the populations grow. This type of local variation in areas of intergrading populations was not found by HAMRICK (1966) or DANIELS (1969), although local variation of growth-related characters associated with environment (expressed as elevation) was found in Sierran *A. concolor* (HAMRICK and LIBBY 1972). Morphology varied clinally with latitude in their study, but not so obviously with local environment (again expressed only as elevation).

General environmental differences between the western and eastern parts of the study area are large. The eastern part of the area has much less precipitation, greater temperature extremes, and a substrate of much more recent origin and less soil development that the western portion (FRANKLIN and DYRNESS 1969). Environmental differences associated with selective pressures in the stands studied can presently only be inferred, but direct measurements of selected factors of stand environment at intensive sampling sites are being made.

The pattern of genetic influence of *A. concolor* in these populations can be shown from morphology. However, more insight into the ecology of the populations studied could be gained from knowledge of more easily interpreted physiological characteristics than from the morphological differences reported here. In *A. concolor,* at least, physiological characteristics may be more liable to vary with local environment than morphology (HAMRICK and LIBBY 1972). Knowing how the physiology of intergrading populations differs, one might better understand the basis for the selective advantage of widespread intermediate populations in this area of geologically recent disturbance in the central Oregon Cascades. Furthermore, past studies of physiology of ecodemes (populations occupying a specified habitat) of a given taxon have been valuable for elucidating basic differences in adaptation to contrasting environments (e.g., as reviewed by HIESEY et al. 1971, pp. 185–186). Ecological differences in east- and west-side populations are apparent in their different tolerance to balsam woolly aphid attack (MITCHELL 1966), degree of dominance in the vegetation (FRANKLIN and DYRNESS 1969), and type of conditions where reproduction is successful. This study should provide an understanding of the variation pattern around which ecological and physiological studies of grand fir can be planned and interpreted.

Acknowledgments

JERRY FRANKLIN and WILLIAM CRITCHFIELD, U.S. Forest Service, have encouraged and aided this study from its inception. Thanks are given them and to KENTON CHAMBERS for their comments on the manuscript. Financial support has been provided by an Oregon State University Faculty Development Grant, the U.S. Forest Service, and the Oregon State University Department of Forest Management.

LITERATURE CITED

ANDERSON, E. 1949. Introgressive hybridization. Wiley, New York.

BENSON, L., E. A. PHILLIPS, PATRICIA A. WILDER, et al. 1967. Evolutionary sorting of characters in a hybrid swarm. I. Direction of slope. Amer. J. Bot. **54:**1017–1026.

CHANG, Y. 1954. Bark structure of North American conifers. U.S. Dep. Agr. Tech. Bull. 1095.

DANIELS, J. D. 1969. Variation and intergradation in the grand fir–white fir complex. Ph.D. diss. University of Idaho. 235 pp.

DAUBENMIRE, R. 1972. On the relation between *Picea pungens* and *Picea engelmannii* in the Rocky Mountains. Can. J. Bot. **50:**733–742.

DYRNESS, C. T., J. F. FRANKLIN, and W. H. MOIR. 1973. Forest communities of the central portion of the Western Cascades in Oregon. Coniferous Biome, Int. Biol. Program Bull. (in press).

FRANKLIN, J. F., and C. T. DYRNESS. 1969. Vegetation of Oregon and Washington. USDA Forest Service Res. Paper PNW-80. 216 pp.

HAMRICK, J. L., III. 1966. Geographic variation in white fir. Master's thesis. University of California, Berkeley. 143 pp.

HAMRICK, J. L., III, and W. J. LIBBY. 1972. Variation and selection in western U.S. montane species. I. White fir. Silvae Genet. **21:**29–35.

HIESEY, W. M., M. A. NOBS, and O. BJORKMAN. 1971. Experimental studies on the nature of species. V. Biosystematics, genetics and physiological ecology of the Erythranthe section of *Mimulus.* Carnegie Inst. Washington Publ. 628.

LACAZE, J. F., and R. TOMASSONE. 1967. Contribution a l'étude de la variabilité infraspécifique d'*Abies grandis* Lindl. Caractéristiques juvéniles. Ann. Sci. Forest. Paris **24:**277–325.

LITTLE, E. 1971. Atlas of United States trees. I. Conifers and important hardwoods. U.S. Dep. Agr. Forest Service Misc. Publ. 1146.

MANLEY, S. A. M., and D. P. FOWLER. 1969. Spruce budworm defoliation in relation to introgression in red and black spruce. Forest Sci. **15:**365–366.

MITCHELL, R. G. 1966. Infestation characteristics of balsam woolly aphid in the Pacific Northwest. USDA Forest Service Res. Paper PNW-35. 18 pp.

MORGENSTERN, E. K., and J. L. FARRAR. 1964. Introgressive hybridization in red spruce and black spruce. University of Toronto, Fac. Forestry Tech. Report 4. 46 pp.

MULLICK, D. B. 1969. Studies on periderm. II. Anthocyanidins in secondary periderm tissue of amabilis fir, grand fir, western hemlock and western red cedar. Can. J. Bot. **47:**1419–1422.

———. 1971. Natural pigment differences distinguish first and sequent periderms of conifers through a cryofixation and chemical techniques. Can. J. Bot. **49:**1703–1711.

ROCHE, L. 1969. A genecological study of the genus *Picea* in British Columbia. New Phytol. **68:**505–554.

SCHEPLITZ, V. B. 1956. Uber einen naturlichen *Abies*-Bastard: morphologische und holztechnologische Untersuchung an Art-bastarden von *Abies concolor* × *Abies grandis.* Z. Forstgenetik **5:**71–79.

SHERMAN, R. J. 1969. Spatial and developmental patterns of the vegetation of Black Butte, Oregon. Ph.D. diss. Oregon State University. 80 pp.

SWEDBERG, K. C. 1961. The coniferous ecotone of the east slope of the northern Oregon Cascades. Ph.D. diss. Oregon State University. 118 pp.

WEST, N. E. 1964. An analysis of montane forest vegetation on the east flank of the central Oregon Cascades. Ph.D. diss. Oregon State University. 272 pp.

———. 1969. Successional changes in the montane forest of the central Oregon Cascades. Amer. Midland Natur. **81:** 265–271.

ZOBEL, D. B. 1969. Geographical distribution of *Abies grandis* and its ecotypes on and around H. J. Andrews Experimental Forest. Report on file with Pacific Northwest Forest and Range Experiment Station, U.S. Forest Serv. 8 pp.