

Variation and Selection in Western U. S. Montane Species

I. White Fir

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Introduction

White fir (*Abies concolor* [GORDON and GLEND.] LINDL.) is a middle-to-high-elevation species found throughout the central and southern mountains of the western United States, and to a lesser extent in the northern mountains of Mexico. In the past, the frequency of decay in old-growth white fir and the invasion of tolerant young white fir in forests where fir was excluded have led to regard it as an undesirable species. Recent commercial acceptance of many white fir products, and an increasing appreciation of forest ecology, have created a heightened interest in the biology of this species. As more white fir is planted, it will become important for the forester to know where he can obtain seed which will develop into healthy trees with desired attributes.

A knowledge of the amount and pattern of genetic variation found between trees from differing geographic and climatic areas is prerequisite to a genetically-sound reforestation program with any species. In studying white fir, we have been led to question some general concepts about ecotypes, clines, and the uniformity of variation pattern among different characteristics of the same populations. We offer several hypotheses in this paper which suggest possible causes of the observed patterns of variation.

Native white fir in the Rocky Mountains is morphologically different from native white fir in the Sierra Nevada Mountains of California (LAMB, 1914). Some botanists (LARSEN, 1956; GATHY, 1957) have considered the Rocky Mountain white fir a distinct species (*A. concolor*) from the California and Oregon firs (*A. lowiana*). Others (LAMB, 1914) felt that the differences found between the white fir of these geographic regions only warranted separation into two varieties (*A. concolor* var. *concolor* and *A. concolor* var. *lowiana*).

In addition to such descriptions of intra-specific variation, there have been several reports (ELIOT, 1938; LAMB, 1914; MÜLLER, 1939) of natural populations in central Oregon and northwest California which have characteristics intermediate between *A. concolor* var. *lowiana* and *A. grandis* (DOUGLAS) LINDL. LARSEN (1956) and CRITCHFIELD²⁾ have made controlled crosses between *A. concolor* var. *lowiana* and *A. grandis*, which produced viable F₁ offspring with apparently intermediate characteristics. Two cases of spontaneous hybrids have occurred in European arboreta (GATHY, 1957; and SCHEPLITZ, 1956). In both cases, the seed parent was a Rocky Mountain white fir and the probable pollen parent was a nearby *A. grandis*. GATHY observed that his hybrids resembled Sierra white fir.

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²⁾ Personal communication, W. B. CRITCHFIELD, Institute of Forest Genetics, Placerville, California, 1970.

³⁾ A 1961 collection organized by Prof. J. W. WRIGHT, Michigan State University, East Lansing.

The study reported here demonstrates that the range of white fir can be broken into at least four geographic Groups, based upon certain characteristics measured on seedlings growing in a common garden at Placerville, California. However, other characteristics had clinal patterns of variation throughout the sampling range. This study also verifies that there are large geographic areas where trees are intermediate between *A. concolor* and *A. grandis*. Both common-garden and field data indicate that these populations could be fairly stable hybrid swarms between white and grand fir.

Seed Collections

In the autumn of 1962, white fir had a heavy cone crop in the western part of its range, but few cones in the east. Wind-pollinated cones were obtained from 35 natural stands in the western part of the species range and from 8 scattered stands³⁾ in the eastern part of the range (Figure 1). Most stands were represented by seed from 10 or more randomly chosen trees. The seeds were stratified for 90 days in moist sand.

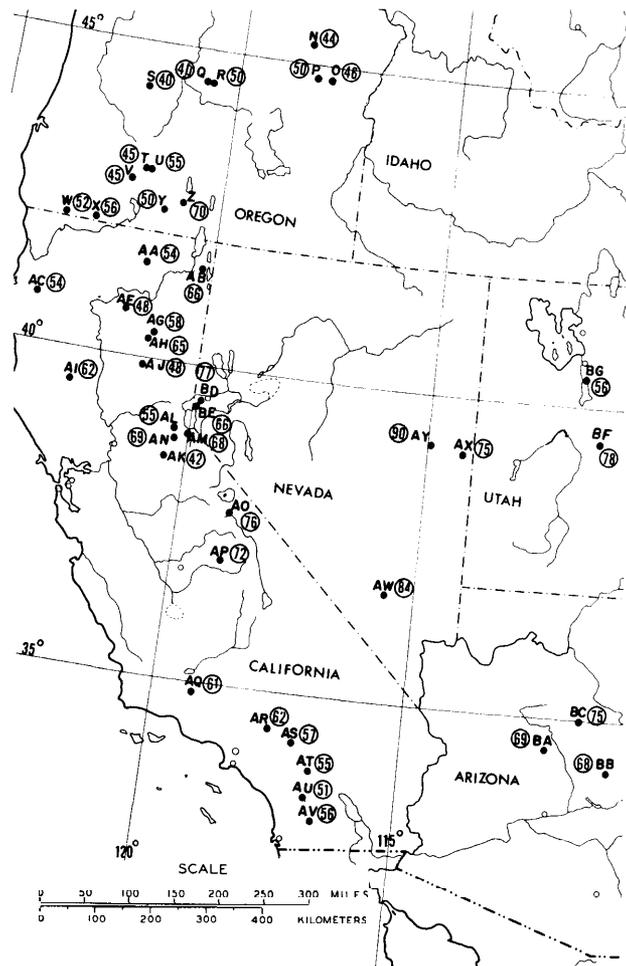


Figure 1. — Letters identify the geographic location of areas where viable seed was collected. Numbers within the circles indicate the elevation of the collection in hundreds of feet.

Nursery Design and Characteristics Analyzed

In early May 1963, part of each collection was broadcast-sown into two rows in each of two nursery beds at the Institute of Forest Genetics, Placerville, California. (Sufficient seed was sown in additional beds for later out-planting at five locations in northern California.) In each row, five newly-germinated seedlings, spaced at approximately equal intervals, were designated for subsequent measurement. Of the many characteristics measured during the first two years, 13 were sufficiently variable and were considered sufficiently independent of each other to be included in the analyses reported below (see Table 1 for list of characteristics). All 13 characteristics were statistically significant at the 1% level for the "between population samples" component of the analyses of variance performed. Descriptions of the procedure for designating seedlings to be measured, of the methods used in obtaining the measurements, and the model for the analysis of variance, are given in HAMRICK (1966⁴).

Comparing white fir to other conifers in similar experiments at Placerville and elsewhere, white fir proves to be a highly variable species, both locally and across the species range. Of the 13 characteristics analyzed, the most variable within single population samples were *lateral bud number* (characteristic 8), *growth of epicotyl* (characteristic 11), *needle-tip shape* (3), *adaxial stomata rows* (2), and *second-year height* (13), with coefficients of variation⁵ of 0.745 to 0.390, respectively. The least variable was *needle width* (4) with a coefficient of variation of 0.070. The relative variation between population samples was calculated by dividing the between-population-sample component of variance by the within-row component of variance. The characteristics *adaxial stomata rows* (2) and *needle-tip shape* (3) had ratios of 1.95 and 0.89, indicating a high degree of variability between populations. Ratios for the other 11 characteristics were between 0.51 and 0.32.

Clines, Ecotypes, and Population Architecture

The following proposals were stimulated by our observations and data in this study. They are offered as hypotheses, and as such are in no way proved by the data which suggested them. Additional work on three other species is in progress.

Ecotypic and clinal patterns of variation have frequently been discussed as if they were properties of species, or of a group of populations within a species. It is thereby implied that where ecotypic variation is demonstrated, all characteristics of those populations will vary ecotypically (if they vary in other than random fashion). After all, genes affecting all characteristics of a plant are transported together in a pollen grain or in a seed. But genetic recombination occurs, and subsequent selection among the recombinants is usually stronger for some characteristics than for others. Thus, among populations which are exchanging genes, recombination and differential selection may allow different patterns of non-random variation to develop for different characteristics of the same plants.

Both ecotypic and clinal patterns of variation simultaneously occur in the same populations of white fir. This became apparent when population means for each character-

istic were plotted against latitude (HAMRICK, 1966⁴). The characteristics *needle-tip shape* and *adaxial stomata rows* did not develop strong patterns of between-population variation within each of three regions (central Oregon and northwestern California — Group I, below; south-central Oregon and central and northeastern California — Group II, below; and southern California — part of Group III, below). Major discontinuities in these two characteristics did occur between Groups I and II, and between Groups II and III, providing a good case of ecotypic variation. The characteristics *needle length*, *resin-duct diameter*, and *cytledon number* also varied ecotypically in the vicinity of the Group I-II border, but showed a clinal pattern of variation across the Group II-III border. The characteristics *needle width*, *maximum hypoderm*, *hypocotyl length*, *days until germination*, *epicotyl growth*, *days to growth termination*, and *second-year height* all varied clinally along the entire western part of the species range, with no apparent discontinuities at the Groups I-II and II-III borders. Figure 2 illustrates these two variation patterns for *adaxial stomata rows* and *second-year height*, as expressed by exactly the same seedlings growing in the common-garden experiment at Placerville.

Since white fir frequently grows over an elevational range of 2000 feet or more within a local region, the elevational as well as latitudinal dimension must be considered when analyzing patterns of variation. When the

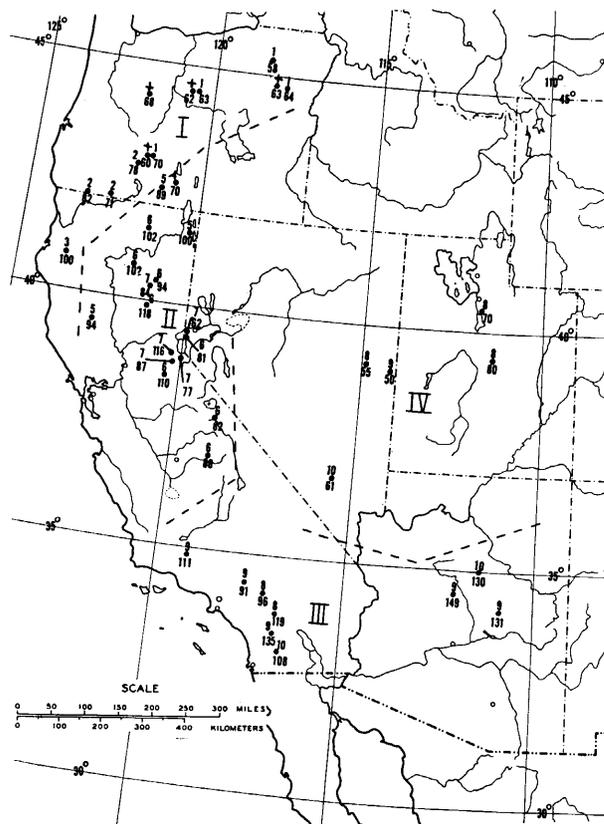
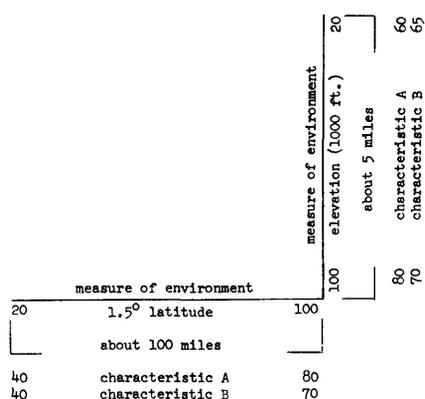


Figure 2. — Mean values by collection for the characteristics *adaxial stomata rows*¹⁾ (above) and *second-year height* (below, in mm.). *Adaxial stomata rows* has an ecotypic pattern of variation, while *second-year height* has a clinal pattern of variation. *Second-year height* is also more affected by elevation of the population. Roman numerals indicate the four Groups, based on results reported in Table 2. — Dashed lines indicate the borders between the Groups.

¹⁾ The + symbol indicates presence of stomata on the upper needle surface occupying short rows, generally near the needle tip.

⁴⁾ M. S. Thesis, University of California, Berkeley. "Geographic variation in white fir". 143 p. (1966).

⁵⁾ This coefficient of variation was calculated by dividing the within-row standard deviation by the overall mean of the characteristic.



Ratio: $\frac{\text{change with elevation}}{\text{change with latitude}}$ char. A = $\frac{20}{40} = 0.50$; char. B = $\frac{5}{30} = 0.17$

Figure 3. — Variation Patterns in Two Hypothetical Characteristics. Selection in the different environments acts much more strongly on variation in characteristic A than it does on variation in characteristic B. The environment changes 80 units in each dimension from the common point in the lower right of the diagram.

U. S. Forest Service uses non-local seed for reforestation, seed origin and planting site are matched by taking lower-elevation seed from a higher latitude, or higher-elevation seed from a lower latitude, according to the relationship: 1000 feet of elevation equals 1.5 degrees of latitude (HOPKINS, 1938). If this "rule of thumb" is correct, a native tree will resemble native trees 1000 feet lower at 1.5 degrees greater latitude more than it resembles local native trees growing 1000 feet lower at its own latitude. But the geographic distance associated with a 1000-foot difference in elevation in a local region is much shorter than the nearly 100 miles represented by a 1.5 degree difference in latitude. (See Figure 3 as an aid in visualizing the concepts discussed here.)

Selection is constantly adapting a local population to its environment against various disruptive forces, including immigration of genes adapted to another environment. Such immigrants are much more likely to come from a local population differing 1000 feet in elevation than from a

population at the same elevation 1.5 degrees latitude distant. As stated above, genes affecting all characteristics will immigrate together in the seed or pollen grain. But selection will operate on their various combinations such that differences in some characteristics may be maintained over short distances, and possible differences in others may be swamped by migration. If selection cannot maintain differences in the face of local migration, a native tree will resemble the local trees 1000 feet lower more than it resembles trees 1.5 degrees latitude distant (at any elevation).

Of the 13 characteristics analyzed, the variation in 12 of them was correlated with latitude at the 1% level of significance (Table 1). If local differences between populations at different elevations were maintained against migration, the correlation coefficient of the characteristic with latitude should be increased by properly adjusting the latitude for elevation. Therefore, exactly the same data were analyzed by correlating population means with latitude adjusted by the "1.5 degrees = 1000 feet" rule. If local variation with elevation is random, such an adjustment of latitude for elevation would decrease the correlation.

In the calculation of the two correlation coefficients (with adjusted and unadjusted latitude) for each characteristic, the dependent variables were identical, and the independent variables (adjusted and unadjusted latitude) were related. Thus, the usual statistical test to compare correlation coefficients is inappropriate. Furthermore, we are not interested in whether the two correlation coefficients are different (changing the values of the latitudes is very unlikely to keep them the same), but we wish to have some confidence in the sign of the difference. We therefore applied an approximate test to determine the likelihood that a change in correlation coefficient is due to chance, and accepted the 50% level of probability as indicating the sign of the change is likely to be correct (Table 1).

It is clear that the adjustment of latitude for elevation did not produce the same result for all characteristics. The absolute values of the correlation coefficients of three characteristics increased, five decreased, and five changed relatively little. Thus, non-random variation with eleva-

Table 1. — Characteristics Analysed, and their Correlation with Latitude and Adjusted Latitude.

Characteristic	Correlation With		P ²⁾	Sign of Change ³⁾
	Latitude	Adjusted Latitude ¹⁾		
1. Needle Length	— .52**	— .51**	.93	0
2. Rows of Stomata on Upper (adaxial) Surface of Needle	— .90**	— .67**	<.01	—
3. Needle-Tip Shape	+ .82**	+ .72**	.12	—
4. Needle Width	— .69**	— .64**	.58	0
5. Diameter of Largest Resin Duct	— .71**	— .53**	.06	—
6. Maximum Hypoderm Layer	— .82**	— .66**	.02	—
7. Cotyledon Number	— .84**	— .84**	1.00	0
8. Lateral Bud Number	— .23N.S.	— .22N.S.	.95	0
9. Hypocotyl Length	— .58**	— .44**	.15	—
10. Days Until Germination	+ .69**	+ .81**	.10	+
11. Growth of Epicotyl in First Year	— .46**	— .61**	.21	+
12. Days Until Growth Termination	— .45**	— .66**	.06	+
13. Second Year Height	— .78**	— .74**	.62	0

** Significant at 1% level N.S. Non-significant
(1.5) (elevation in feet)

¹⁾ Adjusted latitude = degrees latitude + $\frac{\text{elevation}}{1000}$

²⁾ The approximate statistical likelihood such a change in the correlation coefficient is due to chance alone.

³⁾ A plus or minus indicates the absolute value of the correlation was increased or decreased, respectively, and a zero indicates the change was too small to have confidence in its sign.

Table 3. — Group Means, and Ranges of Population-sample Means.

Group Characteristic	I		II		III		IV	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
1. <i>Needle Length (mm)</i>	20—25	22.1	22—33	26.6	22—32	27.5	18—26	22.8
2. <i>Rows of Stomata on Upper (adaxial) Surface</i>	0.4—3.8	1.4	5.0—7.3	6.2	7.8—9.6	9.1	8.0—10.4	8.9
3. <i>Needle Tip Shape¹⁾</i>	2.8—4.2	3.6	1.2—2.9	2.0	1.0—1.6	1.1	1.1—2.6	1.6
4. <i>Needle Width (units, 55 units = 1 mm)</i>	79—90	82.3	78—92	85.8	83—94	88.3	80—83	81.9
5. <i>Diameter of Largest Resin Duct (units, 55 units = 1 mm)</i>	3.7—4.4	4.1	4.1—5.0	4.6	4.8—6.2	5.4	5.6—6.8	6.0
6. <i>Maximum Hypoderm Layer</i>	1.4—2.0	1.7	1.8—2.2	2.0	2.0—2.6	2.3	1.8—2.0	2.0
7. <i>Cotyledon Number</i>	5.6—6.6	6.0	6.5—7.8	7.0	7.2—8.0	7.6	6.4—7.2	6.7
8. <i>Lateral Bud Number</i>	0.6—2.8	1.9	1.7—6.6	3.0	0.7—6.4	2.7	0.4—1.0	0.8
9. <i>Hypocotyl Length (mm)</i>	14—23	17.9	16—23	19.6	18—26	21.1	14—19	15.7
10. <i>Days Until Germination</i>	21—28	23.8	18—24	20.3	14—24	17.1	14—18	16.5
11. <i>Growth of Epicotyl in First Year (mm)</i>	4—18	9.7	6—26	13.1	10—28	17.4	2—9	5.6
12. <i>Days Until Growth Termination</i>	53—88	73.0	59—108	79.8	65—113	97.2	49—80	63.0
13. <i>Second-Year Height (mm)</i>	58—100	70.0	62—118	92.7	91—149	119.0	50—80	63.0

Number of populations sampled: I = 13, II = 16, III = 9, and IV = 5.

Italics indicate characteristics particularly useful in delineating the Groups.

¹⁾ 1.0 = pointed; 3.0 = blunt; 5.0 = deeply notched.

continuities may be more a reflection of discontinuous sampling and distribution than they are of large and abrupt changes in the characteristics. Group means and the range of population means within each group for the 13 characteristics studied are presented in *Table 3*.

There are several possible alternative taxonomic interpretations of the results described above. These range from the proposal that three species of fir (*A. concolor*, *A. lowiana*, *A. grandis*) occupy different parts of western North America and interbreed along areas of contact, to the proposal that the observed data are indicative of one large complex species with several races or varieties.

MÜLLER (1939) suggested that many of the intermediate populations are a race of *A. grandis*. Furthermore, he stated that much of the intermediate variation is caused by environmental conditions. This common-garden study has demonstrated that much of the variation is genetic. We feel that it is unlikely that *A. grandis* has evolved a race intermediate between itself and white fir without the contribution of white fir genes. MÜLLER'S conclusion is especially suspect in light of the hybrids between *A. grandis* and *A. concolor* var. *lowiana* produced at Placerville and Hørsholm.

Speculation that *A. concolor* and *A. grandis* are all part of a large species complex has more merit. The very similar morphological and chemical characteristics of these taxa (ZAVARIN and SNAJBERK, 1965), as well as the results of controlled crosses, indicate that they have evolved from the same ancestral taxon. However, the discontinuous patterns of variation observed between Groups I and II indicate there may have been separate evolution occurring at one time between the taxa now called *A. concolor* and *A. grandis*. Furthermore, within Group I the coefficients of variation for all needle characteristics (characteristics 1—6, *Table 1*) averaged 45%. The two most variable characteristics were *adaxial stomata rows* (with a coefficient of variation [C. V.] of 175%) and *needle-tip shape* (C. V. of 48%). Group II, by contrast, had an average C. V. of 22%, with *adaxial stomata rows* having a C. V. of only 36% and *needle-tip shape* a C. V. of 41%. The greater amount of

variation for these characteristics in Group I as compared to Group II indicates that Group I populations may have resulted from the formation of a large hybrid swarm following contact of *A. concolor* var. *lowiana* with *A. grandis* in the recent geologic past.

Foliage samples were collected from seedlings in natural stands throughout Oregon and northwestern California in order to see if the pattern of variability observed in the nursery occurs in the field. Additional collections were made of "good" white fir in the central Sierra Nevada Mountains of California and of "good" grand fir along the California coast. The results are presented in *Figure 4* and in *Table 4* in the form of hybrid index values based on measurements of *adaxial stomata rows* and *needle-tip shape*. The populations with mean hybrid index values intermediate between grand fir and white fir have some individual trees which resemble white fir and others which resemble grand fir in these two characteristics. This does not occur in the "good" species collections (A & I, *Figure 4* and *Table 4*). Since the field collections were more extensive, *Figure 4* presents a better representation of the distribution of intermediate populations than does *Figure 2*.

We propose the following speculation on the evolution of this species complex (*Figure 5*). Over geological time the populations now classified as *A. grandis* evolved from a common ancestral taxon with *A. concolor* into a morphologically distinguishable species to the north. Here *A. grandis* became adapted to a moist cool climate, and now occurs mostly as scattered trees in generally dense coniferous forests. The southern California and eastern populations of *A. concolor* evolved different characteristics from the central California populations. The southern California — Arizona Group and the Rocky Mountain Group can be called *A. concolor* var. *concolor* to distinguish them from the Sierra Nevada — northeast California trees, which most properly should be called *A. concolor* var. *lowiana*. These two varieties became adapted to drier warmer climates than did *A. grandis*, and they often make up a major proportion of stands in these areas. In more recent times, the ranges of *A. grandis* and *A. concolor* var. *lowiana* have

Summary

Seedlings from 43 geographic locations within the range of white fir (*Abies concolor*) were grown in a nursery at Placerville, California and were measured or scored for thirteen morphological and growth characteristics.

The results indicate that white fir is a highly variable species, and that the variation is significantly correlated with latitude of seed origin for 12 of the 13 characteristics. Three major differences in variation pattern were observed: (1) Some characteristics varied ecotypically; (2) Some characteristics, particularly those associated with growth, varied clinally relative to both elevation and latitude; (3) Others, particularly those associated with morphology of the seedlings, varied clinally with latitude, but were fairly uniform over a range of elevations at a given latitude. It is postulated that characteristics which vary significantly over local differences in elevation have high selection pressures acting upon them. Those characteristics with little or no variation associated with elevation either are not selected by environmental factors which vary with elevation, or such selection is insufficient to offset migration.

It is concluded from needle characteristics of seedlings in the nursery, and also from measurements made on needles collected in the field, that *Abies concolor* has at least four major morphological divisions. Those we investigated are provisionally designated as: (I) Central Oregon and northwestern California; (II) South-central Oregon, and central and northeastern California; (III) Southern California and Arizona; (IV) Eastern Nevada and Western Utah. The data also suggest that the Group I populations have resulted from the hybridization and introgression of the Group II populations with *Abies grandis*.

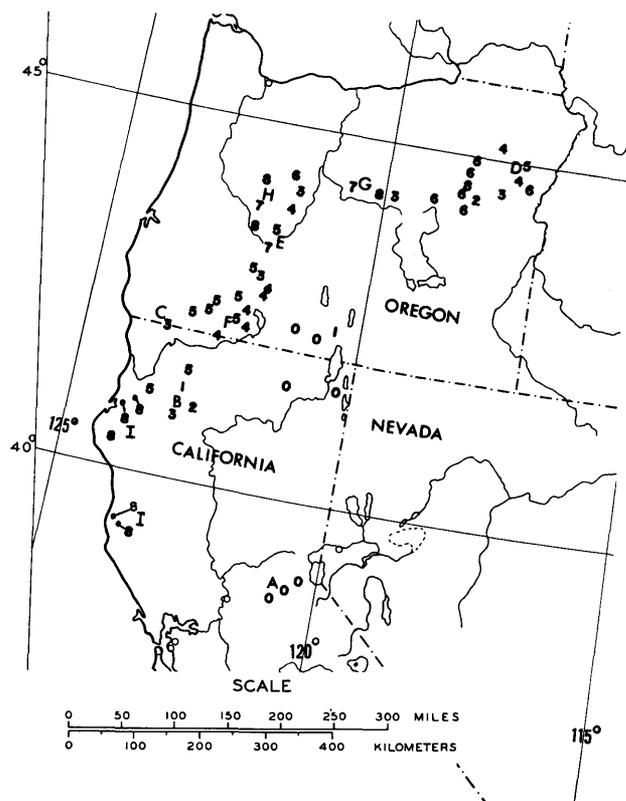


Figure 4. — Average hybrid index values of field collections at their geographic locations. 0 = *A. concolor*, 8 = *A. grandis*. Letters designate location of transects presented in Table 4.

come into contact, and intermediate populations have developed through hybridization and subsequent crossing among the hybrid derivatives and trees of both species. These intermediate populations, which make up a major proportion of their forest stands, are found in the drier warmer parts of Oregon and northwestern California.

Estimates of the relative contribution of genes by *A. grandis* and *A. concolor* var. *lowiana* to these intermediate populations, and more exact correlations of morphology with ecological conditions, await further experimentation.

Acknowledgements

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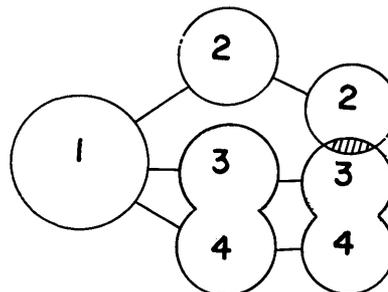


Figure 5. — A possible evolutionary relationship: The original *Abies* population evolved into the taxa now called *A. concolor* and *A. grandis*, which have more recently begun to interbreed. 1. *Abies* sp.; 2. *A. grandis*; 3. *A. concolor* var. *lowiana*; 4. *A. concolor* var. *concolor*. Crosshatch indicates intermediate hybrid derivatives.

Table 4. — Hybrid Index Distributions on Eight Transects.

Transect	Rows of Adaxial Stomata	Needle-Tip Shape	Hybrid Index Class								Average Transect Index		
			0	1	2	3	4	5	6	7		8	
A. Eldorado Co., Calif.	8.43	2.10	23	7	—	—	—	—	—	—	—	—	0.23
B. Sawyers Bar Rd., Calif.	5.42	2.94	5	2	6	2	1	2	1	—	—	—	2.05
C. Cave Jct., Oregon	5.15	3.50	1	—	3	—	3	2	1	1	—	—	3.73
D. Antony Lakes, Oregon	1.38	3.12	1	1	—	3	—	—	3	—	7	—	4.94
E. Odell Butte, Oregon	2.11	3.29	2	—	1	—	2	1	3	2	3	—	5.07
F. Lake of the Woods, Oregon	2.38	3.76	—	—	1	3	1	3	5	3	3	—	5.53
G. Prineville, Oregon	1.87	3.96	—	2	—	2	3	2	2	12	12	—	6.04
H. Oakridge, Oregon	0.00	3.61	—	—	—	—	3	1	2	8	8	—	6.64
I. California Coast	0.00	4.36	—	—	—	—	—	—	1	2	19	—	7.82

Means of the two characteristics for each transect, and the distribution of trees by hybrid index values is presented for 9 elevational transects. Each transect was three or more field collections of at least three trees each along a local elevational gradient. Collections were made at intervals of roughly 500 feet elevation. See Figure 4 for location of the transects. A hybrid index value of 0 is typical of Sierra *A. concolor*, and 8 is typical of coastal *A. grandis*.

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Crossing Among Loblolly Pines Indigenous to Different Areas as a Means of Genetic Improvement

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Introduction

Of the several plant breeding procedures that can be used to improve outcrossing species, the one currently most employed in first generation selection of loblolly pine (*Pinus taeda* L.) is mass selection within locally adapted stock. This breeding method is applicable because there are large amounts of between-tree and within-population variability of a genetic nature.

Economically important differences also exist among geographic races within this species. WELLS and WAKELEY (1966) reported results for loblolly pine that indicated there may be benefits from using non-local seed sources in certain areas. Among their results were: (1) trees of western origin and from one far northeast area were consistently least infected with fusiform rust; (2) in practically all plantations, trees of western origin survived best; (3) in all but the coldest location, the trees from coastal areas grew fastest.

These and similar results indicate that hybridization among trees indigenous to different areas might be an additional breeding method for loblolly pine. First generation among-area crosses (wide crosses) conceivably could combine parental characteristics thus producing new genotypes having superior growth performance, drought or cold hardiness, or disease resistance. Likewise, new genetic combinations which would be useful in later breeding cycles could be expected to be created.

The results reported here are from a juvenile assessment of loblolly pine crosses among seed orchard selections indigenous to three different areas of the Southern United States: the Coastal Plain, the Piedmont, and west of the Mississippi River.

In a juvenile analysis, germination characteristics of sound seed were evaluated to see if there were any indications of genetic incompatibilities resulting from wide crossing. A measure of first year height growth hybrid vigor was obtained by evaluating a control cross-pollinated family as a percent of the wind-pollinated families collected from the parental clones. Duration and distribution of growth were assessed to see if hybrids of North Carolina sources with more southern sources would have a period of physiological activity that would allow them to be grown at latitudes more northern than the origin of their most southern parent.

Materials and Methods

Parental Population

Control pollinations for the wide crosses were made according to mating design II of COMSTOCK and ROBINSON (1948). Each of several seed orchard clones used as female parents were pollinated by a set of clones used as male parents. The geographic origin of the ortets is shown in *Figure 1*. Four female parents of Piedmont origin were crossed with 5 males from the Piedmont, ten males from the Coastal Plain, and 4 males of Western origin. Four female parents of Coastal Plain origin were crossed with



FEMALE PARENTS	Source Number	Number of Clones
Coastal Plain Source	8	4
Piedmont Source	6	4
MALE PARENTS		
Coastal Plain Sources	11	4
	8	4
	10	2
Piedmont Sources	3	2
	5	4
	1	2
	12	3
Western Source	13	4

Figure 1. — Southern states showing origin of the trees used as female and male parents. The dark lines delineate the areas within which the ortets were selected.