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Variation and Selection in Western Montane Species II. Variation within and between Populations of White Fir on an Elevational Transect

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Summary. Four populations of *Abies concolor*, white fir, were sampled along an elevational transect in the central Sierra Nevada mountains of California. This paper is based on data taken during the first two years' growth in a nearby nursery at Placerville, California. Ten of the thirteen growth, size, and needle morphological characteristics had significant differences between population samples, while eleven characteristics had significant differences between open-pollinated families within the population samples. High-elevation population samples were smaller in size and needle measurements, had fewer adaxial stomatal rows, blunter needle tips, and a shorter growing season. Most characteristic values were distributed ecotypically between the two lower- and the two higher-elevation population samples. Analyses of the patterns of variation demonstrated that characteristics of size and growth showed greater differentiation between population samples than did characteristics of needle morphology. It was concluded that the differences between characteristic patterns were caused by the more intense selection pressures acting upon the characteristics of size and growth. No consistent differences were discovered between these population samples in terms of total amounts of within-population genetic variation. The failure to find differences in intra-population variation may be due to the high rates of migration that probably exist within such a transect, and the fact that none of the populations included in this study are truly marginal. There were large differences between characteristics for total within-population variation; a positive but non-significant correlation was found between high coefficients of variation and those characteristics with much differentiation between populations. It is postulated that the maintenance of this intra-population variation was caused by microhabitat adaptations and gene flow. Evidence for increased genetic variation within open-pollinated families due to pollen immigration is presented, and its implications discussed.

Introduction

White fir (*Abies concolor* Gordon and Glend. Lindl.) is one of the most common and geographically widespread montane tree species in the western United States. Its range extends from central Oregon and northern California south along the Sierra Nevada mountains into southern California and northern Mexico, east into the mountains of Arizona and New Mexico and north throughout the Rocky Mountains into southern Idaho (Fowells 1965, Griffin and Critchfield 1972). It is also a common element of the floras of many of the mountain ranges of the Great Basin region of Nevada and Utah (Critchfield and Allenbaugh 1969). Throughout its geographic range, *A. concolor* has a wide elevational range, with the greatest range occurring in the mountains of central and southern California, e.g. its range in the Sierra Nevada is between 3000 and 8000 feet.

In a recent paper, Hamrick and Libby (1972) demonstrated that white fir is a highly variable species whose patterns of genetic variation in a common garden are often correlated with the latitude and elevation of the collection site. In this earlier paper we divided the western part of the range of white fir into four morphologically distinguishable geographic regions: central Oregon and northwestern California; south-central Oregon, northeastern California and the Sierra Nevada of California; southern California and Arizona; eastern Nevada and western Utah. We also demonstrated that within each of these four regions there were smaller, but important differences between populations for most of the characteristics measured. Some of this within-region variation was correlated with the latitude of origin. However, differences in elevation between populations within a region seemed to account for most of the intra-regional variation. Furthermore, characteristics concerned with growth were influenced to a greater degree by changes in the elevation of the populations than were characteristics of needle morphology. A similar pattern of variation has been described by Conkle et al. (1966) for the response of these seedlings to winter injury.

The present paper reports the results of a common-garden nursery study which measured the distribution of genetic variation for 13 quantitative characteristics within and between four populations of white fir from an elevational transect of the central Sierra Nevada of California (Region II, Hamrick and Libby 1972). Data from the first two years of growth in the nursery indicate that, although the populations are significantly different for most characteristics, characteristics of growth and size have much greater differentiation along this transect than do characteristics of needle morphology. The conclusion reached is that those characteristics with greater variation between populations have more intense selection pressures acting upon them.

Materials and Methods

During the fall of 1962, four stands of white fir located along an elevational transect of the Sierra Nevada of California (Eldorado Co.) were selected for study. (See Table 1 for the geographic location and elevation of these stands.) Cones were collected from 10 trees in each stand by the staff of the Institute of Forest Genetics (IFG), Placerville, California. The trees were no closer to each other than 100 meters, and no attempt was made to select for any particular characteristics. It was an excellent seed year and thus the ideal of a scattered random sample was obtained. Sub-samples of the open-pollinated families were bulked for each population sample to provide collections (AK, AL, AM, AN) which were included in the geographic variation study (Hamrick and Libby 1972). The remainder of the seed were kept separate by seed parent, were assigned an IFG lot number, and were stratified for 90 days in moist sand for use in the present study.

In the spring of 1963, the seeds were sown into the IFG nursery. In this experiment, each open-pollinated family occurred in two broadcast-sown rows located randomly within a single nursery bed. Five spots were systematically located within each row. Seedlings which germinated nearest those spots were designated the experimental seedlings. Thus, with this design each open-pollinated family was represented by 10 randomly-chosen seedlings on which all nursery measurements were made. Additional seeds of each family were sown into other nursery beds to provide seedlings for planting into experimental plantations.

Thirteen characteristics were measured during the first two years of nursery growth (Table 1). These included characteristics of needle morphology, and size and growth characteristics measured at various developmental stages. (See Hamrick 1966 for methods of measurement.)

The analyses of variance used to analyse the variation of all nursery measurements contained four sources of variation: (1) between populations, (2) between open-pollinated families within a population, (3) between nursery rows of an open-pollinated family, (4) within nursery rows. This was a nested design in which source of variation (4) tested source of variation (3), source of variation (3) tested (2), and (2) tested (1).

At the end of the second season of growth (1964), all available seddlings from each family were lifted from the nursery beds and were either placed into transplant beds at IFG or were planted directly into experimental plantations. These plantations were established in five locations in California during the two succeeding years (1965 and 1966) and will be the subject of subsequent papers.

Results

Population means and standard deviations are given in Table 1 for each of the 13 nursery characteristics measured. The analyses of variance demonstrated that the between wind-pollinated families component of variation was significant at the 1% level for 11 of the 13 characteristics (only characteristics (5) resin duct diameter and (6) hypoderm thickness were nonsignificant) whereas 10 of the 13 characteristics were significant at the 1% level for the between-population component (characteristics (5) resin duct diameter, (7) cotyledon number and (10) days until germination were nonsignificant). An examination of Table 1 indicates that the two collections from the lower elevations (AK and AL) were similar to each other for all 13 characteristics. Collections AM and AN from the higher elevations also had similar means. However, AK and AL had quite different means from AM and AN for a number of characteristics. Generally the results indicate the plants with low-elevation origins have longer, wider and more pointed needles which have somewhat greater numbers of stomatal rows on their adaxial surface. Furthermore, during the first year of growth the low-elevation seedlings had a growing period which averaged approximately 30 days longer than that of the high-elevation seedlings. The longer growth period coupled with a more rapid growth rate produced an epicotyl elongation in the low-elevation plants approximately three times (25 mm vs 8 mm) that of the high-elevation plants. The differences in growth rate carried over into the second growing season, for at the end of the second year the low-elevation populations averaged about 60 mm (2 1/3 inches) taller than the high-elevation populations. In fact, although there was a significant amount of variation between families within a population, there was virtually no overlap of the family means between seedlings from the high- and the low-elevation sites for second-year height (AK, 107 to 164 mm; AL, 100 to 205 mm; AN, 61 to 95 mm; AM, 52 to 101 mm).

From the analyses of variance, estimates of the variance due to the within-family, the between-families-within-populations, and between-population sources of variation have been obtained (Table 2, note that the variance between rows of the same family [source 3 above] is not included). Ratios were calculated which demonstrate the relative amounts of variation contributed by each source to the total variation. On the average, 80% of the total variation for the transect is found within the populations $\left(\sigma_w^2/V_G + \sigma_f^2/V_G\right.$, Table 2). Furthermore, it can be seen that at least 40% and usually more (average 69%) of the total variation and 70% or more (average 86%) of the within-population variation is due to the within-family variance. The within-family variance estimate is, however, confounded by the local micro-environmental differences found within a row. The environment of the nursery beds was generally uniform with common soil properties, watering regimen, and sunlight throughout. However, one must always expect some microsite va-

Table 1. Population locations, means and standard deviations for 13 characteristics measured during nursery growth. Population means include data from 100 individuals. Standard deviations were calculated from the sum of the within-family plus the between-family estimates of genetic variance for each population. All characteristics are actual counts or are measured in mm except for characteristics (4) and (5) which were measured in units where 55 units = 1 mm

		Population							
		AK[1]		AL[1]		AN[1]		AM[2]	
	Latitude	38°33'		38°54'		38°48'		38°51'	
	Longitude	120°26'		120°14'		120°14'		120°00'	
	Elevation	4200'(1280 M)		5500'(1676 M)		6900'(2103 M)		6800'(2073 M)	
	Nearest Town	Omo Ranch, Ca.		Kyburz, Ca.		Kyburz, Ca.		Meyers, Ca.	
	Characteristics	mean	sd	mean	sd	mean	sd	mean	sd
1.	Needle Length	34.05	5.92	32.72	5.46	24.85	4.44	26.57	3.81
2.	# Rows of Stomata on Upper (adaxial) Surface of Needle	7.19	1.84	7.26	2.76	6.26	2.05	6.95	1.44
3.	Needle-Tip Shape[3]	1.25	0.47	1.49	0.77	2.14	1.28	2.20	1.07
4.	Needle Width	89.26	10.14	91.49	11.60	80.53	7.98	82.81	8.39
5.	Diameter of Largest Resin Duct	5.10	1.05	4.92	1.29	4.75	1.10	4.81	0.93
6.	Maximum Hypoderm Layer	2.14	0.36	2.09	0.32	2.01	0.10	2.01	0.10
7.	Cotyledon #	7.43	0.75	7.24	0.76	6.97	0.77	7.36	0.83
8.	Lateral Bud # (end of 1st year)	5.78	3.55	6.30	3.53	2.24	1.81	2.21	1.46
9.	Hypocotyl Length	20.06	4.09	18.96	4.85	15.22	2.47	16.93	4.50
10.	Days Until Germination	19.30	3.66	18.38	4.46	21.24	7.98	21.51	4.80
11.	Growth of Epicotyl in First Year	27.34	12.78	24.12	13.75	8.10	5.24	8.35	5.04
12.	Days Until Growth Termination	101.44	29.94	96.79	24.79	70.49	31.15	66.32	29.60
13.	Second Year Height	129.89	52.96	136.36	59.65	75.92	30.90	76.56	26.68

1 west side of Sierra crest

2 east side of Sierra crest

3 1 pointed
3 blunt
5 deeply notched

riation in these environmental factors. What microsite variation that did exist would be expected to be greatest between nursery rows because of the pattern of watering. Some within-row microsite variation did exist at the margins of the beds where wooden rails were embedded into the soil. However, since the phenomena had been previously observed, the sampling spots were established internally away from the rails. Thus, the section of the rows from which data were collected should have been quite uniform. The usual procedure used to obtain an estimate of the within-family genetic variation in such a situation is to assume an additive model of inheritance and to estimate the within-family genetic variance from the between-family variance on the basis of genetic relationships. In the case of open-pollinated families the degree of relationship between progeny is taken as being somewhere between $\frac{1}{4}$(half-sibs) and $\frac{1}{2}$ (full-sibs) because of the possibility of selfing and kin mating. A genetic relationship of 1/3 is the degree of relationship usually used in such situations, and thus the expected within-family genetic variance would equal 2 times the between-family variance estimate. However, this calculation assumes that the variance of the pollen gene pool is equal to that estimated from the seed trees, i.e. that there is no gene flow between populations. Such an assumption is questionable in a wind-pollinated tree such as white fir. Although the contribution of pollen flow is unknown, its effect would be to raise the within-family genetic variation. Since the available evidence suggests that the environmental effect may be relatively small (the between-row source of environmental variation, measuring much larger microsite environmental differences, was significant at the 5% level for only four of the 13 characteristics) -- it is reasonable to assume that much or even most of the within-family variation is due to genetic differences beween the progeny. The ratio σ^2_w/σ^2_f is therefore of interest, with ratios much over 2.0 either indicating a large microenvironmental contribution to the variation or additional genetic variation being produced via pollen immigration (Table 2). Note that only the ratio for characteristic 10, germination time, is less than 3.0, and that eleven of the ratios are

Table 2. Variance estimates and ratios of selected variances to the between-family variance, the within-population variance and the total variance. Where: σ_w^2 = an estimate of the variation between wind-pollinated seedlings of a single tree (this consists of genetic differences between such seedlings, at least half-sibs, plus variation due to the local nursery microenvironment); σ_f^2 = an estimate of the genetic variation between wind-pollinated families of the same population; σ_p^2 = an estimate of the genetic variation between the four populations along the Eldorado transect; V_G = total variance = $\sigma_w^2 + \sigma_f^2 + \sigma_p^2$; V_S = total within-population variance = $\sigma_w^2 + \sigma_f^2$. See Table 1 for a description of the characteristics indicated by number below

Characteristic	Variance estimates			Ratios						
	σ_w^2	σ_f^2	σ_p^2	$\frac{\sigma_w^2}{V_G}$	$\frac{\sigma_w^2}{V_S}$	$\frac{\sigma_f^2}{V_G}$	$\frac{\sigma_w^2}{\sigma_f^2}$	$\frac{\sigma_p^2}{\sigma_f^2}$	$\frac{\sigma_p^2}{V_G}$	$\frac{\sigma_p^2}{V_S}$
1	21.89	4.63	19.63	.475	.825	.100	4.73	4.24	.425	.739
2	3.70	0.69	0.36	.779	.843	.145	5.36	0.52	.076	.082
3	0.81	0.13	0.20	.711	.862	.114	6.23	1.54	.175	.212
4	72.71	13.46	24.36	.658	.844	.121	5.40	1.82	.220	.282
5	1.28	0.02	0.00	.985	.985	.015	> 10.0	0.00	.000	.000
6	0.150	0.000	0.003	.980	1.000	.000	> 10.0	----	.020	.020
7	0.500	0.084	0.002	.853	.856	.143	5.95	0.02	.003	.003
8	5.29	1.63	4.30	.471	.764	.145	3.25	2.64	.383	.621
9	17.31	1.87	4.21	.740	.903	.080	9.26	2.25	.180	.220
10	22.81	9.55	1.05	.683	.705	.286	2.39	0.11	.031	.032
11	79.46	17.37	95.67	.413	.821	.090	4.57	5.51	.498	.992
12	666.43	96.84	302.73	.625	.873	.091	6.88	3.13	.284	.397
13	1663.76	329.73	1030.49	.550	.835	.109	5.05	3.12	.341	.517

larger than 4.5. Germination time probably has a large maternal effect and thus would be less influenced by the paternal contribution.

Ratios of the between-population variance to between-family variance $\left(\sigma_p^2/\sigma_f^2\right)$, the between-population variance to the within-population variance (σ_p^2/V_S) , and the between-population variance to total variance (σ_p^2/V_G) were calculated (Table 2) for each characteristic. These ratios are of interest for they indicate those characteristics whose patterns of genetic variation are most highly influenced by changes in environmental components that are in elevation. These three ratios provide roughly equivalent results and demonstrate that the characteristics can be grouped into four rather distinct ratio classes. correlated with changes in elevation. These three ratios provide roughly equivalent results and demonstrate that the characterstics can be grouped into four rather disctinct ratio classes. Those characteristics with the largest between-population/between-family ratios (>4.0) include (11) growth of the epicotyl during the first growing season and (1) needle length. Those characteristics with higher intermediate ratios (2.2-3.2) include (12) days to growth with lower-intermediate ratios (1.0-2.0) include (3) needle tip shape and (4) needle width. Characteristics with the lowest ratios (< 1.0) include (2) number of adaxial stomatal rows, (10) days until germination, (7) cotyledon number, (5) resin duct diameter, and (6) maximum hypoderm width. When considered as a whole, there is a striking dichotomy between these four groups of characteristics in regards to the type of characteristic in each. Growth and size characteristics predominate in the high or higher-intermediate ratio classes while needle morphological characteristics are generally in the lowest ratio classes.

Discussion

The patterns of variation described above are consistent with those of our earlier work (Hararick and Libby 1972). The high evaluation population samples (AM and AN) are quite different from the lower elevation population samples in a number of their characteristics. It is somewhat surprising to find populations AK and AL so similar in their characteristics, since there is more than a 1,000' difference between their elevations of origin. This suggests that the pattern of variation on the Eldorado transect is ecotypic and is reminiscent of the results of Clausen, Keck and Hiesey (1948). This pattern is even true of those characteristics which varied clinally throughout the geographic range of the species. An examination of climatic data for the region indicates that all the climatic factors one would think might be important are distributed clinally. However, weather data in such a mountainous area is at best sketchy in nature and some important climatic factors may in truth be distributed in a discontinuous fashion. Therefore, before conclusions can be made, more populations would need to be sampled at intermediate elevations and better climatic information should be obtained. Nevertheless, the trends demonstrated in this study correlate quite well with those trends described for populations distributed over a latitudinal gradient. In other words, the higher elevation populations (AM and AN) on the "Eldorado transect" have characteristics which are more similar to populations found at the lower elevations of higher latitudes than they are to the low elevation populations (AK and AL) located at approximately the same latitude. This pattern is not unexpected and has been noted for many other plant species.

The present results vary from those reported earlier for latitude in the relative amounts of change found between populations for the different characteristics. On the latitudinal gradients all characteristics showed considerable differentiation between geographical locations. However, on the Eldorado transect the relative proportion of the total variation contributed by the between-population component varies significantly between characteristics. Mechanisms which could influence patterns of variation between populations such as those described, are gene flow, selection, and genetic drift. However, gene flow should have an equal effect on all characteristics and genetic drift should be unimportant in natural populations as large as these. Furthermore, if drift were an important force, we would not expect to find the consistent ecotypic patterns illustrated by Table 1. Therefore the presence of such different responses between characteristics is undoubtedly produced by different intensities of natural selection acting upon the traits. This conclusion finds additional support when one examines those characteristics involved. The characteristics with high between-population to between-family variance ratios are characteristics which are components of size and growth, whereas those with low ratios are predominantly those concerned with needle morphology. The environmental factor most likely to be imposing such selection pressures is the growing period, which varies from approximately 150 days at 4,000 feet to approximately 70 days at 7,000 feet (note the correspondence of characteristic 12 [Table 1], growing period, with this environmental parameter). This is the same relationship we reported earlier based on 43 populations sampled at various geographic locations and elevations and analysed by regression and correlation (Hamrick and Libby 1972), i.e. that growth and size characteristics varied with both elevation and latitude whereas the characteristics of needle morphology varied mostly with latitude. Evidently the short-term adaptive importance of needle morphology is low, and the resulting selection pressures which act on needle morphology to produce the observed variation with latitude are not great enough to overcome the effects of the higher levels of gene flow that occur along the Eldorado transect.

That there are high levels of gene exchange between collection areas is demonstrated indirectly by the large amount of variation within an open-pollinated family relative to that between open-pollinated families within a population (Table 2). If the assumption re the relative unimportance (based on the measured between-row environmental effects) of local nursery microenvironmental effects is valid then much of the within-population variation that exceeds 2 × the between-family variance is due to gene flow between populations. Although it is impossible to measure the level of gene flow from the present data, the existence of high rates of gene flow between populations should not be surprising in the central Sierra Nevada. *A.concolor* is a common component of the California mixed conifer forest and occurs continuously throughout the 4,000 to 7,000 feet section of its elevational range. Furthermore, one can find quite different elevations within quite small horizontal distances and, although the prevailing winds are upslope (west to east), downslope (east to west) winds are common in the evenings. Thus, there should be considerable pollen mixing between stands. Barber and Jackson (1957) have shown similar high rates of migration between populations of animal-pollinated *Eucalyptus* species occurring on a similar elevational transect, as have Tigerstedt (1973), Koski (1970) and Silen (1962) in the wind-pollinated conifers, *Picea abies*, *Pinus silvestris*, and *Pseudotsuga menziesii*. With the possibility of such high migration rates, it should not be surprising to find characteristics with lower adaptive significance with less differentiation between popu-

Table 3. Coefficients of variation (%) for all characteristics. Each coefficient of variation is the ratio of $\sqrt{V_S}$ /mean. See Table 1 for a description of the characteristics indicated by number below.

Population	Characteristic													
	1	2	3	4	5	6	7	8	9	10	11	12	13	mean
AK	17.4	25.6	37.6	11.4	20.6	16.8	10.1	61.4	20.4	19.0	46.7	29.5	40.8	27.5
AL	16.7	38.0	51.7	12.7	26.2	15.3	10.5	56.0	24.3	25.6	57.0	25.6	43.5	31.0
AN	17.9	32.7	59.8	9.9	23.2	5.0	11.0	80.8	16.2	37.6	64.7	44.2	40.7	34.1
AM	14.3	20.7	48.6	10.1	19.3	5.0	11.3	66.1	26.6	22.3	60.4	44.6	34.8	29.5

lations. However, it should be stressed, as Ehrlich and Raven (1969) pointed out, that even with a situation where gene flow may be as high as it ever occurs in nature, that characteristics with high selection intensities acting upon them can differentiate to such an extent that there is virtually no overlap between the family means of the population samples.

A question which is often neglected in studies of geographic variation, is whether there are differences between the populations in terms of total amounts of genetic variation. Factors which are most likely to effect levels of genetic variation in large populations are selection intensities, gene flow and environmental heterogeneity within the area sampled. Increased selection intensities, reduced gene flow, and environmental uniformity would produce reduced levels of genetic variation. Thus, marginal and isolated populations are expected to have less variation than would centrally-located populations (Carson 1955 and 1959, Soulé 1973). Since the present study does not include any truly marginal or isolated populations (white fir on this transect ranges from 3000 feet to at least 7,700 feet), one would not expect to find striking differences between the populations in regards to the levels of genetic variation maintained. This expectation is borne out by the data (Table 3) which fails to show any large differences between the average coefficients of variation. The low-elevation population, AK, and the high-elevation east-side population, AM, do have slightly less variation but the differences certainly are not significant. Thus, it appears that all of the populations have similar levels of genetic variation. Evidently the combined effects of selection, gene flow, and environmental heterogeneity are roughly equivalent for all the populations studied.

A factor which appears when one examines the coefficients of variation (Table 3) is that some characteristics are highly variable whereas others are less so. One would expect those characteristics with the highest selection pressures to have the least within-population variation due to directional selection. This trend is observed if one compares the within-population variation to the total variation ($\sigma_w^2/V_G + \sigma_f^2/V_G$, in Table 2). But since this is the method by which we originally defined those characteristics of high selective importance, we have a circular argument. Thus, a comparison between the coefficients of variation within populations and the ratio of between-population variance to between-family variance $\left(\sigma_p^2/\sigma_f^2\right)$ is valuable. However, the comparison does not reveal the expected negative relationship between the ratio of variances and the coefficient of variation (Spearman's coefficient of rank correlations = +.41 with a probability of .10). This is surprising if relatively less within-population variation is expected in those characteristics which are undergoing intense directional selection. In fact the trend, though nonsignificant, is in the opposite direction; those characteristics with high variance ratios tend to have higher coefficients of variation. A number of situations can be thought of which could produce such a result. First, the result may mean that the response of some characteristics to the within-row environmental variation may be greater than the response of other traits. However, a similar result is found if the unconfounded between-family standard deviation is used to calculate the coefficients of variation. Thus, it does not appear that the within-row environmental effect is an important consideration in this regard. A second, and probably more important, consideration in explaining the positive correlation between selection intensity and variation is the possible adaptation of white fir to microhabitats. The existence of microhabitat differences over short distances in the Sierran conifer forest would favor the maintenance of a variety of genotypes within a population. Also we would expect those characteristics with more intense selection acting upon them to be more sensitive to local environmental variation as well. The present data would seem to support this conclusion. Thus, the effects of the directional selection which would act to reduce within-population variability on the elevational transect may be counteracted by the effects of local microhabitat selection which would maintain genetic variability within populations. Such a situation has been reported for allozyme variation patterns in *Avena barbata*. In the *Avena* case, Hamrick and Allard (1972) and Allard et al. (1972) have demonstrated the maintenance of genetic polymorphism by microhabitat differences in populations distributed along a moisture gradient.

A final topic that needs consideration is the implications that arise from the estimates of the within-family variance. It is possible that a substantial proportion of the within-family variance was due to gene flow from outside the collection area. With the design of the present study it is impossible to quantify the magnitude of this contribution. However, with a properly designed experiment, using cloned seedlings, it would be possible to partition the genetic and environmental contributions to the within-family variance. If the within-family genetic variance remains above approximately 2 times the between-family genetic variance, a number of interesting and valuable interpretations can be made. First, the differences between the expected $\left(2 \times \sigma_f^2\right)$ and actual genetic variances provides an excellent method to estimate levels of pollen immigration. Second, assuming that the populations under study are at an equilibrium (i.e. reasonably well adapted to the local environment), the differences between the expected and the observed variance can be used to estimate the selection intensities acting upon the population. Thus the use of open-pollinated families provides a powerful tool in studies of gene flow and selection, and as such may give valuable insights into evolutionary strategies and population structure.

In conclusion, it appears that white fir is a highly variable species on the Eldorado transect as well as on the latitudinal transects studied earlier by Hamrick and Libby (1972). Not only was the species found to be quite variable between populations from different elevations, but there is a relatively large amount of variation within each population sample. The majority of this variation is found within open-pollinated families. The mechanism for the maintenance of this variation in the face of natural selection is not obvious, but may be related to the high levels of migration and gene exchange found within the species, coupled with microhabitat selection. When the characteristics were examined, certain ones had relatively more between-population variation than did others. Those characteristics which were demonstrated to have greater amounts of between-population variation are the same characteristics which were previously postulated by Hamrick and Libby (1972) to have high selection pressures acting upon them. Together these two studies show that selection intensities vary between characteristics within the same population, and that studies which compare patterns of variation provide a method by which differences in selection intensities can be illustrated.

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