

THE IMPORTANCE OF LOCAL GENETIC VARIABILITY IN DOUGLAS-FIR

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ABSTRACT

Analyses of genetic variability in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) indicate that a large proportion of it is within stands. This is probably due, at least in part, to the highly heterogeneous habitat conditions within those stands. Two examples of this heterogeneity are provided.

A case study of two pairs of adjacent sites illustrates the differences between early-successional sites, burned in about 1900, that support meadows containing Douglas-fir and adjacent mid-successional, close-canopied forests. There were significant differences between early and later successional sites in the genetic constitution of the trees and in the spatial organization of this genetic variability.

We also present a survey of patterns of damage by herbivores and other pests to Douglas-fir and to other forest trees. The results indicate that (1) in natural forests there is extensive variability in the susceptibility of individuals to pest damage and (2) individual trees that are resistant to the attacks of one pest are often susceptible to the attacks of another.

These studies support the idea that the establishment and maintenance of healthy forests depends upon the maintenance of high levels of genetic variability. Management policies must keep this point in mind, for example, (1) reforestation with seeds of a narrow genetic base, or with nonlocal seeds should be avoided, (2) searching for "supertrees" that are simultaneously resistant to several insects and diseases may not be worthwhile.

Keywords: Genetic variability, succession, pest pressure, reforestation, *Pseudotsuga menziesii*

INTRODUCTION

Douglas-fir is a highly variable species. As foresters interested in Douglas-fir, we need to understand why this species is so variable, and the implications of this variability for forest management. Table 1 illustrates the difficulty of this task by listing some of the major environmental variables that Douglas-fir has to deal with. Many of these variables operate simultaneously and affect growth, survivorship and reproduction, thereby generating natural selection, and shaping genetic variability. This list is actually an underestimate for at least two reasons. First, several factors can interact; for example, drought-stressed trees are often more susceptible to insect attack. Secondly, only a few categories of animals are listed in the table. Within any one stand, many species can damage or kill trees: these include budworm (*Choristoneura*), bark beetles

(*Dendroctonus*), tussock moth (*Orgyia*), cone beetles (*Conophthorus*), and cone moths (*Dioryctria*). Over the whole range of the species, at least 230 species of insects are known to damage Douglas-fir (Furniss and Carolin 1977).

Table 1.—Factors affecting survival, growth and reproduction of a forest tree such as Douglas-fir.

Physical Factors	Biotic Factors
Temperatures	Competition
Daily variation	intra-specific
Yearly variation	inter-specific
Cold = freezing	Allelopathy
High = desiccation	Mycorrhizal Infection
Light	Defoliation
Low = etiolation	Vertebrates, e.g. deer
High = desiccation, uv damage	Insects, e.g. western spruce budworm
Water	Cone and Seed Feeders
Low = drought	Vertebrates
High = flooding	Insects
Wind	Phloem Feeders
Desiccation	Porcupine
Breakage	Bark beetle
Fire	Gall Makers
Soil Characters	Root Feeders
Particle composition	Fungal Diseases
pH	
Levels of specific elements	Dwarf-mistletoe parasites
low, high	

Attempts have been made to partition genetic variability in forest trees into within-stand and among-stand components. Results show that in Douglas-fir, as in many other conifers, a considerable proportion, and sometimes the majority of the variation is within stands, both in morphological (Campbell 1979) and in allozyme (Yeh and O'Malley 1980) characters. However, until recently, most studies of variability in Douglas-fir have concentrated on the among-stand component, by comparing stands over large geographic scales. Studies using this regional perspective have emphasized the role of extremes of temperatures, moisture, and exposure which Douglas-fir encounters, in shaping genetic variability in this species (Wright *et al.* 1971; Rehfeldt this volume).

To obtain a more complete perspective on variability, patterns must also be studied on a local scale. In this essay we examine some of these patterns operating at a scale of a few hectares or less, and their impacts upon genetic variability. We illustrate some of the impacts of local ecological heterogeneity upon Douglas-fir by discussing:

1. A case study of small scale variability associated with fire, succession and localized selection.
2. The impact of pest pressure upon Douglas-fir and other conifers of Western North America as examples of local selection.

FIRE, SUCCESSION, AND GENETIC STRUCTURE OF LOCAL STANDS

Goals

We compared genetic variability in Douglas-fir stands occupying pairs of adjacent sites at two locations. At each location, one site, termed early successional, was in a meadow established in an opening created by a fire circa 1900. The adjacent site was a close-canopied stand unaffected by the fire, and termed later-successional. We examined stand structure and genetic differences associated with tree age, successional status and spatial patterning. We asked the following questions:

1. What are the differences in age structure between stands on the sites?
2. With respect to genetic variability, is there genetic differentiation between early and later successional sites?
3. Are there spatial differences detectable among groups of trees within a site?

Materials and Methods

Field Sites

Our study locations are in the Front Range of the Colorado Rocky Mountains, in Boulder County, Township 1 N, Range 72 W. The Lefthand Canyon location is in Section 9. The Bald Mountain location is in Section 27. There was an early and a late successional site at each location (Table 2). The fact that early and late successional sites were immediately adjacent to each other at each location provided a control for environmental factors unrelated to succession, such as rainfall, aspect, and seed sources of new colonizers. All four sites were at an elevation of about 2,600 meters on NNE facing slopes (Davis 1981). Both early successional sites consisted of meadows, with scattered Douglas-fir and a variety of shrubs, herbs, grasses, and occasional ponderosa pine (*Pinus ponderosa*, Laws. var *scopulorum*); at Lefthand Canyon, there were also occasional limber pine (*Pinus flexilis*, James) and spruce (*Picea engelmannii* (Parry) Engelm.). These sites had been burned by small-scale fires around 1900. Such localized fires are very common in this region, whereas extensive fires (over 1,000 ha) are uncommon. The late successional sites were in adjacent mature

forest which escaped the fire. They consisted of dense stands with little understory vegetation. These forests are different from the old, open, climax forests of the Pacific Northwest. The oldest trees are usually 120-150 years and of modest size. They are representative of mid-succession in the Central Rocky Mountains.

Field Data

Data for a total of 1,519 trees were collected in 1979 and 1980. These trees were a complete census of all the individuals within the boundaries of the study sites. The location of individual trees on the sites was determined using the mapping program of Rohlf and Archie (1978). Foliage samples and increment cores or cross sections were collected. Increment cores were taken on the western side of each tree 10 cm above ground level. Seedlings were sectioned at ground level. A subsample of the sectioned trees for each site were sectioned at both ground level and at 10 cm above ground level. The average differences in the number of annual rings at these two levels for each site was calculated. This number was added to the age of trees, determined by counts of rings from increment cores, to provide a more accurate estimate of age. For analyses, trees were divided into three classes: seedlings (ages 1-10 yrs), saplings (11-30 yrs), and adults (over 30 yrs). These divisions are appropriate at these sites, as individuals to 10 years old are often 10 cm tall or less, and trees can reproduce at 30 years.

Genetic Data

The genetic constitution of trees was determined at four enzyme loci that showed Mendelian inheritance using starch gel electrophoresis. These loci included an esterase (FE), phosphohexose isomerase (PHI), glycerate dehydrogenase (GlyDH) and Shikimate dehydrogenase (SkDH). Protein extracts were made from foliage samples, according to the methods of Mitton *et al.* (1979). The details are provided in Davis (1981).

Genetic diversities for specific age classes at the four sites were calculated by the formula $H = 1 - \sum P_i^2$ where P_i is the frequency of the i^{th} allele. H can vary from 0 to 1. The greater the number of alleles and the more intermediate the frequencies, the higher H will be. That is because under such conditions, there will be a greater diversity of genotypes.

Tabulation of allelic and genotypic frequencies was performed using the frequencies subprogram of SPSS (Nie *et al.* 1975). Chi² tests for heterogeneity were performed on allele frequencies (Sokal and Rohlf 1969). In cases where a cell size was less than five and experimental design fit a 2 X 2 contingency table,

Table 2.—Characteristics of study sites. We indicate locations, successional status, area in hectares, numbers of individuals in three age and size classes defined as seedlings (ages 1-10 years), saplings (11-30 years) and adults (over 30 years), and density of all individuals per hectare.

Location of Sites	Successional Status	Size (age) Categories			Total Trees	Area (ha)	Density
		seedlings	saplings	adults			
Lefthand Canyon	Early (Burned)	98	210	47	355	1.2	295.8
	Late (Unburned)	40	27	210	285	0.3	950.0
Bald Mountain	Early (Burned)	143	205	15	364	0.4	910.0
	Late (Unburned)	246	183	79	515	0.3	1716.7

Fisher's exact test (Sokal and Rohlf 1969) was used. In both the χ^2 test for heterogeneity and Fisher's exact test, the frequency of all less common alleles were combined to obtain frequencies for only two classes of alleles. In all cases, the frequencies of the third and fourth most common alleles were less than 0.1, and in most cases, less than .05. The χ^2 test of goodness of fit (Sokal and Rohlf 1969) was used to compare the distribution of genotypes to those expected under Hardy-Weinberg equilibrium conditions. Classes were combined as necessary to eliminate classes with expected values of less than five.

Successional Stage and Stand Age Structure

The late successional sites had no trees older than 145 years, and few trees older than about 110 years. In late-successional or climax forests, one would expect trees several hundred years old. Their absence from these sites is presumably a reflection of previous fires, set by early European settlers in the 1860s (Bates 1918).

As expected because of the fires, at both locations the early successional sites had no trees older than 75 years. At all four sites, there were many seedlings (Table 2), but most were 7-10 years old. The youngest (1-3 years) age classes were either missing or had very few individuals (Davis 1981). The most likely explanation for this lack of very young seedlings is that it was due primarily to the increasingly severe spruce budworm infestation, which started approximately 20 years before this study. Spruce budworm defoliates trees and destroys buds bearing strobili, so that heavily infested trees produced few or no cones. Similar effects of spruce budworm have been observed in Balsam fir (Ghent 1958).

The relatively low density of seedlings at the late successional site at Lefthand Canyon (Table 2) was probably due to a dense canopy associated with a less severe budworm infestation at Lefthand Canyon than at Bald Mountain, and a higher density of adult trees at this site (adult density = 693/ha) than at Bald Mountain (adult density = 261/ha). As a result, much less light was reaching the forest floor, and few seedlings were establishing under these low light levels.

Genetic Change During Succession

The potential for genetic change was tested in two ways. One involved the comparison of allele and genotype frequencies between early and late successional sites. The other involved a comparison of genetic diversity, as calculated by H , at these sites.

There were no significant differences in allele frequencies between sites for three out of four loci (Davis 1981). At the SkDH locus, significant differences occurred between early and late successional stands; the differences were especially marked at the sapling and adult stages (Table 3).

The fit of genotype frequencies to those expected under Hardy-Weinberg equilibrium conditions was also tested. The test indicates relatively consistent results between locations. In three out of four loci there were no deviations from expected frequencies (Davis 1981). At SkDH, there are deficiencies of heterozygotes. These deficiencies are significant at three of four

sites, and are therefore not associated with successional status *per se*. Consequently, they cannot be ascribed to biological changes going on during succession (Davis 1981).

Overall levels of genetic diversity were determined for all loci allele frequencies and separately for seedlings, saplings and adults. A summary of comparisons shows that trees in specific size classes at early successional sites are more variable than their corresponding size classes in paired, late successional sites, in 17/24 cases (Table 4).

A variety of possible underlying ecological and/or genetic variables could cause genetic divergence between early and late successional stands: these include (1) genetic differences among age classes within a site combined with (2) major differences in age structure between sites, (3) differences in seed sources, and (4) differences between sites within specific age class. Each of these possibilities was considered, and the results are as follows:

1. There were no marked genetic differences among seedlings, saplings, or adults within any given successional site (Table 3, $\chi^2(w)$, and Davis 1981). However, at SkDH there is a consistent trend: in the early successional sites, the frequency of the most common allele decreases with increasing age and in the late successional sites it increases with age (Table 3, Figure 1). As noted above, genotype frequencies showed no deviations from Hardy-Weinberg expectations at three of four loci (Davis 1981). At SkDH there were significant deficiencies of heterozygotes at three sites. The sites as a whole show no deviations from Hardy-Weinberg expectations associated with successional stage (Davis 1981). Level of diversity (H) is higher in most early successional conditions except in adult trees at Bald Mountain and saplings at Lefthand Canyon (Table 4)
2. There are differences in numbers of individuals of the three size classes between sites at both locations (Table 2). However, all three classes are present at all sites, and genetic differences at SkDH are only significant between specific size classes (Table 3, saplings and adults). Thus the patterns between sites are not similar to the patterns among age classes within sites. Consequently, it seems safe to conclude that the observed differences are not due to differences in age structure *per se* between populations in different successional stages.
3. Trees in the early and late successional stands could have developed from seed of different genetic constitutions. The age-specific genetic comparisons (Table 3, Figure 1) show that, at both locations, the allele frequencies in the seedling classes were essentially the same in early and late successional sites and that the frequencies became increasingly different with age. These results indicate that there are no detectable differences in the seed source of current seedlings. This lack of difference is consistent with the fact that these trees are wind pollinated, highly outcrossed, and have small, wind-dispersed seeds which can travel far. As a result, seed pools at adjacent sites are not likely to be very different.
4. Genetic differences between comparable age classes in the two sites explain the patterns observed. There are no differences between seedlings in early and late successional sites. But there are differences between sapling classes and

Table 3.—Genetic variation at SkDH at each site in each of the three major age classes, seedling (1-10), sapling (11-29), adults (30 on). For allele frequencies, two χ^2 tests of heterogeneity were performed $\chi^2(w)$ compares age classes within sites. $\chi^2(B)$ compares individual age classes within locations between sites, e.g., early seedlings to late seedlings, etc. . . . For genotype frequencies, data are presented as observed and (expected) values. Expected values are reported only for the largest class, since other classes have been combined as necessary to eliminate cells with expected values of less than five.

Location	Site	N	Age Class	Allele Frequencies			$\chi^2(B)$ P	Genotypes						Level of Significance
				1	2	3		11	12	22	23	33	13	
Lefthand Canyon	Early	98	seedling	.036 ± .013	.724 ± .032	.240 ± .031		1	2	53 (51)	34	5	3	P > .50
		210	sapling	.026 ± .008	.712 ± .002	.262 ± .021		3	2	114 (106)	69	19	3	P < .02
		47	adult	.012 ± .018	.691 ± .048	.277 ± .046		1	1	23 (22)	18	4	0	a
		$\chi^2(w)$		P > .9										
Lefthand Canyon	Late	40	seedling	.000	.750 ± .048	.250 ± .048	>0.50	0	0	23 (23)	14	3	0	a
		27	sapling	.000	.796 ± .055	.204 ± .055	>0.10	0	0	17 (17)	9	1	0	a
		210	adult	.017 ± .006	.793 ± .020	.190 ± .019	<0.05	1	3	138 (132)	54	12	2	p > .05
		$\chi^2(w)$		P > .5										
Bald Mountain	Early	143	seedling	.042 ± .012	.801 ± .024	.157 ± .022		1	7	97 (92)	28	7	3	p < .10
		205	sapling	.037 ± .009	.788 ± .020	.175 ± .019		4	5	139 (127)	40	15	2	p < .005
		15	adult	.133 ± .062	.667 ± .086	.200 ± .073		1	1	8 (7)	3	1	1	a
		$\chi^2(w)$		P > .1										
Bald Mountain	Late	246	seedling	.019 ± .006	.809 ± .018	.172 ± .017	<0.70	1	4	157 (154)	64	7	3	p > .70
		183	sapling	.008 ± .005	.843 ± .019	.149 ± .019	>0.05	1	1	133 (129)	40	7	0	p < .025
		79	adult	.095 ± .072	.861 ± .028	.044 ± .016	>0.01	6	3	63 (69)	7	0	0	p > .005
		$\chi^2(w)$		P > .2 ^a										

^a) χ^2 test not calculated, since expected values for certain cells were < .

between adult classes in early and late successional sites (Table 3). Results are consistent between locations. There are no significant differences at the other three loci (Davis 1981). The more common allele at SkDH decreases with increasing age at the early successional sites, whereas at the late successional sites, it increases with age (Figure 1). The differences between sites in the sapling class at Lefthand Canyon is not statistically significant probably because the sample size is small at the late successional site. These results support the hypothesis that there has been site specific natural selection acting on a relatively homogeneous seedling pool which has created increasingly large differences at later age classes. In this scenario, the differences between the sites have more selective impact in older age classes.

An alternative explanation is that there were large differences in biotic (e.g., intense intraspecific competition in later

successional sites) and physical (e.g., heavy influx of nutrients into soil, and soil covered by ashes in early successional sites) conditions between the two sites at the time of establishment of the earliest seedlings which have now become the adult trees. Since that time, biotic and physical conditions have become more similar so that the allele frequencies of the younger age classes gradually converge. We consider the latter explanation the less probable one, since there are still striking differences between the two kinds of sites in many biotic and physical characteristics (e.g., soil conditions, vegetation composition, amount of light, presence of canopy). Many of these differences involve the same characteristics that differentiated these sites immediately after the fires, and should therefore produce genetic differentiation in seedling class. We cannot exclude either alternative with certainty. However, in both scenarios, differences in selective regimes associated with fire and successional stage

result in the present genetic differences between the sites. Such genetic differentiation in association with succession has also been documented in other species (Redfield 1973; Gray 1987).

Table 4.—Level of genetic variability as determined by H in early (E) and late (L) successional stands in seedlings, saplings and adults at four enzyme loci. The site with the higher level of variation is indicated with the appropriate letter.

Location	Age Class	FE	PGI	GDH	SkDH
Lefthand Canyon	seedling	E	E	E	E
	sapling	L	L	L	E
	adult	E	E	E	E
Bald Mountain	seedling	E	L	E	E
	sapling	E	E	E	E
	adult	L	L	L	E

to disturbance mosaics, soil patchiness, and related factors (Connell 1978; Cooper 1960; Denslow 1980; Forcier 1975; Harper 1977; Sprugel 1976; West 1969; Linhart 1989). Individuals within such an area can be randomly distributed, evenly distributed, or aggregated. Although there is no ideal way to analyze such data statistically (Goodall 1952; Clark and Evans 1954; Meagher and Burdick 1980), one can look for obvious clustering. Individuals can be distributed so that they form groups that are physically separated from one another and easily discernable by eye. One can then ask whether these groups may be genetically different from one another (Linhart *et al.* 1981, 1989). Such differences may be caused by differences in the age of the groups, characteristics of germination sites, intra or interspecific competition, limited seed dispersal and consequent clustering of related individuals, or random genetic differences. Many of these factors can also cause genetic differentiation even when individuals are not obviously spatially clustered in their distribution.

We studied the genetic consequences of small scale diversity by analyzing the spatial distribution of individuals at Lefthand Canyon and testing the possibility of genetic differences among spatially-associated groups. Individuals in both early and late successional sites show such groupings and the genetic constitution and the genetic heterogeneity of the groups were compared. Trees at the early successional site were easily divided into eight distinct groups and a collection of outliers. At the late successional site, three groups were recognizable, although less distinct (Davis 1981). Significant genetic differences occurred among groups in the early successional stand at two loci (Table 5), but not in the late successional stand (Table 6). Some of the genetic differences among groups are quite striking. The magnitude of the differences in allele frequencies among groups is similar to, or larger than, the magnitude of the differences between the early and late successional stands (compare Table 5 and Table 3).

Genetic differences among visually identifiable groups could be caused by a number of factors. Sometimes such groups are composed of individuals of similar ages. Differences in times of establishment among such even aged groups are common in many forest trees (Cooper 1960; Harper 1977; Linhart *et al.* 1981). However, when the individuals in this study are mapped by 10 year age classes, there is no noticeable clustering of age classes at either site (Davis 1981). Thus, the differences among groups are not associated with differences in the age composition of these groups.

It is possible that localized seed dispersal from one or a few seed trees contributed to differences among groups. This pattern has been seen or postulated for other tree species (reviewed in Linhart 1989). However, the absence of differences between spatially separated early and late successional stands in the seedling class (Table 3) and among groups within the late successional stand (Table 6) suggests that localized dispersal is not a major contributor to differentiation. Microhabitat differences between the sites may have played a role in causing differences between groups: the early successional site is more spatially heterogeneous in both physical and biotic features than the late successional site. Another possibility is that, though the area of the groups is comparable between stands, the number of individuals is not. Consequently, this difference could be contributing to the lack of differentiation between groups of the

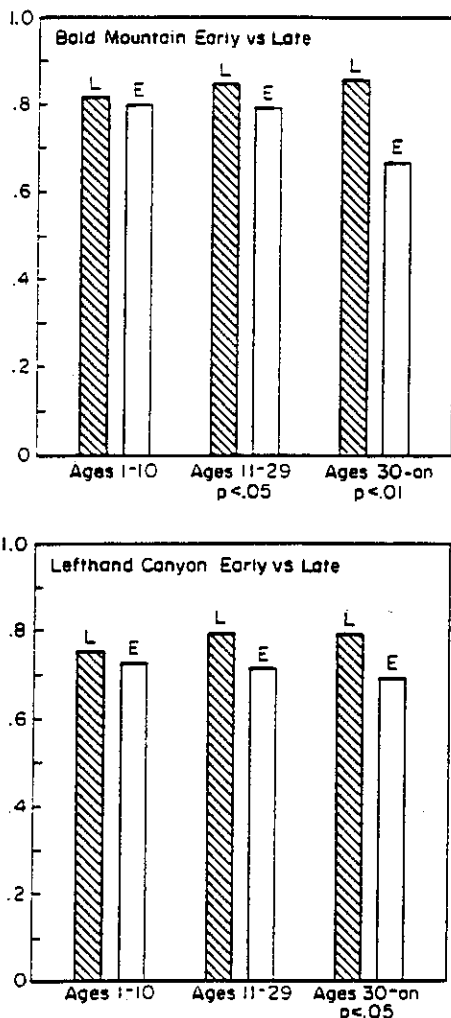


Figure 1.—Frequencies of the most common allele at shikimate dehydrogenase for the three major age classes. For each age class the frequency is shown in the early (E) and mid-late (L) successional stands.

Spatial Variation and Succession

Small scale diversity, often over a single hectare or less, is common in forest trees. This diversity is frequently attributed

Table 5. - Allele frequencies within groups at the Lefthand Canyon early successional site for four loci. Data are presented as the frequency of the allele the standard error. Chi² values, levels are all included for a Chi² test of heterogeneity among groups.

Group	FE				PHI			GlyDH			SkDH			
	N	1	2	3	0	1	2	3	1	2	3	1	2	3
1	35	0	1.0	0	.029 ± .02	.043 ± .02	.928 ± .03	0	.286 ± .05	.714 ± .05	0	.071 ± .03	.729 ± .05	.200 ± .05
2	28	0	1.0	0	.018 ± .02	.018 ± .02	.964 ± .02	0	.250 ± .06	.750 ± .06	0	0	.821 ± .05	.179 ± .05
3	36	0	1.0	0	.014 ± .01	.153 ± .04	.833 ± .04	0	.403 ± .06	.597 ± .06	0	.014 ± .01	.792 ± .05	.194 ± .05
4	16	0	1.0	0	0	.344 ± .08	.654 ± .08	0	.438 ± .09	.563 ± .09	0 †	.063 ± .04	.875 ± .06	.063 ± .04 †
5	50	.010 ± .01	.980 ± .01	.010 ± .01	.03 ± .02	.02 ± .01	.950 ± .02	0	.340 ± .05	.660 ± .05	0	.040 ± .02	.710 ± .05	.250 ± .04
6	27	0	1.0	0	0	.037 ± .03	.944 ± .03	.019 ± .02	.204 ± .05	.796 ± .05	0	.019 ± .02	.759 ± .06	.222 ± .06
7	16	0	1.0	0	0	0	1.0	0	.219 ± .07	.781 ± .07	0 †	.031 ± .03	.719 ± .08	.250 ± .08 †
8	36	0	1.0	0	0	0	1.0	0	.111 ± .04	.899 ± .04	0	.014 ± .01	.625 ± .06	.361 ± .057
Outliers	111	0	.982 ± .01	.018 ± .01	.023 ± .01	.045 ± .01	.914 ± .02	.018 ± .01	.306 ± .03	.689 ± .03	.005 ± .03	.027 ± .01	.649 ± .03	.324 ± .03
Chi ²		†				†				19.844			12.576	
D.F.		†				†				6			6	
Level of Significance				†		†						p < .005		p < .05

† Results of the Chi² test are not evaluated for FE and PHI since the expected values for many of the cells were less than five and this test is not valid under those conditions.

‡ Gene frequencies for groups where N = 16 were not included in the Chi² test for GlyDH and SkDH because the values for some of the cells were less than five.

Table 6. - Allele frequencies within groups at the Lefthand Canyon late successional site for four loci. Data are presented as the frequencies of the allele the standard error. Chi² values are also included for a Chi² test of heterogeneity among groups.

Group	FE				PHI			GlyDH			SkDH		
	N	1	2	3	0	1	2	3	1	2	3	1	2
1	109	0	1.0	0	.009 ± .01	.028 ± .01	.954 ± .01	.009 ± .01	.335 ± .03	.665 ± .03	.004 ± .00	.803 ± .03	.193 ± .03
2	93	0	1.0	0	.005 ± .00	.065 ± .02	.919 ± .02	.326 ± .03	.674 ± .03	.016 ± .01	.753 ± .03	.231 ± .03	
3	80	.006 ± .01	.963 ± .01	.031 ± .01	.031 ± .01	.037 ± .01	.919 ± .02	.013 ± .01	.250 ± .03	.750 ± .03	.019 ± .01	.806 ± .03	.175 ± .03
Chi ²		†				2.604				3.552		1.962	
D.F.		†				2				2		2	
Level of Significance				†		p > .2				p > .1		p > .3	

† Results of the Chi² test are not evaluated for IE since the expected values for many of the cells were less than five and this test is not valid under those conditions.

late successional site where the number of individuals per group is large, whereas the small number of individuals per group at the early successional site may have caused random genetic differences. It is not possible to distinguish between these explanations without more detailed information. However, we think that genetic differences between groups in Douglas-fir may be caused in part by selection associated with microhabitat differences. As noted earlier, Douglas-fir has light seeds that can be dispersed relatively long distances (Levin and Kerster 1974; Campbell 1979), and the Lefthand Canyon site is very windy. Additional support for the selective role of microhabitat comes from the fact that the late successional stand, which is dense and tends to limit air movement, and thus should have more restricted gene flow than the early successional site, shows no genetic differences between groups, perhaps because it is more homogeneous in vegetation and physiognomy.

SELECTION BY LOCAL PEST PRESSURE

Douglas-fir serves as a host to many insects, mammals, fungi and other pests and parasites. Whenever the impact of these species has been studied in detail, it has been noted that, within a given area, there are marked differences among trees in the extent to which they are damaged by the pest in question. The same observations have been made with other tree species. Examples of such selective damage are listed in Table 7.

The budworm *Choristoneura* is a case in point. Certain individuals can be almost completely defoliated, while adjacent trees are scarcely touched. Although the reason for these differences was not known in early studies, it was surmised to have a genetic basis. More recently, the careful studies of Cates and his collaborators (this volume) have begun to demonstrate the

role played by various secondary compounds present in foliage in determining insect choice. Most of their work has dealt with inter-stand comparisons, but intra-stand comparisons also show that nearby trees present very different biochemical profiles (Cates and Zou 1990)

Other species of pests which show avoidance of, differential preference for, or distaste for, individual Douglas-fir are listed in Table 7. In some of these cases, a genetic basis for inter-tree differences in palatability has been demonstrated, either because different seed sources are exposed to a pest in a common garden or because clonal replicates show the same results. In other cases, genetic bases are inferred but not demonstrated. It also should be stressed that, in at least some tree x pest interactions, individual trees that are susceptible to specific pests are not automatically susceptible to others. In fact, in some instances, trees susceptible to one pest species are simultaneously resistant to another (Stephan 1987). This is to be expected if different pests have different enough physiologies and behaviors so as to generate different host choices. This pattern has been termed species-specific host selection, has been observed in several tree species and herbaceous plants as well, and is discussed in detail elsewhere (Linhart 1989).

Pest-generated selection may also be important in the context of reforestation with non-local seeds. This is of special concern if these introduced individuals cross with native trees to produce hybrid progeny. Studies of hybrid zones between either varieties or species of both animals (Sage *et al.* 1986) and plants (Whithman 1989) show that hybrid individuals are often much more heavily parasitized than are individuals of either parental taxon. This presumably happens either because co-adapted complexes of genes are broken down by hybridization, or because

Table 7. – Examples of differential host utilization in trees of Western North America. Intraspecific variability in a host plant is associated with interspecific differences in host preference by species of parasites or herbivores referred to, in the aggregate, as dependent species.

Host species	Dependent Species	Preference Pattern	References
<i>Pseudotsuga menziesii</i>	Deer (<i>Odocoileus hemionus</i>) Hare (<i>Lepus americanus</i>)	No correlation between herbivore spp. in preference for specific clones.	Dimock <i>et al.</i> 1976
	Woolly aphid (<i>Gilletteella cooleyi</i>)	Populations resistant to aphid are susceptible to fungus.	Stephan 1987
	Needle cast fungus (<i>Rhabdocline pseudotsugae</i>)		
<i>Pinus radiata</i>	<i>O. hemionus</i> Porcupine (<i>E. dorsatum</i>)	The herbivores prefer different clones.	Hood and Libby 1980
<i>Pinus ponderosa</i>	<i>O. hemionus</i> Rabbit (<i>Sylvilagus nuttallii</i>) <i>E. dorsatum</i>	<i>O.h.</i> and <i>S.n.</i> prefer trees of same origin. <i>E.d.</i> preferences very different.	Squillace and Silen 1962
	<i>O. hemionus</i> Wolly aphid (<i>Pineus coloradenis</i>)	Feeding tree distributions show no significant correlation.	Linhart, in prep.
	Porcupine (<i>E. dorsatum</i>) Squirrel (<i>S. alberti</i>)	<i>E.d.</i> and <i>S.a.</i> feed on trees with different resin and phloem characteristics.	Linhart <i>et al.</i> 1989 Habeck 1990 Snyder 1990
<i>Pinus contorta</i>	<i>Arceuthobium americanum</i> <i>Dendroctonus ponderosae</i>	Mistletoe-infected trees are less susceptible to beetle attack.	Hawksworth & Johnson 1989

the two parental genomes are somehow "uncoordinated" so that the hybrids function poorly at the physiological level, and are unable to repel pests and parasites. These findings suggest that the introduction of non-local seeds may lead, in the next generation, to the production of dysgenic or maladapted progeny that may be especially attractive to pests. We are attempting to study such non-local populations and nearby hybrid progeny to see if this prediction is worthy of concern; any information about such situations in Douglas-fir or other tree species will be appreciated.

MANAGEMENT IMPLICATIONS

Fire and succession-associated differences in habitat conditions have generated marked genetic differences between Douglas-fir stands occupying adjacent sites. The precise role of individual factors in generating the genetic differentiation cannot be identified. However, it is clear that observable habitat conditions, associated with fire or lack of it, provide good clues to the existence of differences in stand structure and genetic constitution of Douglas-fir.

Genetic differentiation over short distances is common in forest trees. It has been observed repeatedly (Hermann and Lavender 1967; Campbell 1979; Linhart 1988), except in cases where the species in question have little or no genetic variability (Fowler and Morris 1977), or where sample sizes are small. Normally, the differentiation is detected when populations span obvious environmental contrasts such as variation in slope, soils or elevation. The results reported here suggest that more subtle patterns of heterogeneity associated with stand history need to be recognized as well.

When genetic variability is apportioned to within-population and among-population components, the former tends to be the larger of the two forest trees. Our results suggest that one reason for this finding is that within stand variability can be very high because of locally complex environmental conditions. This result must not be used to conclude that, since most variation is within stands, seeds from any one location can be used for reforestation elsewhere, and the trees will be able to adapt to their new locations. Repeated failures of reforestation using non-local seeds attest to the flaws in this approach.

The results presented here along with those Rehfeldt and Cates and his collaborators (this volume) illustrate the need to recognize that phenotypic and genetic variability are necessary components of Douglas-fir forests. Consequently, reforestation must involve a broad genetic base. Care must be taken to prevent inadvertent reduction of the genetic base, a periodic problem in reforestation (Stern and Roche 1974; Silen and Osterhaus 1979). In this context, reforestation with a small number of cones or a small number of seed trees (one or two per hectare) do not appear to be a reasonable option.

Patterns of damage generated by insects, fungi and other damaging species suggest the existence of species-specific host selection. This means that individual trees can be simultaneously resistant to one pest species but susceptible to another. This implies that there are not likely to be "super trees" that can withstand the attacks of all their biotic pests.

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