AN ABSTRACT OF THE THESIS OF

TIMOTHY LEE WHITE for the degree of DOCTOR OF PHILOSOPHY

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Title: GENECOLOGY OF DOUGLAS-FIR FROM SOUTHWESTERN OREGON

Abstract approved: Kim K. Ching

This thesis is divided into three chapters. For all chapters, the experiments described deal with the responses of all or a subset of 72 wind-pollinated Douglas-fir families from 36 different locations in southwestern Oregon. Wind-pollinated seed was collected from each of two trees at each of the 36 locations. The 36 locations were chosen to give a broad regional sample of southwestern Oregon. The two families were considered a sample of the Douglas-fir population present at each location.

All experiments described herein were aimed at defining and patterning the genetic variation among these families and populations as it occurred in various test environments.

GENECOLOGY OF DOUGLAS-FIR FROM SOUTHWESTERN OREGON

by

TIMOTHY LEE WHITE

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements of the
degree of

Doctor of Philosophy

Chapter 1

In the Chapter 1 experiments, 30 populations (60 families) were grown in each of three test environments (growth room, greenhouse and nursery) to examine the influence of the environment on the genetic variation in first-year height growth. Overall, the populations differed markedly in their first-year height growth, with the estimated variance among populations being about four times greater than both the estimated family within population and population x environment variances.

Regression models indicated that populations originating from higher elevations and southerly latitudes in the sampled region tended to grow slower in all test environments. While the trends were consistent in all test environments, the models for the nursery data were not as efficient in accounting for the variation in population means.

Chapter 2

Several experiments, conducted in both the growth room and greenhouse test environments and employing from 50 to 70 of the families, are reported in Chapter 2. The Dry and Drought Survival experiments in both test environments examined genetic variation in several traits when the seedlings were growing in dry soil conditions. The greenhouse Moist experiment examined genetic variation in some of these traits as expressed under well-watered conditions. All of the experiments used seedlings in their second growing season.

Populations differed markedly in second-year height growth and in time of budset. In general, populations originating from higher elevations and southerly latitudes grew slower and set bud earlier. The exact nature of the elevational and latitudinal trends varied among experiments. Generally, both higher elevation and low latitude populations also accumulated less shoot dry weight over two growing seasons.

Although the Drought Survival experiments were characterized by large amounts of experimental error, trends seem clear. High elevation and low latitude populations survived better during extended soil drought. Because the elevation and latitude of the 36 population locations were so closely linked ($r = -0.80^{**}$), it was impossible to separate the influences of these two variables on the gene pool of southwestern Oregon Douglas-fir.

Chapter 3

Four drought resistant and four drought susceptible families (as judged by their performance in the greenhouse Drought Survival experiment) were chosen for intensive investigation of several drought avoidance characteristics associated with needle morphology and transpiration control. No differences between drought resistant and drought susceptible genotypes were found for 1) number of stomatal rows, 2) number of stomata per unit of needle surface area, 3) number

of stomata per needle or 4) length of the stomatal antechamber opening.

Leaf conductance and plant water potential were monitored on two overcast days at the end of the growing season. Under well-watered conditions, seedlings from drought resistant families transpired more per unit of needle surface area than did seedlings from drought susceptible families. This may reflect the fact that drought resistant families maintained higher (more favorable) evening water potentials.

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APPROVED:

Professor of Forest Science, in charge of major

Head of Department of Forest Science

Dean of Graduate School

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CHAPTER 1. FIRST-YEAR HEIGHT GROWTH IN THREE TEST ENVIRONMENTS

Introduction

Many studies report geographic variation in juvenile height growth of coastal Douglas-fir (Pseudotsuga menziesii). Most of these studies sampled provenances from the western portions of British Columbia, Washington and Oregon (Campbell and Sorensen 1978, Rowe and Ching 1973) or California (Griffin and Ching 1977, Sweet 1965). Because southern Oregon has received much less attention, even though it is an important timber producing area, I undertook, in cooperation with the Bureau of Land Management, a regional study to investigate the patterns of genetic variation in Douglas-fir in this limited area of southern Oregon.

Campbell and Sorensen (1978) point out that initial attempts to reveal and characterize adaptive genetic variation among plant populations should be conducted in environments (common gardens) with high resolution. That is, by limiting environmental variation in the test environments and by choosing test environments which discriminate among the populations being tested, we can better describe and pattern the factors associated with the populations' differences. For instance, if some populations are more able to respond to long photoperiods, then an environment with long photoperiods will tend to differentiate among the populations which can and can't respond. However, because genetic expression can vary in different test environments (genotype x environment interaction), it is necessary to use more than one test environment.

Chapter I reports results dealing with genetic variation in first-year height growth as expressed in three contrasting test environments: growth room, greenhouse, and outdoor nursery.

Materials and Methods

Sampling Scheme

In the fall of 1976, wind-pollinated seed was collected from two mother trees at each of 36 sample population locations distributed throughout southwestern Oregon (Figure 1). All of the population locations were between 42.00 and 43.12°N latitude and ranged from 475 to 1630 m elevation, from 61 to 162 Km from the Pacific Ocean, and from 80 to 130 ft site index[1].

I intended that the 36 population locations should systematically sample the range of sites on which Douglas-fir grows in this region. Therefore, although slopes and aspects of the locations were randomly chosen, some constraints on the elevations, latitudes and distances from the Ocean insured a broad regional sample. Because of the geography of the region, the topographic variables associated with the population locations are not independent of each other (Table 1). In particular, compared to lower elevation population locations,

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[1]Site index, in feet at 100 years of age, was determined from 7-10 trees at each population location as described by McArdle and others (1961).

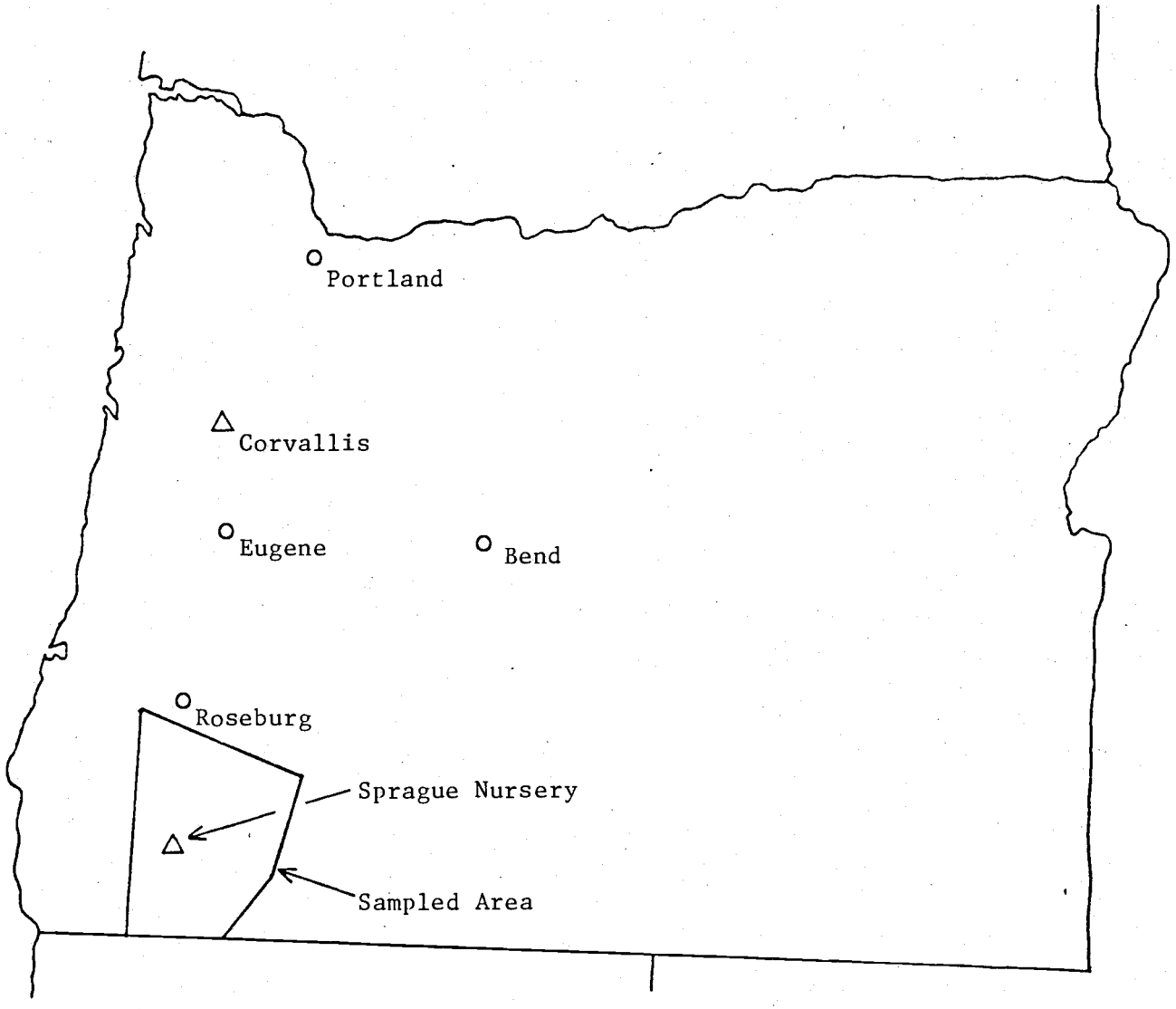

Figure 1. Map of Oregon showing area sampled in study.

higher elevation locations tended to be located in the southern portion of the region and to a lesser extent tended to be further from the Pacific Ocean.

Within each of the 36 populations, we collected wind-pollinated seed from two randomly selected parent trees located at least 120 m apart. Because 1976 was only a moderate seed crop year, some inadvertent selection may have occurred for the ability to produce seed.

Experimental Designs in the Test Environments

After extraction and cleaning, I cut open a sample of at least 100 seeds from each of the 72 wind-pollinated families and weighed the filled seed to obtain a family average of sound seed weight. In mid-March, 1977, stratified seeds destined for the growth room and greenhouse test environments were individually sown into 45 cm^3 tubes (2.5 cm diameter x 10 cm long) containing a 3:2 peat: vermiculite rooting medium. In the growth room, 35 populations (70 families) out of the total of 36 were represented, while only 31 populations (62 families) were included in the greenhouse experiment. In both the growth room and greenhouse test environments, family row-plots were organized in a completely randomized design. In the growth room, three ten-tree row-plots represented each family, while in the greenhouse, each family had eight row-plots of eight seedlings each. Seedlings were watered weekly and fertilized periodically with a liquid fertilizer (approximately 10% Hoagland's solution). Growth room seedlings experienced a 16 hr photoperiod and a 25/20°C thermoperiod.

Greenhouse seedlings experienced natural photoperiods.

In mid-April, 1977, seeds from 35 populations (70 families) were sown at the Bureau of Land Management's Sprague Nursery in Merlin, Oregon (Figure 1). The randomized complete block design meant that within each of four blocks (nursery beds), 70 family row-plots were randomly assigned positions.

At the end of the first growing season, epicotyl length (hereafter, first-year height growth) was measured to the nearest 0.5 cm in each of the three test environments. All seedlings were measured in the growth room and greenhouse, while in the nursery, only the first 15 seedlings in each family row-plot were measured.

Table 1. Correlations among the topographic variables associated with the 36 population locations.

	Elevation	Latitude	Distance from Ocean	Site index	Aspect
Elevation	1.0	-0.80[a]	0.44	-0.34	-0.16
Latitude		1.0	-0.28	0.45	0.12
Distance from the Ocean			1.0	0.04	0.02
Site index				1.0	-0.14
Aspect					1.0

[a]All correlations have 34 df.
r = 0.33 significant at P = 0.05.
r = 0.42 significant at P = 0.01.

Statistical Analyses

Individual tree measurements served as the experimental units for the analyses of variance of first-year height growth for both the growth room and the nursery test environments. Unfortunately, because the trees in the greenhouse were rearranged for use in another experiment prior to measurement, an analysis of variance employing individual tree measurements was precluded and only family means could be obtained for this test environment.

For the 60 families common to all three test environments, the family means within each test environment served as the basis (experimental unit) for an analysis of variance combined over environments. The population x environment interaction sum of squares was partitioned into various components by regressing the population means from each environment onto the means of the test environments (Finlay and Wilkinson 1963, Mandel 1961). The rationale behind this type of joint regression analysis has been previously discussed in the forestry literature (Mergen and others 1974, Morgenstern and Teich 1969, Owino 1977).

Population means within each test environment were obtained by averaging the two family means from each population. I regressed these population means against the topographic variables associated with the population locations to establish trends relating population origin to height growth in the test environments. Regression models, built individually for each of the three test environments and also for the combined population averages, employed standard forward and backward stepwise multiple linear regression techniques. Only variables

with significant partial correlation coefficients (P = 0.01) were allowed to enter a model. The independent variables available to each model included elevation, latitude, distance from the Pacific Ocean, site index, aspect and all of the first order interactions. Transforming aspect to a cosine function of the true azimuth in degrees set the optimum at true north. In addition, weighting aspect by the percent slope insured that aspects from steeper slopes were given more weight (Stage 1976).

Results and Discussion

Seed Weight

An analysis of variance revealed that differences in seed weight among the 36 sample populations were significant when tested against the family within population mean square (F = 1.95* with 35, 36 df[1]). Sound seed weight averaged 0.015 and ranged from 0.011 to 0.019 g per seed for the 36 populations. The average population seed weights correlated weakly to moderately with the topographic variables of the population locations. Values of 0.35*, -0.38*, and 0.47** (with 34 df) for the correlations of population mean seed weight with elevation, latitude and distance from the Ocean indicate that seed collected from cold parts of the region (high elevation, and farther inland) tended to be slightly heavier. Several investigators (Birot 1972, Ching and Bever 1960, Griffin and Ching 1977, Sweet 1965) reported similar

[1]Throughout this thesis, ns = not statistically significant, * = significant at P = 0.05, ** = significant at P = 0.01.

trends either with elevation or distance from the Ocean for Coastal Douglas-fir.

Because the seed developed in different locations, the differences among the population seed weights may be either genetic or environmental. On one hand we can speculate that a faster growth start after germination, such as might be conveyed by genetically heavier seed, would benefit seedlings in harsher (for example, colder) environments by allowing for more height growth in the shorter growing seasons. On the other hand, seed weight differences among the 36 populations and the trend with the topographic variables may manifest the different environments in which the seed matured. At any rate, these population differences and topographic trends were not strong.

Family mean seed weight did not correlate strongly with family mean height growth in any of the three test environments ($r = -0.44^{**}$ with 68 df, 0.09^{ns} with 68 df, and -0.21^{ns} with 60 df in the growth room, nursery and greenhouse). The only significant correlation, that in the growth room, indicated decreasing height growth for families with heavier seed. Because seed weight apparently did not influence height growth on a family mean basis, it was not used as a covariate in the following analyses.

Influence of Test Environments on Height Growth

The combined analysis of variance employing family means from each of the test environments (Table 2) shows, as expected, a marked effect of the test environment on first-year height growth. The average heights in the growth room, nursery and greenhouse were 8.67 cm, 5.62

Table 2. First-year height growth combined analysis of variance based on family means from the three test environments.

Source	df	Mean Square	Intraclass[a] Correlation (% S_T^2)[c]	Expected Mean Square
Environments (E)	2	383.080**		
Population (P)	29	5.265**[b]	46.2	$(K\sigma_c^2 + \sigma_{EF/P}^2) + 2\sigma_{EP}^2 + 3\sigma_{F/P}^2 + 6\sigma_P^2$
Family/Population (F/P)	30	.924**	10.8	$(K\sigma_c^2 + \sigma_{EF/P}^2) + 3\sigma_{F/P}^2$
E*P	58	.786*	12.0	$(K\sigma_c^2 + \sigma_{EF/P}^2) + 2\sigma_{EP}^2$
Slopes	29	.827*		
Concurrence	1	14.452**		
Nonconcurrence	28	.340^{ns}		
Remainder	29	.745*		
E*F/P	60	.447	31.0	$(K\sigma_c^2 + \sigma_{EF/P}^2)$

[a] $S_T^2 = S_P^2 + S_{F/P}^2 + S_{EP}^2 + (KS_c^2 + S_{EF/P}^2)$

Table 2. (Continued)

[b] Population mean square was tested using Satterthwaite's Approximate F-Test (Anderson and McClean 1974, p.117).

[c] Each of the variance components is estimated by a sample variance component;

S_P^2 estimates σ_P^2 = variance among populations,

$S_{F/P}^2$ estimates $\sigma_{F/P}^2$ = variance among families within populations,

S_{EP}^2 estimates σ_{EP}^2 = variance due to the interaction of test environments with populations,

$S_{EF/P}^2$ estimates $\sigma_{EF/P}^2$ = variance due to the interaction of test environments with families within populations,

S_c^2 estimates σ_c^2 = composite variance resulting from several families within test environment sources.

cm and 3.52 cm; the average height in the growth room was about 2.5 times larger than in the greenhouse. With these large differences among environments, the potential exists for a large genotype x environment interaction (Shelbourne 1972). The estimated variance component associated with differences among the populations (S_P^2) was about four times larger than that associated with the population x environment interaction (S_{EP}^2). Populations, families within populations and the interaction of test environments with populations accounted for 46%, 11% and 12% of the variance not associated with environments. The component of variance due to the interaction of families within populations with environments could not be estimated because of other inseparable variance components included in that mean square.

I explored the nature of the population x environment interaction by regressing population means from each environment onto the environmental means. For the 30 populations involved there are 30 such regressions, each regression having three points (two populations are plotted as examples in Figure 2). Each of the three points through which a line is fitted represents the average height of a population in one of the environments. The highly significant concurrence and the lack of non-concurrence (Table 2) reveal that the 30 lines tend to have a common intersection which occurs below the lowest environment. The lines fan out from that point becoming increasingly further apart in the larger environments. Thus, the lines do not tend to overlap in the inference space. The concurrence mean square is identical to that obtained from Tukey's "one degree of freedom for non-additivity" (Tukey 1949).

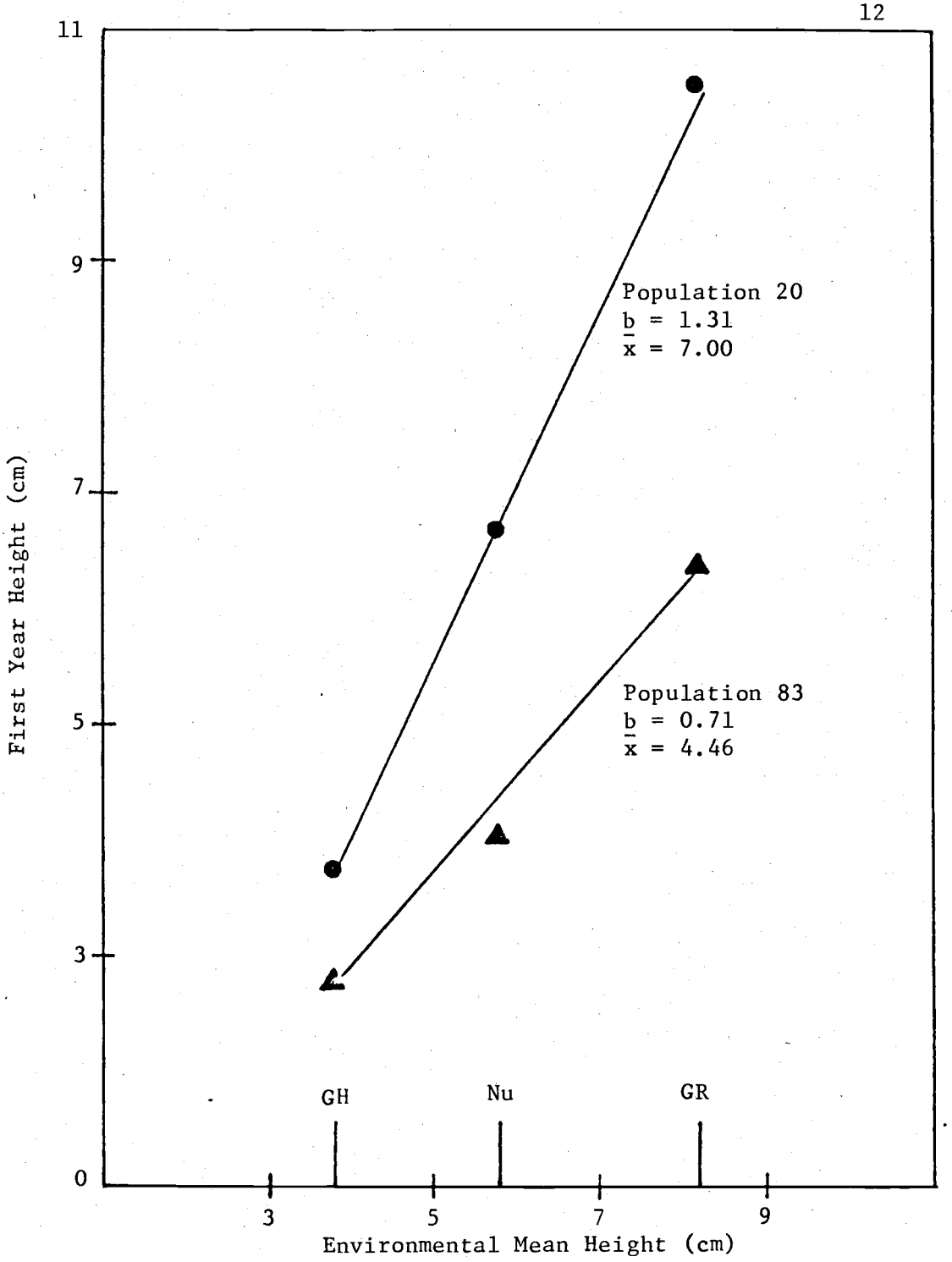

Figure 2. Height growth and stabilities of two example Douglas-fir populations grown in three test environments.

This analysis indicates that the portion of the population x environment interaction which is accounted for by slopes is best characterized as a scale effect and not by changes in population rankings in the different environments. A population which was taller in the poor environment (greenhouse), tended to be progressively taller in magnitude, relative to shorter populations, in the better environments. There was a small but significant portion of the population x enviroment interaction (the remainder in Table 2) which we could not explain in this fashion.

Figure 2 shows that the slopes of the regressions tell us something about the genetic responsiveness of a population to the more favorable environments. In this context, a favorable environment was one which resulted in good height growth; the growth room was the most favorable. The average of the slopes for all 30 populations is 1.0. A population with a slope (b) greater than 1 had an above average genetic responsiveness to the environmental change. If b is less than one, the population was relatively more stable to the environmental change. A b = 0 indicates complete stability; the population would have the same height in all of the test environments.

All of the populations in this study grew faster in more favorable environments; b values ranged from 0.66 to 1.36. A strong correlation ($r = 0.78^{**}$, 28 df) between the population b values and the overall population mean heights (averaged over the three test environments) indicates that taller populations tended to be more responsive to environmental change by growing progressively taller in the better environments. This information is identical to that given by the

"concurrence" degree of freedom in the combined analysis of variance (Table 2). In fact, the coefficient of determination ($R^2 = 0.78^2 = 0.61$) for the relationship between population heights and population b values defines the fraction of the "slopes" sum of squares accounted for by "concurrence".

Finally, the population b values correlated moderately to strongly with the topographic variables from the population locations. Values of -0.72**, 0.70** and -0.32* (all with 28 df) for the correlations between the population b values and the population elevation, latitude and distance from the Ocean indicate that the genetic responsiveness of populations to environmental change depended upon the original population locations. The biological implications of this will be discussed in the next section.

Examination of the population mean height and family mean height correlations among environments (Table 3) indicates significant correspondence between performance in one environment and performance in another environment. Approximately 74% (the coefficient of determination) of the variation in the population height means in the growth room could be accounted for by population height means in the greenhouse. As will be discussed in a later section, I believe that family and population heights from the nursery correlate less well with the other two environments because of the relatively large experimental error associated with the nursery experiment.

Clinal Patterns of Population Variation

The combined analysis revealed that S_p^2 was over four times larger

Table 3. Correlations of first-year height growth population means (below diagonal) and family means (above diagonal) between environments.

	Growth Room	Greenhouse	Nursery
Growth room	1.00	0.81[a]	0.53
Greenhouse	0.86[b]	1.00	0.54
Nursery	0.71	0.65	1.00

[a]Family mean correlations have 58 df., r = 0.33 sig at P = 0.01.
[b]Population mean correlations have 28 df., r = 0.46 sig at P = 0.01.

than $S^2_{F/P}$ indicating marked genetic differentiation among the populations sampled. In other studies of juvenile height growth in western conifers (Campbell and Sorensen 1978, Griffin and Ching 1977, Hamrick 1976, Rehfeldt 1974), this pattern has been interpreted as the result of adaptive genetic modification in response to differential natural selection in the populations' original environments.

When strong differentiation occurs among populations, we attempt to describe this variation by developing clinal regression models relating the performance of a population to its original geography, topography and climate. In all three of our test environments (common gardens), first-year population mean height correlated most strongly with the elevation of its origin (Table 4). Seed collected at higher elevations produced shorter seedlings in all test environments. Shorter seedlings also tended to result from seed collected in southern or

Table 4. Correlations of first-year height growth population means from the three test environments with topographic variables from the population locations.

Test Environment	Topographic Variables from Population Locations				
	Elevation	Latitude	Distance from Ocean	Aspect[a]	Site Index
Growth room (35)[b]	-.868	.777	-.531	.161	.347
Greenhouse (31)	-.817	.709	-.603	.197	.299
Nursery (35)	-.590	.525	-.403	.030	.222
Combined means (30)	-.855	.781	-.563	.200	.341

[a]Variable used was % slope * cosine aspect (Stage, 1976).
[b]Number of populations represented in each environment. For 33 df., r = 0.33 and 0.43 significant at P = 0.05 and 0.01. For 29 df., r = 0.36 and 0.46 significant and P = 0.05 and 0.01.

eastern portions of the sampled region. On the other hand, population height in our test environments was not associated with the aspect or site index of the population seed collection location. The correlations (multi-collinearity) existing between elevation and latitude ($r = -0.80^{**}$) and between elevation and distance from the ocean ($r = 0.44^{*}$) imply the presence of confounding and make it impossible to separate the influences of these three variables on height growth. Indeed these variables are merely imperfect substitutes for more fundamental variables (for example, temperature, photoperiod and precipitation). In this context, note that the correlations between population latitude and height growth are in the reverse direction usually reported. When population latitude correlated with height growth in other investigations (Burley 1966, Campbell and Sorensen

1978, Hamrick and Libby 1972, Morgenstern 1969; see also Wright 1976, p. 255), northern populations were slower growing; however, we found the northern populations to be faster growing. The populations in this study sampled a much smaller latitudinal range (1°) than did populations in many other provenance tests (6-20°). I believe that the faster growth of the northern populations in our study reflected the facts that northern environments tend to be lower elevations and have more summer precipitation.

Regressing population height on the topographic variables demonstrated that in all test environments, a population's height was most closely related to its elevation (Table 5). Elevation accounted for a large portion of the variation in population mean heights in the growth room and greenhouse environments (R^2 = 0.75 and 0.67), but was less effective in accounting for the variation in the nursery data (R^2 = 0.35). For all three test environments, elevation entered the model first and, after elevation was in the model, no other variables added significantly. Also, the models including only elevation seemed to adequately account for the variation in population means as evidenced by the lack of fit tests. In all test environments, populations from higher elevations were shorter (Figure 3). Investigations of Pacific Northwest Douglas-fir (Campbell and Sorensen 1978), California Coastal Douglas-fir (Griffin 1978, Sweet 1965), Rocky Mountain Douglas-fir (Rehfeldt 1974) and Southern Oregon Douglas-fir (Hermann and Lavender 1968) reported similar trends with elevation. In these studies, variables other than elevation were sometimes also important.

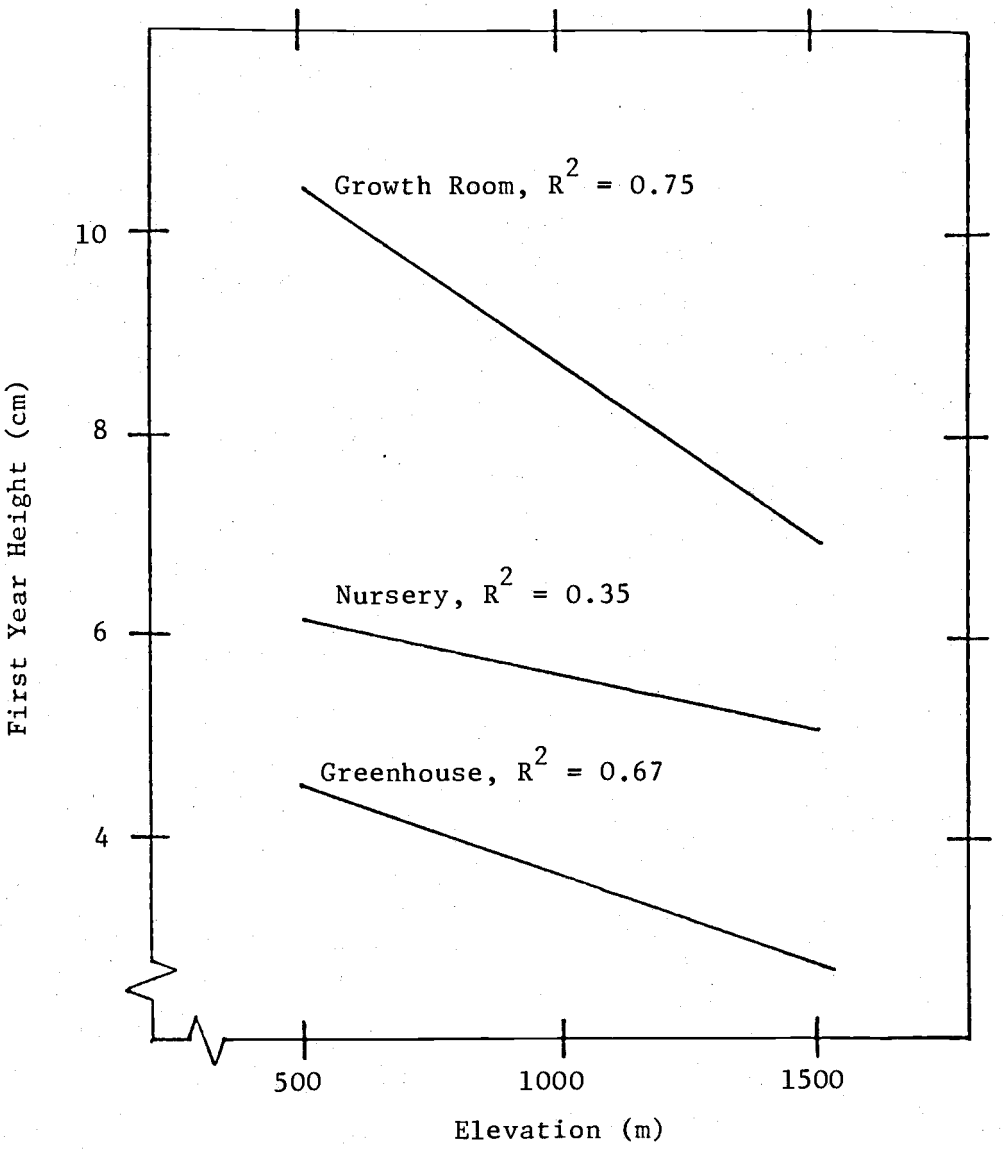

Figure 3. Regressions of first-year population height growth on elevation of population location in three test environments.

Table 5. Regressions of population mean heights from the three test environments on elevation.

Source	Test Environment: Growth Room df	Growth Room MS	Greenhouse df	Greenhouse MS	Nursery df	Nursery MS
Populations	34	12.14**	30	4.16**	34	3.76^{ns}
Elevation	1	311.42**	1	83.33**	1	44.58**
Lack of Fit	33	3.08^{ns}	29	1.43**	33	2.53^{ns}
Family/Population	35	2.98	31	0.64	35	2.89
R^{2a}		0.75		0.67		0.35

[a] R^2 is the fraction of the population sum of squares accounted for by the regression of population means on elevation.

As mentioned previously, the slopes (Figure 2) from the joint regressions of population mean heights on environmental means correlated strongly with population elevation ($r = -0.72^{**}$ with 28 df). This indicates that populations from higher elevations responded less to the favorable environments. Note that all populations responded positively by having taller seedlings in the more favorable test environments, but that lower elevation populations responded more than higher elevation populations. We would expect this result if the temperature regime at higher elevations has resulted in natural selection of genotypes with a more conservative (shorter) developmental cycle (Mangold and Libby 1978). In a study of height growth of eleven jack pine (Pinus banksiana) provenances, northern provenances tended to be more stable (less responsive) to environmental changes than did southern provenances

(Morgenstern and Teich 1969); however, in a study of four other conifers, the situation was less clear (Mergen and others 1974).

Effects of Test Environments on Clinal Models and Population Structure

Having grown the plants in three quite distinct test environments, we can examine similarities among the clinal regression models developed for the different environments. As already described, the overall patterns of our models were similar in all 3 test environments; however, the efficiencies of the models vary dramatically. Correlations between population mean heights and population topographic variables were consistently smaller (in absolute value) for the nursery test environment (Table 4) and the regression model for the nursery data accounted for only 35% of the variation in population mean heights relative to 75 and 67% for the models describing the growth room and greenhouse data (Table 5). Other investigators have also found clinal regression models to vary depending upon the test environments. In a growth room study of four Northeastern conifers, in test environments where trends could be demonstrated, a pattern of decreasing growth with increasing latitude of seed origin was confirmed. However, regressions changed with test environment and in some test environments, no trend at all could be established between growth and latitude (Mergen and others 1974). Decreasing height growth of sitka spruce (Picea sitchensis) with increasing latitude was found in some test environments, but the correlation was not significant in other environments (Burley 1966). Slightly differing clinal patterns and differing effectiveness of models were reported for different test environments

in a study of juvenile height of Pacific Northwest Douglas-fir (Campbell and Sorensen 1978).

To examine the possible reasons why the regression model for the nursery data was less effective than that for the growth room data, I ran individual analyses of variance for both test environments (Table 6). First, more experimental error in the nursery test environment would result in less effective regression models. Roughly assuming only additive genetic variance, then in each test environment $\sigma_w^2 = \sigma_e^2 + 3/4\ \sigma_A^2$ (Becker 1975, p. 32) where σ_e^2 is the variance due to environmental differences among trees within a row-plot and σ_A^2 is the additive genetic variance. Further assuming that $\sigma_{F/P}^2 = 1/4\ \sigma_A^2$, then our estimate of σ_e^2 is $S_e^2 = S_w^2 - 3\ S_{F/P}^2$. So, if for each test environment, S_e^2 roughly estimates the error from tree-to-tree within a row and S_R^2 estimates the error from row-to-row within a family, the $S_e^2 + S_R^2$ estimates the total within-block experimental error. For the growth room and nursery, respectively, $S_e^2 + S_R^2$ = 36% and 46% of the total variation. These rough approximations indicate little, if any, additional experimental error in the nursery test environment.

Second, poorer genetic discrimination among populations in the nursery test environment would lead to less effective regression models. Population differentiation relative to that for families within populations was eleven times greater in the growth room compared to the nursery ($S_P^2/S_{F/P}^2$ = 2.2 and 0.2 in the growth room and nursery). Possibly, low elevation populations were better able to take advantage of the longer growing season in the growth room causing a wide dis-

Table 6. Individual analyses of variance of first-year height growth in growth room and nursery test environments.

Source	Growth Room df	Growth Room MS	Growth Room Intraclass[a] Correlation (% S_T^2)	Nursery df	Nursery MS	Nursery Intraclass Correlation (% S_T^2)	EMS[b]
Population	34	12.15**	22.8	34	3.76ns	2.8	$\frac{\sigma_w^2}{K_1} + \sigma_R^2 + K_2\sigma_{F/P}^2 + K_3\sigma_P^2$
Family/Population	35	2.98**	10.2	35	2.89**	12.8	$\frac{\sigma_w^2}{K_1} + \sigma_R^2 + K_2\sigma_{F/P}^2$
Row within Family	140	.94**	8.1	207	.90**	18.6	$\frac{\sigma_w^2}{K_1} + \sigma_R^2$
Within-row[c]	374	3.94	58.9	543	2.55	65.8	σ_w^{2d}

[a] $S_T^2 = S_w^2 + S_R^2 + S_{F/P}^2 + S_P^2$

[b] For Growth Room $K_1 = 9.9$, $K_2 = 3$, $K_3 = 6$. For Nursery $K_1 = 14$, $K_2 = 4$, $K_3 = 8$. K_1 is the harmonic mean of the number of trees in a row.

[c] Within-row mean squares were estimated from a random sample of rows.

[d] Each of the variance components is estimated by a sample variance component;

S_P^2 estimates σ_P^2 = variance among populations,

$S_{F/P}^2$ estimates $\sigma_{F/P}^2$ = variance among families within populations,

S_R^2 estimates σ_R^2 = variance among row-plots within families,

S_w^2 estimates σ_w^2 = variance among trees within row-plots.

crimination among populations in that test environment. In the shorter nursery growing season, lower elevation populations may not have had the opportunity to outgrow higher elevation populations resulting in poorer discrimination among the populations. Both of these reasons, more experimental error and poorer discrimination among populations, viably explain why the clinal regression model was less effective in the nursery; from these data we cannot say which of the two is more important.

Conclusions

In this study of first-year height growth of Douglas-fir from Southwestern Oregon, variation due to population x environment interaction was only 1/4 of the variation due to population differences. Furthermore, much of the population x environment interaction was explainable as a scale effect rather than as the result of rank changes. However, our test environments did not include a cold environment. Often genotype x environment interaction resulting from rank changes occurs when test environments include both extremely cold and moderate environments (e.g. northern and southern plantations). In these cases height growth is often a function of frost hardiness (Wright 1976, p. 283-311) and differential frost hardiness may lead to rank changes. I found a distinct trend for faster growth for populations from lower elevations and feel that the same sort of clinal pattern would probably be found if these populations were tested in low to mid-elevation field

plantations in this region; however, extrapolating these results to any cold (e.g. high elevation) plantations would be risky.

Even though the clinal regression models demonstrated similar trends in all test environments, the model for the nursery data was less effective in accounting for the variation in population mean heights. In initial attempts to describe and pattern geographical adaptive variation, it is important to choose test environments which have low experimental error and discriminate among the populations being tested (Campbell and Sorensen 1978). If growth room-type test environments are used, they should sample the range of climates of interest. Tentative clinal models based on these "growth room climates" can then be tested in field plantation tests.

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CHAPTER 2. GENETIC VARIATION IN DROUGHT RESISTANCE, PHENOLOGY, AND MORPHOLOGY

Introduction

Environmental conditions vary widely in southwestern Oregon. Over very short distances, differences in aspect, soil parent material and slope result in quite different local environments. Over longer distances, temperature and rainfall gradients associated with elevation, distance from the Ocean and latitude have resulted in a rich mosaic of plant communities distributed throughout the region (Waring 1969). These factors lead to widely varying growing and planting conditions among southwestern Oregon reforestation sites. Drought shortens the growing season for low elevation sites with low soil moisture holding capacity, while late snow melt and early fall frosts shorten high elevation growing seasons.

Douglas-fir nursery seedlings planted on these sites must be properly adapted both physiologically and genetically to ensure good initial survival and growth. Many phenological, morphological and physiological seedling characteristics affect seedling survival during the establishment phase. In this chapter, I report results from several experiments designed to examine genetic differentation in several seedling characteristics of southwestern Oregon Douglas-fir. The chapter is divided into two major sections. First, I discuss genetic variation in some phenological and morphological traits as expressed in dry or moist growing conditions. These traits are important as they relate

to the adaptation of seedling to the planting environment. For instance, phenological adaptations influence frost resistance (Campbell and Sorensen 1973, Drew and Ferrell 1977, Griffin and Ching 1977, McCreary and others 1978). In the second section, I discuss genetic variation in drought resistance, avoidance and tolerance; these are discussed both as they relate to each other and to the previously discussed phenological and morphological traits.

In order to explore the influence of test environment on trait expression, seedlings were grown in two test environments, a growth room and a greenhouse. Common objectives and approaches guided the designs of experiments in both test environments. In both test environments a Dry experiment examined genetic variation in seedling trait expression (other than survival) under conditions simulating those of droughty, low elevation sites in southwestern Oregon. The Drought Survival experiment in both test environments measured genetic variation in seedling survival under an extended soil drought. I intended that the "drought" in both test environments simulate southwestern Oregon growing seasons. Finally, in the greenhouse (but not the growth room), a Moist experiment measured genetic variation in seedling growth and phenology in moist soil conditions.

Drought resistance, drought avoidance and drought tolerance are used as defined by Levitt (1972 p. 10-12 and p. 355). Drought resistance includes both avoidance and tolerance and is used when separation into the 2 components is not feasible. The definitions of drought avoidance and drought tolerance rely on the relationship of the total plant water potential Ψ_t to the water potential of the

environment. If a plant maintains a high Ψ_t (equivalent to a low absolute value of plant water stress) during conditions of low environmental water potential (high environmental water stress), it is avoiding the drought. Drought avoidance mechanisms are plant adaptations which allow the plant to maintain a favorable Ψ_t during drought. Drought tolerance mechanisms allow the plant to grow and/or survive during drought even though Ψ_t becomes low in response to the drought.

Materials and Methods

Experimental Designs

Growth Room Experiments

General: The growth room experiments employed seedlings in their second growing season. The treatment of these seedlings in their first growing season was previously described (the growth-room-grown seedlings in Chapter 1). In order that the seedlings obtain sufficient winter chilling after their first growing season, we moved them into a walk-in refrigerator equipped with fluorescent lights (approximately 1000 ft-c at seedling level) and maintained them there for about two months at 3-6°C with an eight hr photoperiod.

During the second week of February, 1978, seedlings were transferred into one of two experiments, the growth room Dry experiment or the growth room Drought Survival experiment, by extracting them from their plastic tubes and planting them (using a hand dibble) into large,

18 cm deep soil boxes. The seedlings were planted at a five cm x five cm spacing in a clay loam forest soil. One row of buffer trees surrounded the experimental trees. The seedlings in their soil boxes grew in the growth room under a 16 hr photoperiod and 25°C/20°C thermoperiod for the duration of both experiments. Figure 1 depicts a synopsis of the schedule of events for both the Dry and Drought Survival growth room experiments.

Dry Experiment: The completely randomized design for the growth room Dry experiment meant that five to seven seedlings from each of 70 wind-pollinated families representing 35 of the populations described in Chapter I were planted into one large soil box (180 cm long x 75 cm wide x 18 cm deep). All 392 seedlings were measured for all traits.

Bud burst began occurring only seven days after the February 15, 1978 planting and was monitored every two days from February 22 to March 12 (a period of 16 days). A terminal bud was considered burst if the bud scales had parted enough to expose green needles. We recorded the Julian date of bud burst for each seedling. The seedlings were kept well-watered until March 24, 18 days after the average date of bud burst, at which time watering was suspended. Periodically, we monitored the progressive decline in seedling Ψ_t (Figure 1) by measuring the maximum (predawn) Ψ_t of several buffer seedlings with a pressure bomb (Waring and Cleary 1967). On April 24, 32 days after the suspension of watering, we began to harvest the Dry experiment for final measurements. First, on the night of April 24, for each seedling we 1) severed the shoot from the root at the cotyledon scar, 2) measured the length

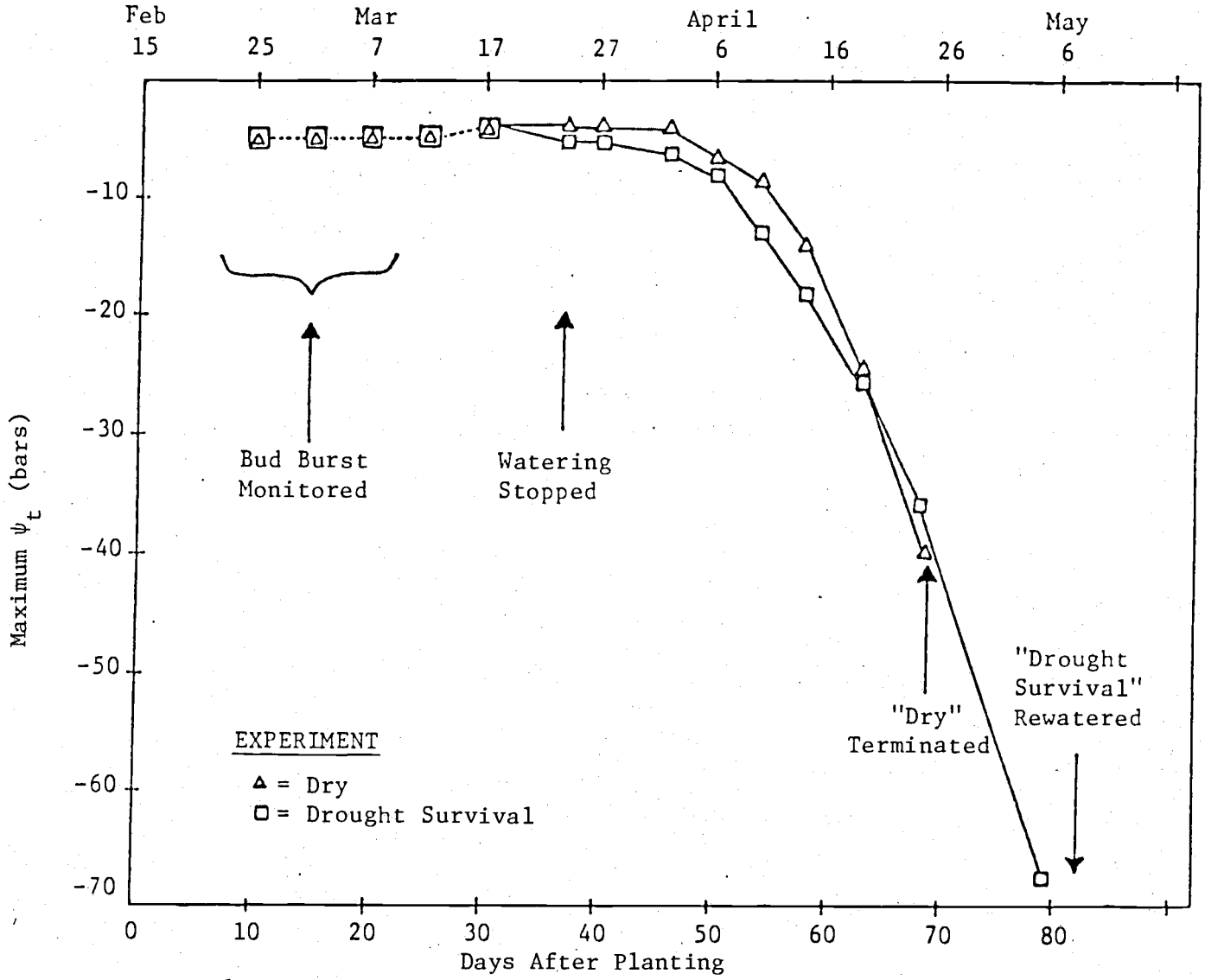

Figure 1. Activity schedule for growth room experiments in relation to ψ_t.

of the epicotyl (two-year height) to the nearest 0.5 cm, 3) removed 20 to 30 current-year needles for relative water content (RWC) determination, 4) measured predawn seedling Ψ_t with a pressure bomb and finally 5) placed the seedling shoot into a labeled bag for ovendry weight determination.

For RWC determination of the 20 to 30 needles, we obtained 1) the actual fresh weight (F), 2) the saturated weight (S) of the needles after they had been placed between wet paper towels and allowed to absorb water for 24 to 36 hr in a dark room and 3) the ovendry weight (D) after drying the needles for 48 hr at 70°C. RWC was calculated after Slayter (1967 p. 150) as

$$RWC = \left(\frac{F - D}{S - D}\right) \times 100.$$

The second stage of harvesting, on the day of April 25, consisted of carefully excavating the root portion of each seedling from the soil box. The root core portion of each seedling was still intact, conforming to the shape of the first growing season's plastic container. In addition, new roots had egressed from this core into the soil during the second growing season. For each seedling we 1) counted the number of egressed roots over 2 cm long and 2) obtained the ovendry weight for the entire root system (core plus egressed roots).

Drought Survival Experiment: The growth room Drought Survival experiment, also planted on February 15, 1978, consisted of a randomized complete block design with three blocks (large soil boxes). Within each box (180 cm long x 75 cm wide x 18 cm deep), a seven tree rowplot represented each of 70 families (35 populations). The seedlings

burst bud and grew under well-watered conditions until March 24 when watering was suspended. Because the buffer trees used to monitor the progressive decline in Ψ_t were under very similar amounts of water stress in the Drought Survival and Dry experiments, average values were plotted in Figure 1.

By May 5, the Drought Survival experiment seedlings averaged -68 bars maximum Ψ_t and many seedlings appeared dead. On May 8, I rewatered and allowed the seedlings to recuperate under well-watered conditions for 6 weeks. At this time, I considered that seedlings which had recuperated had survived the drought, while dead seedlings had succumbed. The two measures of seedling survival, the percentage of trees in a family row-plot which had any green needles and the percentage of trees in a row-plot which had reflushed any buds since rewatering, correlated highly on a row-plot basis ($r = 0.985^{**}$, with 208 df) and I only report the former (hereafter termed survival).

Greenhouse Experiments

General: The greenhouse experiments employed seedlings described as the greenhouse-grown seedlings in Chapter I. In December, 1978, the one-year old seedlings were placed outside at Corvallis, Oregon for their winter chilling requirement. During the first week of March we transplanted the seedlings from their containers into one of three greenhouse experiments, a Dry experiment, a Moist experiment or a Drought Survival experiment. For all three experiments, we extracted the seedlings from their containers and transplanted them to a 5 cm

x 6 cm spacing in 20 cm deep soil boxes containing a clay loam forest soil. In every soil box a row of buffer seedlings which surrounded the experimental seedlings was used to monitor Ψ_t. Figure 2 presents a synopsis of the activities for the three greenhouse experiments.

Dry Experiment: Similar in design to the growth room Dry experiment, the greenhouse Dry experiment consisted of a completely randomized design in which eight to ten seedlings from 45 families representing 29 populations were randomly assigned positions in one large soil box (213 cm long x 122 cm long x 20 cm deep). The seedlings were well-watered throughout the monitoring of terminal bud burst (March 28 to May 2) and up until the suspension of watering on May 27. We measured epicotyl length (height) to the nearest 0.5 cm on May 19 and June 20.

On the night of June 22, we began to take final measurements on each seedling in the greenhouse Dry experiment by 1) removing approximately 30 current-year needles for RWC determination, 2) separating the shoot from the root at the cotyledon scar for ovendry weight determination and 3) measuring the maximum Ψ_t. The next day, we carefully excavated the root portion of each seedling from the soil box, separated the root core from the egressed roots and put these into separately labeled bags for ovendry weight determination.

Drought Survival Experiment: The randomized complete block design of the greenhouse Drought Survival experiment meant that within each of three blocks (244 cm long x 122 cm wide x 20 cm deep soil boxes) a ten-tree row-plot represented each of the 66 families (35 populations). The planting and treatment of this experiment were identical to that of the greenhouse Dry experiment until June 22. Total epicotyl length

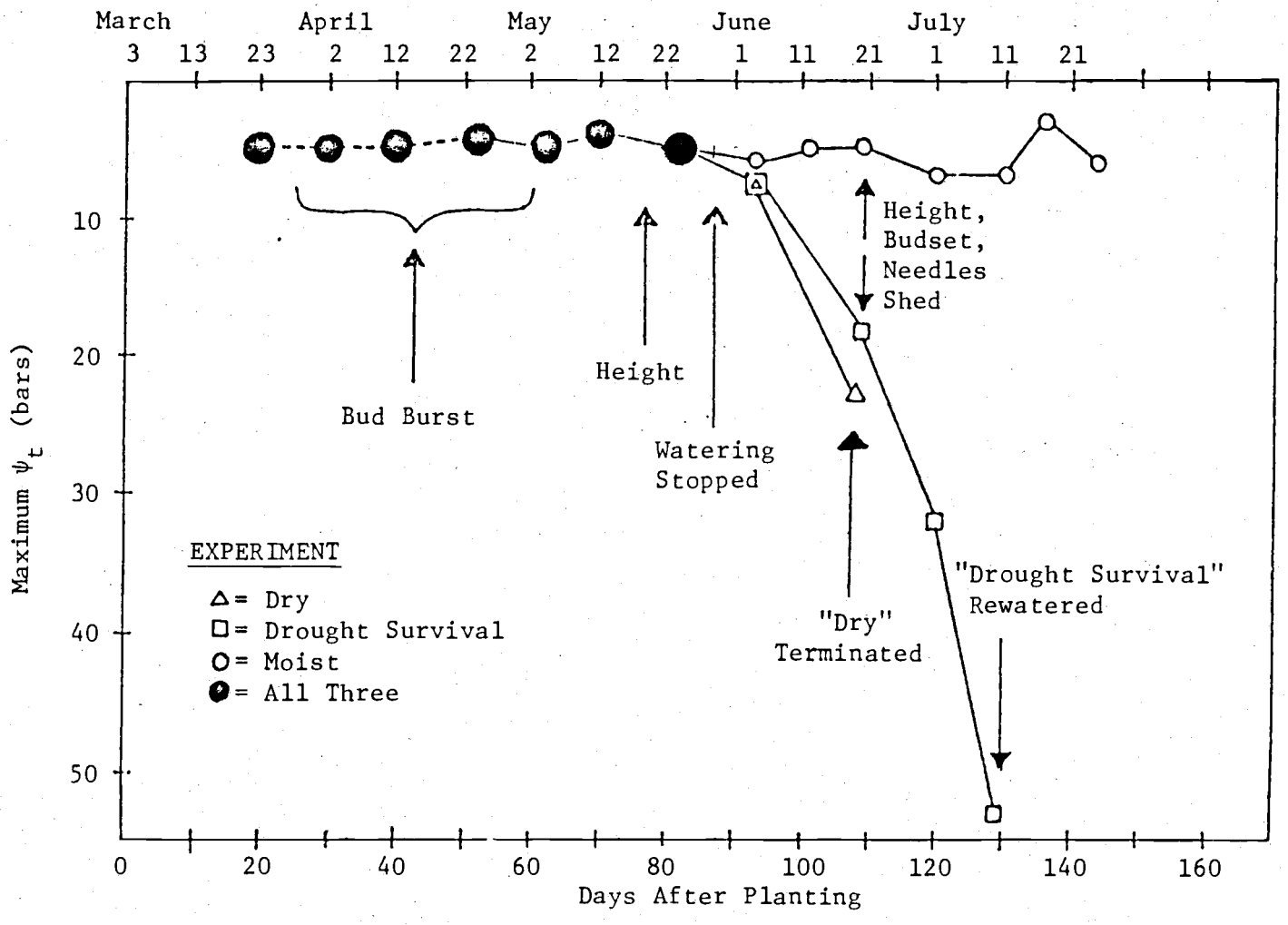

Figure 2. Activity schedule for greenhouse experiments in relation to ψ_t.

(height) was measured on May 19 and June 22. Also on June 22, we measured the status of each terminal bud (0 = flushed, 1 = set) and estimated the percentage of the one-year old (first growing season) needles which were brown or had been shed.

After June 22, the seedlings in the Drought Survival experiment continued to experience drought until I rewatered them on July 11 (Figure 2). After seven weeks of recovery time under well-watered conditions, we scored each seedling for the percentage of live needles and the presence of a newly flushed bud. A seedling was considered alive after the recovery period if it had flushed a bud or if any of its needles were alive and green. On a row-plot mean basis, this measure correlated strongly ($r = 0.96$, with 196 df) with the row-plot mean for the percentage of live needles. Because the percentage of live needles is more nearly continuous, I report it as survival for the greenhouse Drought Survival experiment. Note that for the greenhouse and growth room Drought Survival experiments, survival was a slightly different measure.

Moist Experiment: The randomized complete block design of the greenhouse Moist experiment consisted of three blocks (191 cm long x 66 cm wide x 20 cm deep soil boxes) within each of which a five seedling row-plot represented each of the 50 families (30 populations). This experiment was watered at least weekly throughout the course of the growing season. We measured height, bud condition and percentage of brown year-old needles as described for the Drought Survival

experiment. In addition, height was also measured on July 20 (Figure 2).

Statistical Analysis

Derived Variables

I calculated two derived variables from the height measurements taken during the experiments. Total second-year height growth is the total second-year height minus the first-year height. Late season height growth is that portion of the second-year height growth completed after the first measurement period (May 19) relative to the total second-year height growth; it is calculated as

$$\text{Late Season Height Growth} = \frac{\text{Final Height} - \text{May 19 Height}}{\text{Second-Year height Growth}}.$$

Transformation and Analyses of Variance

Several of the measured and derived variables were percentages. For some of these, e.g. RWC and late season height growth, the arcsine square root transformation (Snedecor and Cochran 1967 p. 327) was employed for analyses and this is noted in the analysis of variance tables. All transformed variables were back transformed before the presentation of means.

For the growth room and greenhouse Dry experiments, individual seedling measurements served as the experimental units in the analyses of variance. For all other experiments, row-plot means served as the bases of analysis. Intraclass correlations were obtained by equating the mean square for a given source of variation to its expected value,

solving for the variance component for that source, and dividing this by the sum of the variance components for all sources except blocks. Coefficients for the expected mean squares and the mean squares themselves were obtained by the SAS Varcomp procedure (Barr and Goodnight 1976).

Multiple linear regression procedures were identical to those described in Chapter I except that aspect was eliminated as an independent regressor.

Covariance Models

In both the greenhouse and growth room Drought Survival experiments, some areas of some blocks (soil boxes) dried out much more rapidly than others resulting in large experimental error in survival. No pattern to this intrablock variation could be found in the greenhouse, but in the growth room, the fan which circulated the air caused some portions of each block to experience more evaporative demand than others (Figure 3). The systematic nature of this circulation caused a distinct pattern of survival in each block.

In order to adjust for and reduce the effect of this systematic "experimental error" in the growth room Drought Survival experiment, I built covariance models which related the survival of a family row-plot within a block to the position of the row in the block (soil box). In each block, 70 family row-plots of 7 trees each were positioned in the soil box as 2 row-plots in each of 35 rows. The covariance models varied drastically from block to block as a result

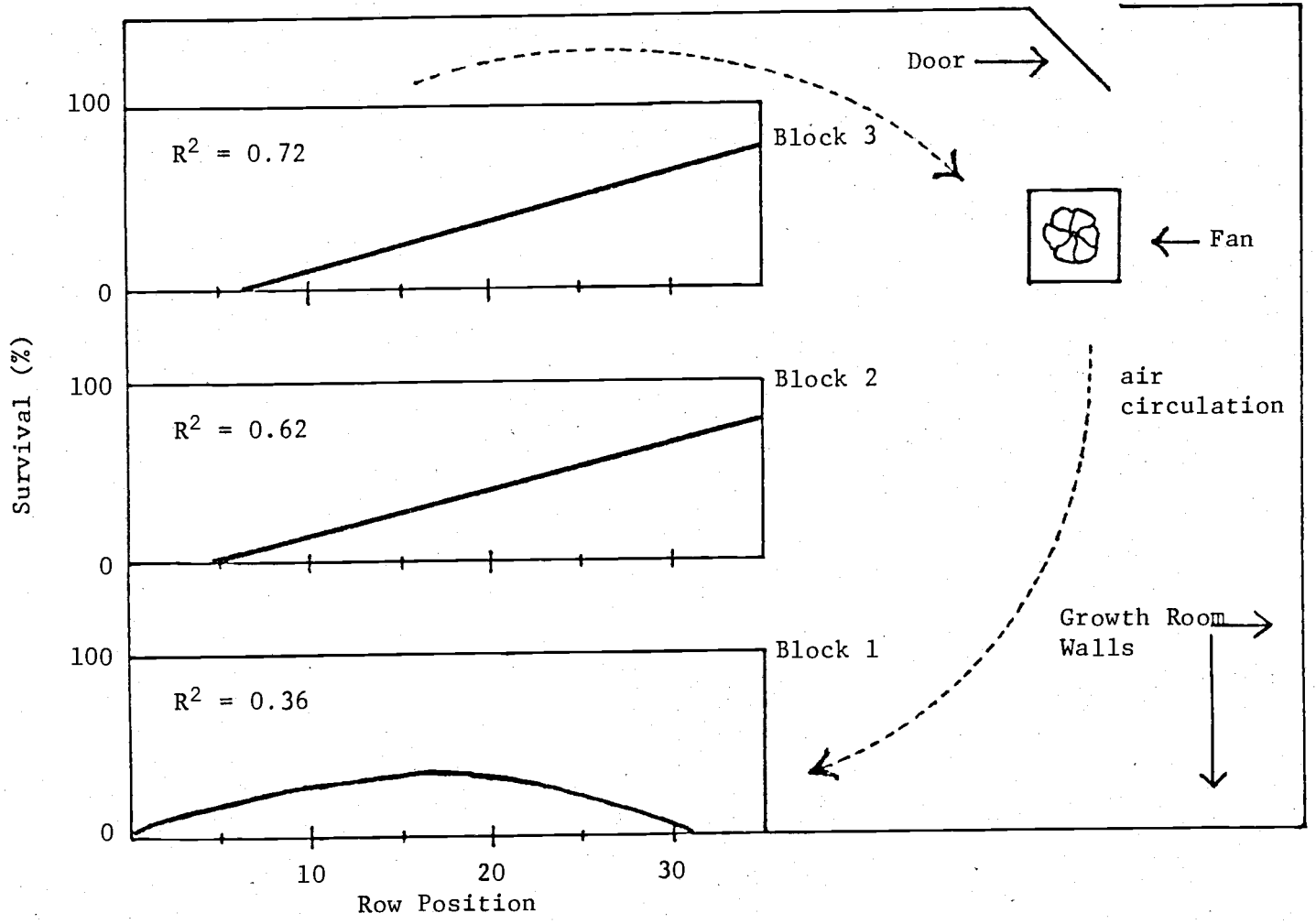

Figure 3. Covariance models depicting seedling survival and the position of the seedling relative to the growth room fan.

of the positioning of the blocks in relation to the fan (Figure 3). The circulating air hit the front end (high row numbers) of block 1 first and in continuing to circulate hit and dried out the back ends of all three blocks. A quadratic model (2 df) relating the position of a family row-plot to the survival of the row-plot accounted for 36% of the variation in family means in block 1. In blocks 2 and 3, linear models accounted for 62 and 72% of the family mean variation. These covariance models were used to obtain adjusted within-block values for survival; these values were further adjusted for additive block effects before being subjected to a completely randomized analysis of variance. In all, six df were used in the survival adjustment: 2 df, 1 df and 1 df for covariance adjustment within blocks 1, 2, and 3, respectively, and 2 df for additive block effects.

Results and Discussion

Comparison of Growth Room and Greenhouse Test Environments

Because throughout this discussion I compare trends as they occurred in the growth room and greenhouse, here I briefly contrast these test environments both in terms of their differential influence on seedling morphology and phenology and in terms of differences in the development of their respective moisture regimes during the present experiments. After two growing seasons in their respective test environments, greenhouse Dry seedlings averaged only 62% as tall as the

growth room Dry seedlings (8.9 cm and 14.4 cm, respectively). Even though taller, the growth room seedlings' shoot and total biomass averaged only 79% and 66% of the greenhouse seedlings. Using weight per unit length of stem as a measure of shoot "stockiness", greenhouse seedlings were more than twice as "stocky" as growth room seedlings (0.064 g/cm and 0.030 g/cm respectively). Differences in seedling morphology between the two test environments are further evidenced by shoot/root ratios of 1.12 and 0.79 for the growth room and greenhouse seedlings.

The divergent seedling morphology may reflect the different light intensities of the two test environments. The 1000 ft-c light intensity in the growth room is well below light saturation for Douglas-fir (Krueger and Ferrell 1965), while greenhouse seedlings experienced full sunlight. Compared to Douglas-fir seedlings grown in full sunlight, those grown in low light intensity environments tend to 1) grow taller, 2) produce less biomass and 3) have higher shoot/root ratios (Drew and Ferrell 1977); these are exactly the differences between the greenhouse and growth room seedlings.

Regarding moisture regime development in the greenhouse and growth room Drought Survival and Dry experiments, seedlings in the greenhouse grew longer before the drought became severe (compare Figures 1 and 2). Greenhouse seedlings grew 73 days from average bud burst date until severe stress (-20 bars Ψ_t, compared to only 40 days for growth room seedlings. This difference in moisture

regime development could also possibly account for some of the previously described morphological differences between the greenhouse and growth room Dry experiment seedlings.

Phenological and Morphological Traits

Phenology and Second-Year Height Growth

Bud Burst: Bud burst patterns, best exemplified by the greenhouse Drought Survival and growth room Dry experiments, indicate stronger genetic differentiation among families within populations than among populations. In the greenhouse Drought Survival experiment, differences among families within populations accounted for 42% of the within-block variation (Table 1); it was also the only significant source of variation in the growth room Dry experiment (Table 2). The genetic differentiation seemed stronger in the greenhouse. Based on the means of the 64 families common to both experiments, bud burst date in the greenhouse correlated poorly with that in the growth room ($r = 0.21^{ns}$, with 62 df).

A partial explanation of these results might be the fact that the bud burst period was much more rapid in the growth room. Long, cool periods of winter chilling coupled with warm temperatures and long photoperiods during flushing greatly enhance the rate of spring bud burst in Douglas-fir seedlings (Campbell and Sugano 1975, 1979). These conditions in the growth room meant that seedlings began to flush only seven days after planting and that the flushing period

lasted only 15 days. In contrast, the greenhouse flushing period began about three weeks after planting and lasted for over a month. The rapid bud burst in the growth room might have made discrimination among families and populations difficult because everything burst at once (see Campbell and Sugano 1979). This might also explain the poor correlation of family means between the two environments.

Bud burst differences among populations showed up in neither test environment (Tables 1 and 2). In the greenhouse, the estimated family within population variance component was over six times larger than the estimated population variance component. In the growth room test environment (but not the greenhouse), population mean bud burst date correlated loosely with the elevation and latitude of the population locations (Table 3); the slight trend indicated that populations originating from higher elevations and more southerly latitudes within the sampled area tended to burst bud later. Hermann and Lavender (1968) reported a similar trend for an elevational transect sample of Douglas-fir populations from southwestern Oregon.

The facts that the trends were weak in the growth room and that population differences did not show up at all in the greenhouse (where family differences were extremely strong) may be indicative of countering selective influences on the gene pool in this region. In provenance studies of Pacific Northwest Douglas-fir, seed sourses from southwestern Oregon nearly always burst bud sooner in common gardens than more northerly, coastal sources (Campbell and Sugano 1979, Heiner 1968, White and others 1979). We speculated (White and others 1979) that

Table 1. Analysis of variance of phenological traits in greenhouse Drought Survival experiment.

Source	df	Bud Burst (Julian Days) Mean Square	Bud Burst (Julian Days) Intraclass Correlation (%)	Buds Set on 6/20 (%) Mean Square	Buds Set on 6/20 (%) Intraclass Correlation (%)	Late Season Height Growth (%)[a] Mean Square	Late Season Height Growth (%)[a] Intraclass Correlation (%)
Block	2	143.20		2247		53.8	
Population	34	32.18^{ns}	6.6	1808**	29.2	24.9^{ns}	10.8
Family/Population	31	26.62**	42.0	709**	17.8	16.0^{ns}	10.6
Row-plot Error	130	7.71	51.4	352	53.0	11.4	78.5
Experimental Mean		99.7		54.4		4.85	

[a] Analyzed as the arcsin square root of the proportion (Snedecor & Cochran 1967, p. 327).

Table 2. Analysis of variance of bud burst and second-year height growth in the growth room Dry experiment.

		Bud Burst (Julian Days)		Second-Year Height Growth (cm)	
Source	df	Mean Square	Intraclass Correlation (%)	Mean Square	Intraclass Correlation (%)
Population	34	19.73^{ns}	6.2	2.58^{ns}	0.6
Family/Population	35	12.94^{*}	9.1	2.44^{ns}	6.9
Tree-to-Tree Error	322	8.12	84.7	1.73	92.5
Experimental Mean		65.0		6.25	

Table 3. Second-year height growth and phenology: Correlations between population means of measured traits and population topographic variables.

Experiment / Trait	Topographic Variables from Population Locations: Elevation	Latitude	Distance from Ocean	Site Index
Greenhouse Moist (30)[a]				
Bud Burst	0.03[b]	-0.11	-0.06	-0.07
Height Growth by 5/19	-0.28	0.22	-0.09	-0.11
Height Growth by 6/20	-0.49	0.34	-0.30	-0.11
Total Height Growth	-0.59	0.47	-0.37	-0.06
Late Season Height Growth	-0.60	0.48	-0.42	0.01
Greenhouse Drought Survival (35)				
Bud Burst	0.04	-0.05	-0.21	-0.01
Height Growth by 5/19	-0.49	0.38	-0.42	-0.04
Height Growth by 6/20	-0.59	0.48	-0.49	-0.03
Late Season Height Growth	-0.66	0.63	-0.47	0.20
Buds set on 6/20	0.72	-0.78	0.43	-0.32
Growth Room Dry (35)				
Bud Burst	0.52	-0.55	0.13	-0.13
Total Height Growth	-0.44	0.45	-0.29	0.11

[a] Number in parentheses is the number of populations represented in each experiment.

[b] For n = 30, r = 0.36 and 0.46 significant at P = 0.05 and 0.01.
For n = 35, r = 0.33 and 0.43 significant at P = 0.05 and 0.01.

earlier bud burst for southwestern Oregon sources would be of selective advantage by allowing seedlings to exploit the early part of the growing season. This characteristic would have less selective advantage for more northerly, coastal sources whose climates are characterized by more summer precipitation.

Another selective force influencing genetic differentiation in bud burst dates among populations has been indicated in provenance studies of Pacific Northwest Douglas-fir (Campbell and Sorensen 1978), western hemlock[1], and Sitka spruce (Burley 1966). In these studies, provenances from cooler or more continental climates burst bud earlier in warm common gardens. Perhaps provenances from colder climates with early fall frosts have adapted earlier bud burst to exploit the early part of the growing season.

Within the southwestern Oregon region sampled in this study, these two selective forces may counter each other. Perhaps early bud burst is advantageous both at low elevations characterized by hot, dry summers and at high elevations characterized by earlier fall frosts. This would explain why in larger scale provenance studies southwestern Oregon provenances have genetically adapted for earlier bud burst; yet, within the region, population differentiation is weak.

Budset: Time of budset was monitored only in the greenhouse experiments. Two measures of budset, percentage of terminal buds set in a family row-plot on June 20 and late season height growth gave similar but not identical results. The Drought Survival experiment was experi-

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[1]Unpublished research results from John Kuser, Dept. of Forest Science, Oregon State University, Corvallis, OR.

encing considerable moisture stress when budset was measured on June 20 (Figure 1); even seedlings without a terminal bud were not growing. The strong genetic differences in percentage of buds set, among populations and among families within populations, accounted for nearly 50% of the variance in row-plot means (Table 1).

Population means of buds set on June 20 correlated strongly with the elevation and latitude of the original population locations (Table 3). The multiple linear regression model indicates a strong (R^2 = 0.70) clinal pattern in the percentage of buds set (Figure 4). The model estimates that a population originating from a low elevation (500 m), more coastal (70 km from Ocean) and more northerly (43°) location had only 33% terminal budset compared to 80% for a population from 1500 m elevation, 150 km from the Ocean and 42° latitude. Intraspecific genetic variation for earlier budset in populations originating from colder climates has been demonstrated in a number of different species (Burley 1966, Campbell and Sorensen 1978, Cannell and Willett 1976, Hamrick and Libby 1972, Heide 1974, Pollard and others 1975, Sweet 1965). The trend is regarded as an adaptive genetic response resulting from natural selection for earlier budset in cold climates. Provenances of Douglas-fir with earlier budset tend to be more frost resistant (Campbell and Sorensen 1973, Griffin and Ching 1977).

The collinearity of latitude and elevation (r = -0.80**, with 34 df) results in the confounding of the effects of these two variables on budset. The relationship between population latitude and

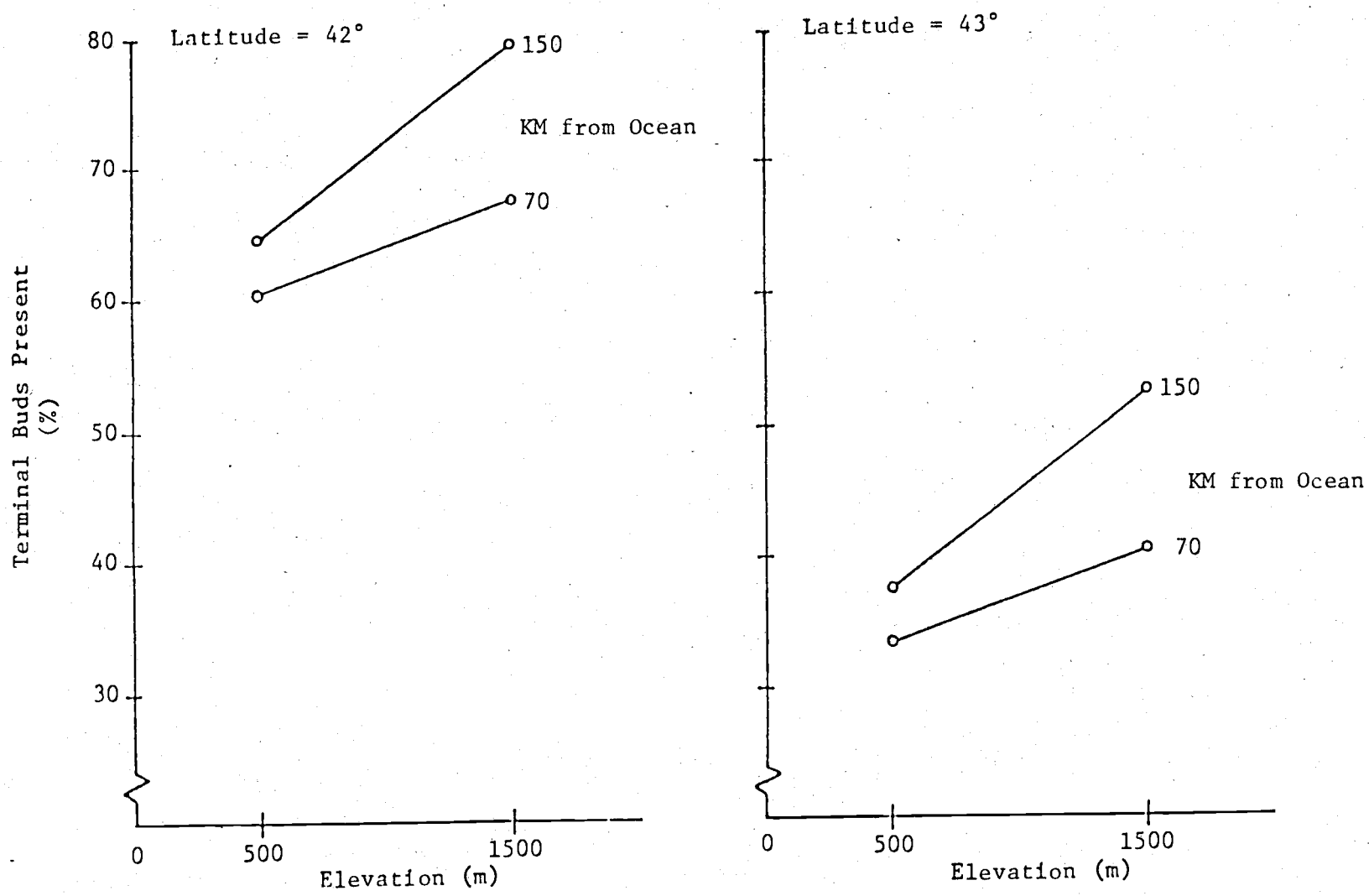

Figure 4. Clinal pattern of terminal buds set on 6/20 in greenhouse Drought Survival experiment (R^2= 0.70).

percentage of terminal budset on June 20 may reflect a temperature gradient because southerly latitudes in the sampled region tend strongly to higher elevations. On the other hand, this relationship may manifest a drought related response, because for a given elevation, southerly latitudes in the region receive less rainfall. Early budset in areas of low summer rainfall may be a drought avoidance mechanism which would be selected for. Compared to Douglas-fir provenances from coastal regions farther north in Oregon and Washington where summer rainfall is more prevalent, southwestern Oregon provenances set bud earlier in common garden experiments (Lavender and others 1968, Lavender and Overton 1972).

Late season height growth was used as the other measure of budset phenology on the assumption that populations which set bud later complete a larger percentage of their height growth in the later part of the season. As expected, compared to seedlings in the greenhouse Drought Survival experiment (Table 1), those in the Moist experiment (Table 4) completed more of their height growth later in the season (22% vs. 5%). The dry soil conditions in the Drought Survival experiment curtailed height growth after May 19, while second flushing in the Moist experiment resulted in appreciable late season growth. In the Moist experiment, strong genetic variation (34% of the total variance in row-plot means) in late season height growth occurred among populations (Table 4). In both the Moist and Drought Survival experiments, population means for late season height growth correlated with elevation, latitude and distance from the Ocean of

the population locations in a similar pattern as described for percentage of buds set on June 20 (Table 3).

Relationship of Height Growth and Phenology: As reported for first-year height growth in Chapter I, population means for second-year height growth consistently correlated with elevation, latitude and distance from the Ocean of the population locations (Table 3). However, in the two experiments (greenhouse Moist and Drought Survival) in which height growth was measured more than once during the growing season, correlations with the topographic variables became stronger later in the growing season. This is best exemplified by the greenhouse Moist experiment (Table 4). At the time of the first height measurement on May 19 (a little over a month after the average bud burst date), the Moist seedlings had completed 75% of their total height growth for the year (4.15 cm out of 5.53 cm). At this time, populations did not differ in height growth and a regression on to elevation accounted for only 6% of the variation in population mean height growth.

Populations differentiated from each other for height growth measured later in the season (Table 4). The plot (Figure 5) of the three regression equations relating population mean height growth at the different measurement times to population elevation estimates that a high elevation (1500 m) population grew less than one cm after the May 19 measurement, while a low elevation population (500 m) grew over 2 cm. These observations indicate that the populations differed most from each other in their ability to take advantage of the later part of the growing season.

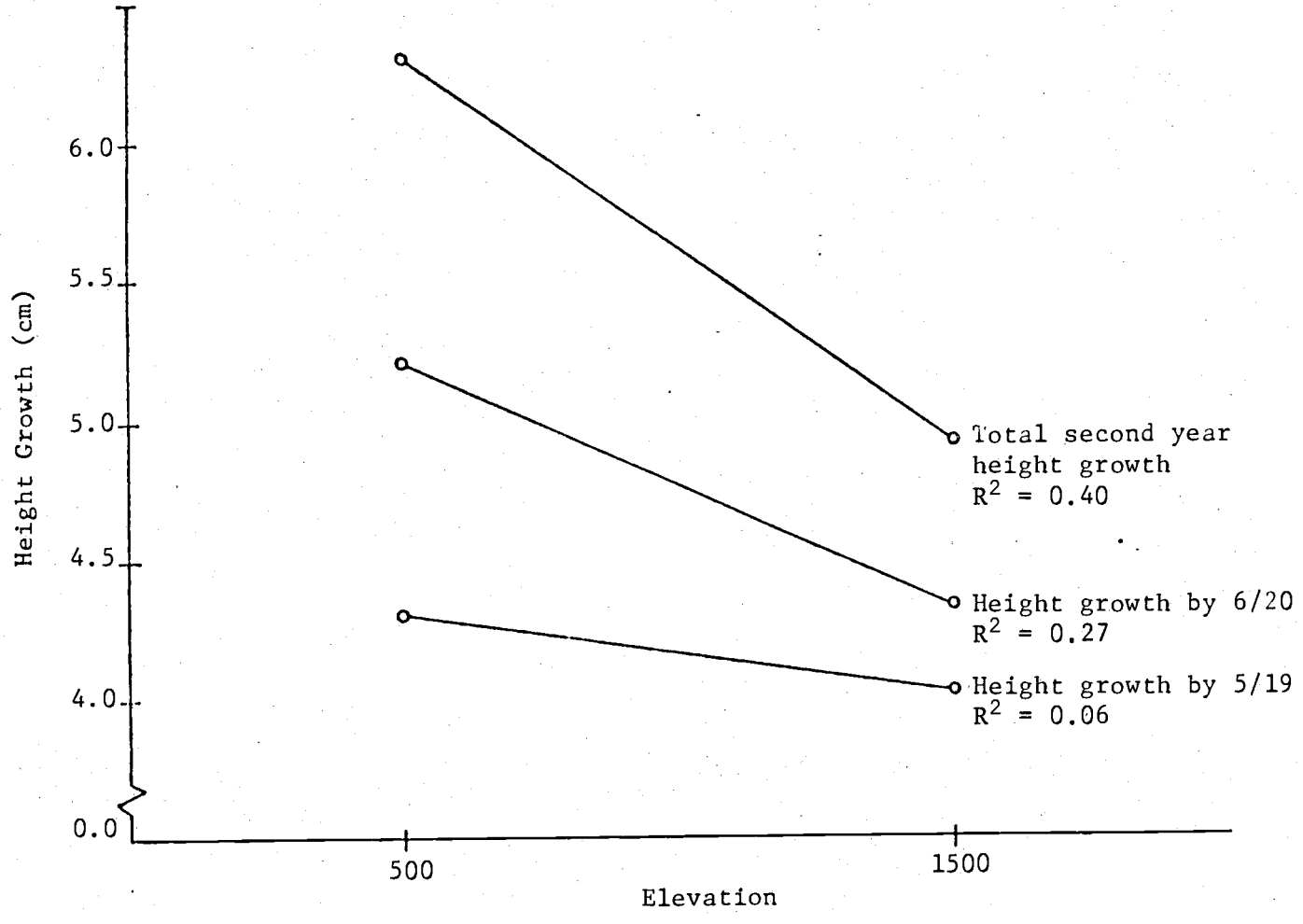

Figure 5. Plot of regression equations relating population height growth to population elevation at three different measurement times in the greenhouse Moist experiment.

Table 4. Analysis of periodic second-year height growth and late season height growth in the greenhouse Moist experiment.

Source	df	Height Growth by 5/19 (cm) Mean Square	Height Growth by 5/19 (cm) Intraclass Correlation (%)	Height Growth by 6/20 (cm) Mean Square	Height Growth by 6/20 (cm) Intraclass Correlation (%)	Total Height Growth (cm) Mean Square	Total Height Growth (cm) Intraclass Correlation (%)	Late Season Height Growth (%) Mean Square	Late Season Height Growth (%) Intraclass Correlation (%)
Block	2	8.20		21.97		21.72		1078.0	
Population	29	0.80^{ns}	4.3	2.12^{ns}	10.3	3.31^{*}	23.6	221.0^{**}	34.2
Elevation	1	1.50^{ns}		16.40^{**}		38.08^{**}		2850.0^{**}	
Lack of Fit	28	0.78^{ns}		1.61^{ns}		2.07^{ns}		130.0^{ns}	
Family/ Population	20	0.69^{*}	20.6	1.50^{*}	16.6	1.44^{ns}	7.2	72.0^{ns}	8.1
Plot Error	98	0.38	75.1	.89	73.1	1.10	69.2	50.0	57.7
R^2		0.06[a]		.27		0.40		0.44	
Experimental Mean		4.15		4.74		5.53		22.2	

[a] R^2 is the fraction of the population sum of squares accounted for by the regression of population means onto population elevation.

In the growth room Dry experiment, populations did not differ in total second-year height growth (Table 2) even though the populations differed quite markedly in first-year height growth (see Chapter I). In terms of total second-year height growth, the growth room Dry experiment contrasted with the previously described greenhouse experiments. Perhaps the quick onset of the drought in the growth room (described in "Comparison of Growth Room and Greenhouse Test Environments") prohibited late season height growth and therefore population differentiation.

On the other end of the phenological cycle, population mean bud burst date never correlated strongly with height growth. Early season height growth correlated better with bud burst date than did total or late season height growth (Tables 5 and 6).

Biomass Relationships

Because dry weights were measured only in the Dry experiments, the following discussion refers only to the greenhouse Dry and growth room Dry experiments. As expected, taller seedlings were heavier; on an individual seedling basis shoot dry weight correlated strongly with total height in both the greenhouse ($r = 0.69^{**}$, with 455 df) and growth room ($r = 0.81^{**}$, with 390 df).

In the growth room, populations differed in shoot dry weight and root dry weight, while families within populations differed in egressed roots and shoot/root ratio (Table 7). Stone and colleagues (see Stone and Schubert 1959) have repeatedly emphasized the importance of root regeneration in seedling survival after planting. To my

Table 5. Pairwise correlations based on population means (above diagonal) and family means (below diagonal) among the traits measured in the greenhouse Drought Survival experiment.

	Bud Burst	5/19 Height Growth	6/20 Height Growth	Buds Set on 6/20	Late Season Height Growth	Needle Shed	Survival
Bud Burst		-0.31[a]	-0.24	- 0.13	0.01	-0.16	-0.25
5/19 Height Growth	-0.26[b]		0.97	-0.33	0.51	0.33	0.11
6/20 Height Growth	-0.19	0.96		-0.47	0.69	0.31	0.06
Buds Set on 6/20	-0.08	-0.37	-0.51		-0.71	0.19	0.49
Late Season Height Growth	0.07	0.42	0.64	-0.68		0.08	-0.14
Needle Shed	-0.10	0.35	0.31	0.12	0.09		0.04
Survival	-0.15	0.09	0.08	0.29	-0.01	0.01	

[a] Population mean correlations have 33 df, r = 0.33 and 0.43 are significant at P = 0.05 and 0.01.

[b] Family mean correlations have 64 df, r = 0.23 and 0.30 are significant at P = 0.05 and 0.01.

Table 6. Pairwise correlations based on population means (above diagonal) and family means (below diagonal) among the traits measured in the greenhouse Moist experiment.

	Bud Burst	5/19 Height Growth	6/20 Height Growth	Total Height Growth	Late Season Height Growth
Bud Burst		-0.50[a]	-0.21	-0.12	0.33
5/19 Height Growth	-0.43[b]		0.85	0.75	0.04
6/20 Height Growth	-0.17	0.83		0.96	0.51
Total Height Growth	-0.11	0.74	0.96		0.68
Late Season Height Growth	0.28	-0.03	0.48	0.64	

[a] Population mean correlations have 28 df, r = 0.36 and 0.46 are significant at P = 0.05 and 0.01.

[b] Family mean correlations have 48 df, r = 0.28 and r = 0.36 are significant at P = 0.05 and 0.01.

Table 7. Analysis of shoot dry weight, root dry weight, egressed roots and shoot/root ratio for the growth room Dry experiment.

Source	df	Shoot Dry Weight (g) Mean Square[a]	Shoot Dry Weight (g) Intraclass Correlation (%)	Root Dry Weight (g) Mean Square[a]	Root Dry Weight (g) Intraclass Correlation (%)	Egressed Roots (#) Mean Square[a]	Egressed Roots (#) Intraclass Correlation (%)	Shoot/Root Ratio Mean Square[a]	Shoot/Root Ratio Intraclass Correlation (%)
Population	34	7.49^{**}	15.3	3.80^{**}	17.0	79.7^{ns}	0.1	0.427^{ns}	0.0
Family/ Population	35	2.94^{ns}	5.9	1.42^{*}	6.8	78.1^{**}	19.4	0.543^{**}	17.2
Tree/Family (Error)	322	2.08	78.8	0.95	76.2	33.5	80.5	0.252	82.8
Experimental Mean		0.45		0.41		12.1		1.13	

[a] Mean squares have been multiplied by 100.

knowledge, strong intraspecific genetic variation in the ability to egress roots after planting has not been previously reported for any North American conifer. In the greenhouse, populations differed only for root dry weight, while families within populations differed for shoot dry weight and shoot/root ratio (Table 8).

That the test environments markedly influenced the genetic expression of these traits is implied in the above discussion and further emphasized by various correlations. In the growth room, shoot dry weight correlated strongly with both root dry weight and the number of egressed roots (Table 9). Further, population means for these response variables correlated at least moderately with the topographic variables of population origin (Table 11). Thus, when growing in the growth room common garden, populations from lower elevations or more northerly latitudes tended to have heavier roots, more egressed roots, heavier shoots and larger shoot/root ratios.

For greenhouse-grown seedlings, similar population trends appeared for shoot dry weight and shoot/root ratio, but the two root parameters did not correlate with any of the other biomass traits (Table 10) nor with the population topographic variables (Table 11).

The tendency for heavier shoots and larger shoot/root ratios for some populations most likely reflects the propensity of these populations to grow later into the growing season. Cannell and Willett (1976) reported that for seedlings of three tree species, shoots were high priority photosynthate sinks during periods of stem elongation.

Table 8. Analysis of shoot dry weight, root dry weight, egressed roots and shoot/root ratio for the greenhouse Dry experiment.

Source	df	Shoot Dry Weight (g) Mean Square [a]	Shoot Dry Weight (g) Intraclass Correlation (%)	Root Dry Weight (g) Mean Square [a]	Root Dry Weight (g) Intraclass Correlation (%)	Egressed Roots (g) Mean Square [a]	Egressed Roots (g) Intraclass Correlation (%)	Shoot/Root Ratio Mean Square [a]	Shoot/Root Ratio Intraclass Correlation (%)
Population	28	9.62^{ns}	0.7	3.67^{*}	5.7	0.553^{ns}	4.5	25.8^{ns}	0.3
Family/ Population	16	9.14^{**}	12.6	1.30^{ns}	0.0	0.301^{ns}	0.0	25.3^{**}	15.3
Tree/Family (Error)	396	3.78	86.6	2.62	94.3	0.359	95.5	9.1	84.4
Experimental Mean		0.57		0.72		0.14		0.82	

[a] Mean squares have been multiplied by 100.

Table 9. Pairwise correlations based on population means (above diagonal) and family means (below diagonal) for traits measured in the growth room Dry experiment.

	BB	HT	SHT	ROOT	EGR	S/R	ψ_t	RWC
Bud Burst Date (BB)		-0.18[a]	-0.11	-0.02	-0.13	-0.08	0.00	0.22
Second Yr. Height Gr. (HT)	-0.17[b]		0.60	0.50	0.44	0.19	0.14	0.25
Shoot Dry Weight (SHT)	0.10	0.50		0.86	0.74	0.43	0.09	0.19
Root Dry Weight (ROOT)	0.14	0.41	0.80		0.80	0.02	0.17	0.18
Egressed Roots (EGR)	0.14	0.34	0.68	0.74		-0.14	0.09	0.10
Shoot/Root (S/R)	-0.06	0.24	0.44	-0.06	0.05		-0.07	0.15
ψ_t	0.11	0.20	0.29	0.20	0.18	0.19		0.39
RWC	0.19	0.37	0.28	0.21	0.23	0.24	0.41	

[a] Population mean correlations have 33 df; r = 0.33 and 0.43 are significant at P = 0.05 and 0.01.

[b] Family mean correlations have 68 df; r = 0.23 and 0.30 are significant at P = 0.05 and 0.01.

Table 10. Pairwise correlations based on population means (above diagonal) and family means (below diagonal) for traits measured in the greenhouse Dry experiment.

	BB	LSHG[a]	HT	SHT	ROOT	EGR	S/R	ψ_t	RWC[a]
Bud Burst Date (BB)		0.55[b]	-0.41	-0.23	-0.25	-0.47	-0.10	-0.26	-0.45
Late Season Height Growth (LSHG)	0.51[c]		0.07	0.19	-0.26	-0.26	0.34	-0.26	-0.55
Second Yr. Height Growth (HT)	-0.36	0.19		0.69	0.34	0.25	0.47	0.06	-0.04
Shoot Dry Weight (SHT)	-0.06	0.22	0.58		0.30	0.37	0.82	0.03	-0.02
Root Dry Weight (ROOT)	-0.15	-0.22	0.15	0.19		0.78	-0.28	0.25	0.06
Egressed Roots (EGR)	-0.39	-0.19	0.23	0.27	0.77		-0.09	0.45	0.23
Shoot/Root (S/R)	0.01	0.30	0.46	0.86	-0.30	-0.12		-0.08	0.02
ψ_t	-0.08	-0.06	0.16	0.18	0.30	0.36	0.04		0.54
RWC	-0.40	-0.43	0.12	0.13	0.07	0.21	0.15	0.50	

[a] Analyzed as arcsin square root of proportion (Snedecor & Cochran 1967, p. 327).

[b] Population mean correlations are based on 27 df; r = 0.37 and 0.47 are significant at P = 0.05 and 0.01.

[c] Family mean correlations are based on 43 df; r = 0.29 and 0.38 are significant at P = 0.05 and 0.01.

Table 11. Population mean correlations between the biomass traits and the population location topographic variables for the growth room and greenhouse Dry experiments.

Experiment Trait	Topographic Variables			
	Elevation	Latitude	Distance from Ocean	Site Index
Growth Room Dry (n = 35)[a]				
Shoot Dry Weight	-0.80[b]	0.63	-0.41	0.34
Egressed Roots	-0.56	0.52	-0.33	0.35
Root Dry Weight	-0.61	0.51	-0.24	0.44
Shoot-Root Ratio	-0.44	0.20	-0.35	-0.03
Greenhouse Dry (n = 29)				
Shoot Dry Weight	-0.53[c]	0.45	-0.35	0.21
Egressed Roots	-0.21	0.00	0.21	-0.12
Root Dry Weight	-0.23	0.06	0.13	-0.08
Shoot-Root Ratio	-0.40	0.43	-0.44	0.20

[a] n = the number of populations in the experiment.

[b] r = 0.33 and 0.43 significant at P = 0.05 and 0.01.

[c] r = 0.36 and 0.48 significant at P = 0.05 and 0.01.

Drought Resistance

RWC and Ψ_t

I measured RWC and Ψ_t, two measures of plant water status, in seedlings being subjected to a sustained drought to ascertain the relative abilities of different genotypes to maintain favorable water balances. These two traits were measured only at harvesting and only in the greenhouse and growth room Dry experiments.

At harvesting of the growth room experiment, I found no difference among populations or among families within populations in the ability to control Ψ_t; however, families within populations differed weakly in their RWC (Table 12). The greenhouse experiment yielded the opposite results, differences among families within populations in Ψ_t and no genetic differences in RWC (Table 13).

I measured these two experiments at drastically different times in terms of their overall drought status and this may explain the differences in their results. This is best exemplified by examining the relationship betwen RWC and Ψ_t in the greenhouse buffer seedlings over the course of the sustained drought (Figure 6). Several investigators (Jarvis and Jarvis 1963, Slayter 1960) have discussed this type of curve, the shape of which depends on the species and on the nature of the drought. During the course of the drought, average Ψ_t for the seedlings dropped from -5 to -55 bars, while RWC decreased from 95 to 60%. This relationship was not linear. That the Douglas-fir seedlings in this experiment maintained a RWC

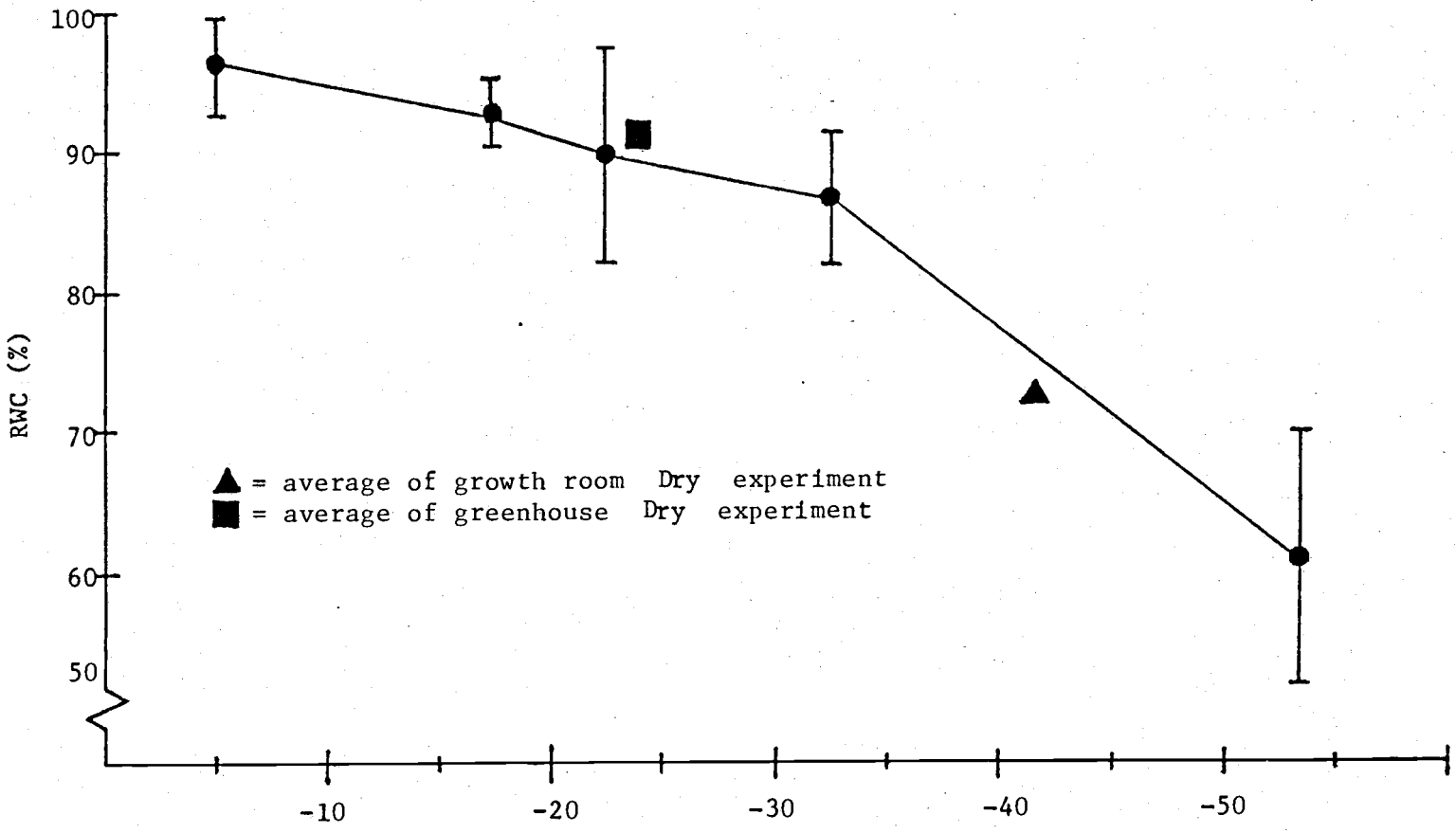

Figure 6. Means and 95% confidence intervals of RWC for decreasing ψ_t of greenhouse buffer seedlings. (The average RWC and ψ_t are also plotted for the two Dry experiments).

Table 12. Analysis of maximum plant water potential ψ_t and relative water content RWC as measured on April 25 in the growth room Dry experiment.

Source	df	ψ_t (Bars) Mean Square	ψ_t (Bars) Intraclass Correlation (%)	RWC (%) Mean Square	RWC (%) Intraclass Correlation (%)
Population	34	29.26^{ns}	0.0	68.9^{ns}	0.0
Family/Population	35	30.56^{ns}	0.9	87.8^{*}	8.0
Tree/Family (Error)	322	29.15	99.1	59.4	92.0
Experimental Mean		41.0		73.6	

Table 13. Analysis of maximum plant water potential ψ_t and relative water content RWC as measured on June 20 in the greenhouse Dry^t experiment.

Source	df	ψ_t (Bars) Mean Square	ψ_t (Bars) Intraclass Correlation (%)	RWC[a] (%) Mean Square	RWC[a] (%) Intraclass Correlation (%)
Population	28	18.57	0.0	20.39^{ns}	4.1
Family/Population	16	21.73**	12.7	12.90^{ns}	1.4
Tree/Family (Error)	396	8.95	87.3	11.32	94.5
Experimental Mean		22.6		92.3	

[a] Analyzed as the aresin of the square root of the proportion (Snedecor and Cochran 1967, p.327).

of 90% even as Ψ_t dropped to -30 bars may reflect their ability to osmoregulate. By reducing the cellular osmotic potential faster than the cellular water potential, cells reduce tissue water loss (see review by Hsaio and others 1976).

Plotting the average RWC and Ψ_t values for the growth room and greenhouse experiments on Figure 6 indicates that the two experiments were measured at quite different points along the curve. Greenhouse seedlings were at a stage where, although the average Ψ_t (-23 bars) indicated considerable moisture stress, RWC remained very high (92%). The 45 family means ranged only from 88 to 93% RWC making it difficult to discriminate among families or populations. The more advanced (stressed) status of the growth room experiment meant more variation among the family means for RWC (66 to 81%). For the 43 families common to both Dry experiments, family mean RWC in the greenhouse did not correlate at all with family mean RWC in the growth room ($r = 0.02^{ns}$, with 41 df). On the other hand, a slight trend ($r = 0.32^{*}$, with 41 df) indicated weak correspondence between average family water potential in the two test environments.

Needle Shed

Leaf damage, one measure of a plant's resistance to a sustained drought has been monitored both as leaf wilting (Townsend and Roberts 1973) and as leaf mortality (Ladiges 1974). In the greenhouse Drought Survival experiment, I noticed that needles produced in the first

growing season began to brown and die in response to the drought. On June 20, only 5.3% of the year-old needles had died on the average seedling in the greenhouse Moist (no drought) experiment compared to 24.2% in the Drought Survival experiment. Families within populations differed strongly in the tendency to shed needles in response to the drought (Table 14) with family means ranging from 10% to 47%.

Care must be exercised in interpreting these results. Families with 47% dead year-old needles may have been experiencing more stress and therefore be less drought resistant than families with 10% dead year-old needles. On the other hand, some families may shed their needles earlier in response to drought to reduce their leaf surface area. Leaf shed as a drought avoidance mechanism is known in several plant species (Larcher 1975 p. 168, Levitt 1972 p. 361). The observed differences may reflect the differential ability of seedlings of some families to shed older needles during a drought to protect newly produced needles.

On a family mean basis, needle shed did not correlate with survival during the drought (Table 5) nor did it correlate with Ψ_t or RWC for the families common to both the Dry and Drought Survival experiments. The strongly inherited tendency to shed needles during drought may be one of a number of compensating drought avoidance and drought tolerance mechanisms operative in Douglas-fir seedlings.

Table 14. Analysis of first-year needles shed and survival in the greenhouse Drought Survival experiment.

Source	df	First-Year Needles Shed (%) Mean Square	First-Year Needles Shed (%) Intraclass Correlation (%)	Survival (%) Mean Square	Survival (%) Intraclass Correlation (%)
Block	2	314.86		7827.3	
Population	34	255.82^{ns}	11.5	1086.3^{ns}[a]	9.2
Elevation	1	154.01^{ns}		4028.9^{*}	
Lack of Fit	33	258.90^{ns}		997.1^{ns}	
Latitude	1	32.28^{ns}		5559.8^{**}	
Lack of Fit	33	262.60^{ns}		950.7^{ns}	
Family/Population	31	174.31^{**}	25.0	638.2^{ns}	0.0
Row-Plot Error	130	79.99	63.6	781.4	90.8
Experimental Mean		24.3		30.4	

[a] Population mean square is significant at P = 0.07.

Survival

One ultimate measure of drought resistance is survival to a sustained drought and I measured survival in both the greenhouse and growth room Drought Survival experiments. The position of a family row-plot within each block substantially affected survival in both of these experiments because some areas of some blocks dried out more rapidly than other areas. This large intrablock variation (partially adjusted for by a covariance model in the growth room experiment) meant large experimental error in both experiments. Consequently, only strong genetic differences were revealed.

In the growth room, population differences in survival were not significant (Table 15), while in the greenhouse (Table 14) populations differed weakly. In both experiments, a weak relationship indicated that populations from higher elevations or lower latitudes tended to survive better under a sustained drought. Closer scrutiny of this relationship indicated that the bulk of the elevational trend stemmed from the superior performance of the high elevation populations (Figure 7). The populations were divided into four evenly-spaced elevational groups as follows: group 1, 475-764m; group 2, 765-1053m; group 3, 1054-1341m; group 4, 1342-1630m. The groups differed significantly in their survival, with the group representing the highest elevation populations surviving best in both experiments (Table 16). Within-group differences between populations were not significant for any of the groups in either experiment.

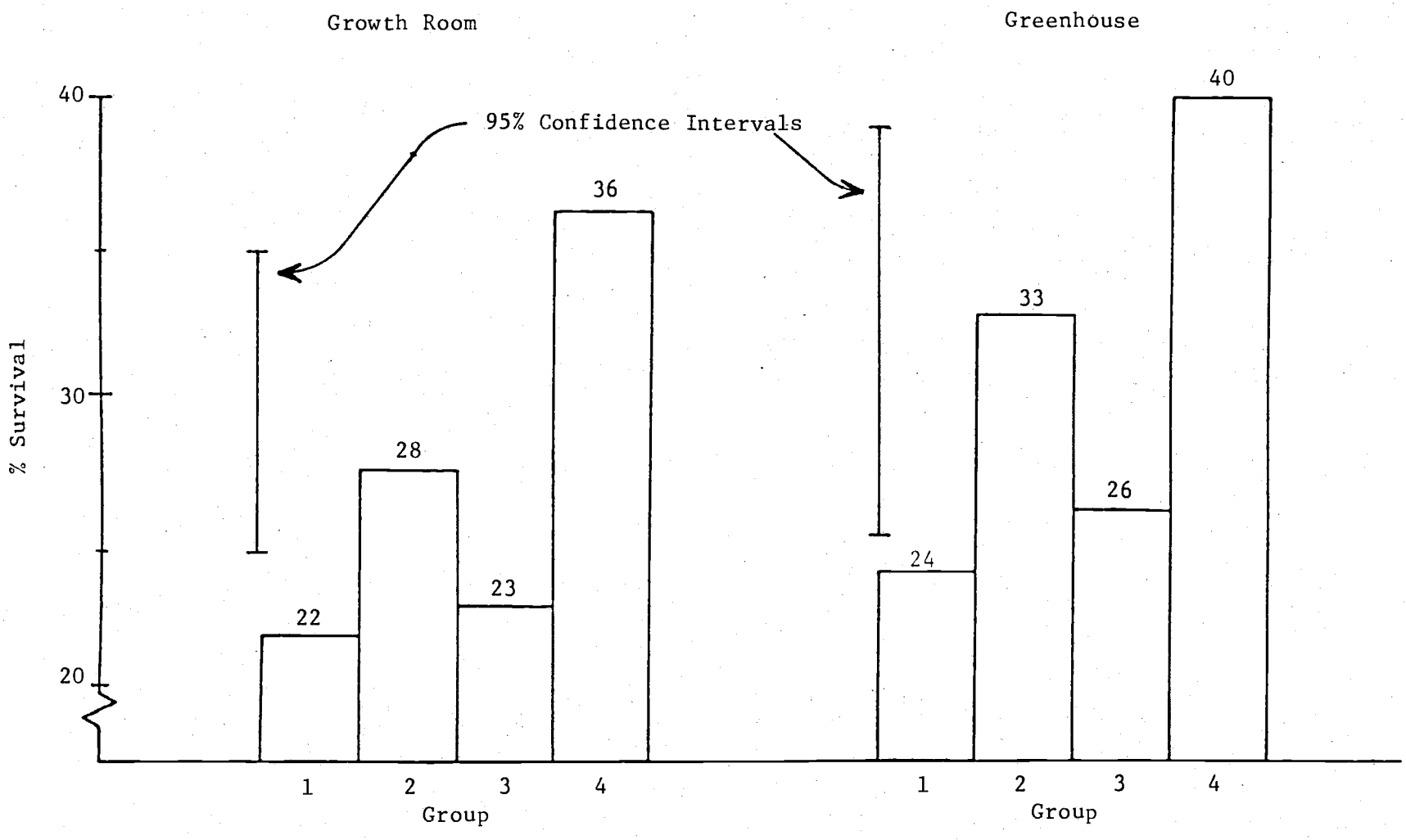

Figure 7. Means and approximate (assuming 18 families per group) 95% confidence intervals for survival of the four elevational groups in the growth room and greenhouse Drought Survival experiments.

Table 15. Analysis of survival in growth room Drought Survival experiment (survival was adjusted with a covariance model).

Source	df	Adjusted Survival (%) Mean Square	Intraclass Correlation
Adjustments	6[a]		
Population	34	450^{ns}	5.2
Elevation	1	3156**	
Lack of Fit	33	368^{ns}	
Latitude	1	3544**	
Lack of Fit	33	356^{ns}	
Family/Population	35	347^{ns}	4.6
Row-Plot Error	134	301	90.3
Experimental Mean		27.1	

[a] The 6 df for adjustments include 2 df for blocks, 2 df, 1 df and 1 df for covariance adjustment in blocks 1, 2, and 3 respectively, for the relationship between the survival of a row-plot and its position (row number) within a block.

Table 16. Partition of population variation in survival in the growth room and greenhouse into four elevational groups[a].

Source	Growth Room df	Growth Room Mean Square[b]	Greenhouse df	Greenhouse Mean Square[b]
Population	34	150.0^{ns}	34	362.0^{ns}
Between Groups	3	677.7**	3	932.7*
Within Group 1	9	138.3^{ns}	9	263.7^{ns}
Within Group 2	8	67.0^{ns}	9	333.7^{ns}
Within Group 3	7	57.0^{ns}	6	489.3^{ns}
Within Group 4	7	126.3^{ns}	7	148.0^{ns}
Family/Population (Error)	35	115.6	31	212.6

[a] The groups represent populations from four evenly spaced elevational groups as follows: Group 1, 475-764 m; Group 2, 765-1053 m; Group 3, 1054-1341 m; Group 4, 1342-1630 m.

[b] Mean squares for Population and Family/Population are scaled down by a factor of 3 from those in Tables 14 and 15 because this analysis was performed on a family mean, not row-plot mean, basis.

Note in Figure 7 that elevational group 2 survived better than expected based on its average elevation. Speculating, group 2 included several low latitude populations and perhaps the fact that low latitude populations survived better on the average (Tables 14 and 15) meant better survival for this group than predicted by its elevation.

I think the elevational and latitudinal relationships with population survival have real biological meaning that was weakened by the large experimental error in both test enviroments. This error may have also reduced the correlation between family means for survival from the two experiments ($r = 0.27^*$, with 62 df).

Relationships Between Drought Resistance and Other Traits

Experiments by other investigators have implicated several phenological, morphological and physiological traits as important in conferring drought resistance, either avoidance or tolerance, to plants. Having measured many of these traits along with drought survival affords me the opportunity to explore the correlation between how these traits are expressed in a family and how the family survives drought. Conclusions of causality drawn from these correlations are speculative on my part, but are interesting when viewed in this light. Lack of consistency or significance in some correlations may reflect experimental error or biological trends.

The shoot-root ratio is a parameter often mentioned as an important drought avoidance mechanism allowing plants to maintain a favorable tissue water balance during drought (Hermann 1964, Levitt 1972, Parsons 1969). In both the growth room and greenhouse Dry experiments, shoot-root ratio failed to correlate on a family mean basis with either RWC or Ψ_t (Tables 9 and 10) even though genetic differences in shoot-root ratio existed. That is, families with smaller shoot-root ratios did not necessarily maintain more favorable tissue water balance during the drought. In the greenhouse, families with more egressed roots tended weakly to have more favorable Ψ_t ($r = 0.36^*$, with 43 df), but this was not true in the growth room. In the greenhouse, for the 43 families common to both experiments there were no significant correlations between a family's egressed roots or shoot-root ratio in the Dry experiment and that family's survival in the Drought Survival experiment. In the growth room, populations with lower shoot-root ratios in the Dry experiment tended weakly to survive better in the Drought Survival experiment ($r = -0.43^{**}$, with 33 df). Rapid root penetration is an important drought avoidance mechanism in several plant species (Daubenmire 1943, Pereira and Kozlowski 1976, Satoo 1966). Limiting the plant rooting depth in shallow pots or boxes hinders the expression of this trait and can influence which genotypes are most drought resistant (Pereira and Kozlowski 1976, Satoo 1966). Because the soil boxes used in these experiments limited rooting depth, drought resistance associated with genetic differences in root penetration could not be measured.

In neither the greenhouse nor growth room were there significant correlations between a family's tissue water status (RWC and Ψ_t) and its survival to drought. That is, families with higher RWC or Ψ_t in the Dry experiments did not necessarily survive better in the Drought Survival experiments.

For Pacific Northwest Douglas-fir seedlings, provenances originating from areas with low summer rainfalls are genetically adapted to early bud burst (Campbell and Sugano 1979, Heiner 1968, White and others 1979). Early bud burst may be a drought avoidance mechanism allowing seedlings to begin growth earlier in the growing season relative to the drought. Bud burst date did not correlate with drought survival in either the growth room or the greenhouse; families with early bud burst did not necessarily survive better. The lack of correlation may reflect experimental error; or, perhaps early bud burst does not confer selective advantage in dry summer climates through drought resistance, but rather by allowing seedlings to complete more height growth prior to the drought. Then, seedlings with early bud burst would derive their competitive edge by being taller.

Provenances of Douglas-fir from southwestern Oregon consistently set bud earlier when grown in common gardens with more northerly, coastal provenances from the Pacific Northwest (Lavender and others 1968, Lavender and Overton 1972). As some other conifers have demonstrated increased tolerance to tissue water desiccation in the dormant state (Oppenheimer 1960, Levitt 1972 p. 393), perhaps early bud set is a drought avoidance mechanism in dry climates. Populations

with less late season height growth (earlier bud set) had more favorable RWC's in the greenhouse Dry experiment (Table 10). The moderate correlation ($r = -0.55^{**}$, with 27 df) indicates that early bud set or some associated trait may have allowed some plants to maintain more favorable water balances during the drought. In the greenhouse Drought Survival (Table 5) experiment, populations which had set a larger percentage of terminal buds on June 20 tended to survive the drought better ($r = 0.49^{**}$, with 33 df).

As discussed earlier, the high elevation and low latitude populations had early budset (Table 3) and tended to survive better under a sustained drought. Perhaps early budset, selected for in high elevation populations in response to early fall frosts, also confers drought avoidance on these populations in some circumstances. The southern (low latitude) locations in this region receive less summer rainfall at a given elevation. And, while it is tempting to speculate that this may have influenced the budset and drought survival characteristics of southern populations, latitude and elevation are too closely linked ($r = -0.80^{**}$, with 34 df) in this region to allow conclusions.

In range-wide provenance studies of seedling Douglas-fir, Rocky Mountain and other interior sources survived drought better than sources from the Pacific Northwest (Ferrell and Woodward 1966, Pharis and Ferrell 1966). Differences in survival were ascribed to both avoidance and tolerance differences among the sources. The interior regions are both drier and colder than the Pacific North-

west and so once again temperature and moisture gradients are confounded.

Conclusions

Moderate to strong population differences in budset, late season height growth, total second-year height growth and shoot dry weight probably reflect the tendencies of some populations to grow later into the growing season. Populations with inherently less late, season shoot growth came from high elevations and low latitudes within the sampled region. These high elevation, low latitude populations also survived better under the sustained droughts imposed towards the end of the growing season.

As previously mentioned, the large amount of experimental error and collinearity between latitude and elevation preclude separating the effects of these two variables on molding the gene pool of southwestern Oregon Douglas-fir. Nevertheless, I speculate that high elevation environments have selected seedlings with early budset and this affects the height growth, shoot dry weight and shoot-root ratios of the seedlings.

These inherent characteristics of seedlings from populations originating from high elevations made these seedlings more drought resistant under our drought conditions; characteristics evolved as frost resistance mechanisms conferred drought resistance in these experiments.

Some of the drought resistance exhibited by the southerly populations may have evolved in response to droughty conditions and I do not mean to imply that drought resistance independent of frost resistance does not occur within the region. The design and power of my experiments just make it impossible to detect genetic differences in drought resistance associated with droughty environments.

In a practical sense, if further testing substantiates that higher elevation populations in this region are more drought resistant, then high elevations become attractive sources of seed for reforesting low elevation, droughty sites. Because the higher elevation populations tend to grow more slowly, the trade-offs between growth rate and drought resistance must be weighed before choosing seed sources.

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CHAPTER 3. SURVEY OF DROUGHT AVOIDANCE CHARACTERISTICS

Introduction

Plant avoid droughts by maintaining favorable tissue water potentials during conditions of unfavorable environmental water potential and previous investigators have implicated several plant attributes as drought avoidance mechanisms. I discussed drought avoidance mechanisms dealing with phenological adjustments and shoot-root ratios, in Chapter 2, but other mechanisms concerning needle morphology and transpiration control were not measured.

Reduction in size (Davies and others 1974) and frequency (van Buijtenen and others 1976, Thomas 1963, Knauf and Bilan 1974) of leaf stomata seemingly confer drought avoidance to some xeric provenances and species. Control of transpirational water loss during drought by regulation of stomatal aperture also varies among species (Kaul and Kramer 1965, Lopushinksy 1969, Running 1975) and among provenances within species (Townsend and Roberts 1973, Unterscheutz and others 1974) and presumably confers drought avoidance to more xeric genotypes.

These characteristics were not measured in the experiments in Chapter 2 because their intensive nature limits the number of seedlings which can be measured. In this Chapter, I report the results of experiments surveying these characteristics on a limited number of wind-pollinated families known to differ in their drought resistance. By investigating how these stomatal traits varied between

four drought resistant and four drought susceptible families, I hoped to learn more about the nature of drought resistance in southwestern Oregon Douglas-fir seedlings.

Materials and Methods

All measurements reported in this Chapter were taken on seedlings of only eight of the 50 families growing in the greenhouse Moist experiments described in Chapter 2. Four of these families were considered drought resistant and four considered drought susceptible as judged by their performance in the greenhouse Drought Survival experiment. Both of these experiments have been fully described in Chapter 2 and I only highlight them here.

Selecting the Drought Resistant and Drought Susceptible Families

In the greenhouse Drought Survival experiment, the randomized complete block design meant that a ten-seedling row-plot represented each of the 66 wind-pollinated families in each of three blocks (soil boxes). About a month after the bud burst of their second growing season, I ceased watering the seedlings and exposed them to an extended soil drought. After about six weeks without water, many seedlings looked dead and all three soil boxes were rewatered. After a month's recovery in well-watered conditions, seedlings with no green needles and no newly flushed buds were considered dead as a result of the drought.

Because of the large intrablock variation in drought-induced mortality (described in Chapter 2), the drought resistant and drought susceptible families were not chosen by overall family means of survival. Instead, each block (soil box) was surveyed row-plot by row-plot to determine family survival characteristics. If a particular family row-plot had good survival in an area of a block which had poor overall survival, it was considered drought resistant. Vice versa, if a family row-plot survived poorly in an area of the block with fairly decent overall survival, that family was classed drought susceptible. No information could be obtained for some families in each block because seedlings in whole areas had lived or died. This information, accumulated over all blocks, was used, along with the overall family survival averages, to choose the drought resistant and drought susceptible families. The overall family survival averages from the Drought Survival experiment, along with the elevation, latitude and site index of the family seed source locations are given in Table 1.

Experimental Methods

In the Moist experiment the randomized complete block design meant that a five-seedling row-plot represented each family in each of three blocks (soil boxes). Only 50 of the 66 families in the Drought Survival experiment were in the Moist experiment. The seedlings were kept well-watered throughout their second growing season.

Table 1. Stand characteristics for family seed source locations and survival in Drought Survival experiment.

Family	Seed Source Location Variables			Survival
	Elevation m	Latitude °	Site Index[a] ft	%
Drought susceptible (DS)				
1	555	42.92	130	57
2	555	42.92	130	17
3	1220	42.68	100	30
4	1020	42.62	105	13
DS Group Average	840	42.79	116	29
Drought Resistant (DR)				
5	1585	42.27	115	73
6	1380	42.30	120	77
7	1560	42.10	80	60
8	1585	42.27	115	40
DR Group Average	1530	42.24	108	62

[a] Height at 100 years.

Because the early stages of the Drought Survival and Moist experiments were concurrent, I measured bud burst and height on all 50 families in the Moist experiment; however, in this Chapter I report these traits only for the eight selected drought resistant and drought susceptible families.

For all seedlings of the eight selected families, we measured bud burst date in their second spring, total epicotyl length (hereafter, height) on May 20 and total height again on July 20 after all seedlings had ceased growing. Late season height growth was calculated as the percentage of a seedling's total second-year height growth completed after May 20.

On August 30, over a month and a half after all seedlings had terminated height growth, we picked three current-year needles from each of two seedlings from each of the three family row-plots of the eight selected families growing in the Moist experiment. We stored the needles in FAA (5% glacial acetic acid, 6% formalin, 44% ethanol and 45% water) and then used an optical micrometer to measure the maximum length, width, and thickness of each needle.

At two different points near the center of each needle, we 1) counted the stomatal rows across the abaxial surface (Douglas-fir is hypostomatous), 2) counted the stomata in a 0.332 mm linear section, and 3) measured the maximum length of the outside opening of the antechamber for 8-14 stomata. To calculate the total number of stomata per needle, I assumed constant stomatal density and rectangular, flat needles.

For the same two seedlings in each family row-plot, we measured leaf conductance on September 1 and 2, two mild, overcast days. Leaf conductance of current-year needles was measured five times each day with the null balance diffusion porometer described and calibrated by Hallgren (1977). The five runs were evenly spaced throughout each day between 530 and 1600. After the final run each day, we measured the plant water potential Ψ_t of each seedling with a Scholander pressure bomb (Waring and Cleary 1967). Projected surface areas of needles used for porometry were measured with a LiCor optical planimeter.

Transpiration per unit of projected abaxial needle surface area was estimated as the product of leaf conductance and absolute humidity deficit. Total daily transpiration per unit leaf area was estimated by trapezoidal approximate integration under the five points forming the daily transpiration curve for each seedling.

All variables were subjected to analysis of variance and the family sum of squares was partitioned into between group and within group differences.

Results

Two-year height, bud burst and late season height growth showed very characteristic trends (Table 2). Relative to the drought susceptible families, drought resistant families were shorter, burst bud earlier and had a lower percentage of their height growth late in the season.

Table 2. Growth, phenological, physiological, and stomatal characteristics for drought resistant and drought susceptible families

Family	2-year height cm	Bud burst date Julian days	Late season growth[a] %	Total Daily Transpiration[b] (g cm^{-2} day^{-1}) X 10^2	Water potential at 1600 bars	Stomata			
						Rows $needle^{-1}$	Number $needle^{-1}$	Number mm^{-2} of leaf surface	Length of opening mm X 10^2
Drought susceptible (DS)									
1	10.8	96.1	13.6	9.85	-11.7	9.69	2832	88	1.29
2	12.4	100.0	21.3	9.46	-13.7	9.75	2746	83	1.29
3	8.3	99.1	8.4	9.20	-11.4	10.36	2572	89	1.26
4	9.9	103.9	12.4	9.04	-12.3	9.36	2392	79	1.42
DS group average	10.3	99.8	14.0	9.39	-12.3	9.79	2636	84	1.31
Drought resistant (DR)									
5	6.9	92.7	9.5	10.24	-11.0	9.53	3114	84	1.25
6	6.9	95.3	8.0	12.41	-9.3	10.28	3506	87	1.28
7	7.6	99.1	6.8	12.47	-9.9	8.61	2276	73	1.28
8	6.7	96.7	5.7	11.95	-11.3	9.64	2802	106	1.24
DR group average	7.0	96.0	7.5	11.78	-10.3	9.51	2924	87	1.26
Statistical differences[c]									
Between groups	**	**	**	ns	**	ns	ns	ns	ns
Within DS group	**	ns	**	ns	ns	ns	ns	ns	ns
Within DR group	ns	ns	ns	ns	ns	ns	*	**	ns

[a] Height growth completed after May 20.

[b] Transpiration per unit leaf area based on projected needle surface area.

[c] Orthogonal partitions of the family sum of squares from the analysis of variance.

The two groups of families also demonstrated different abilities to control their evening water potentials (Table 2). All seedlings in the Moist experiment grew in a moist soil (predawn water potential on neighboring buffer trees averaged -6.5 bars). During the day, water potentials dropped to an average of -14.5 bars before recovering to -11.3 bars at the evening (1600) measurement. As a group, drought resistant families averaged two bars higher (less stressed) than drought susceptible families at the evening measurement.

Drought resistant families seemingly transpired more per unit leaf area than drought susceptible (Figure 1); however, when analyzed on a run by run basis, statistically significant differences between the groups occurred only for the last run of the day. Daily transpiration per unit leaf area did not differ significantly between the groups even though all drought resistant families transpired more (25% more as a group) than all drought susceptible families (Table 2).

Compared to water potential, large measurement error and tree-to-tree variation in the transpiration measurements led to an extremely low statistical power for testing differences between the two groups. Assuming that the family averages and error mean squares we calculated were the true population values, the probability of declaring differences between the two groups (at $P = 0.05$) was only 35% for total daily transpiration but 99% for water potential (Neter and Wasserman 1974 p. 453, 584-5). So, even if the 25% more daily transpiration per unit leaf area by the drought resistant families represented true genetic differences, the large amount of experimental error makes

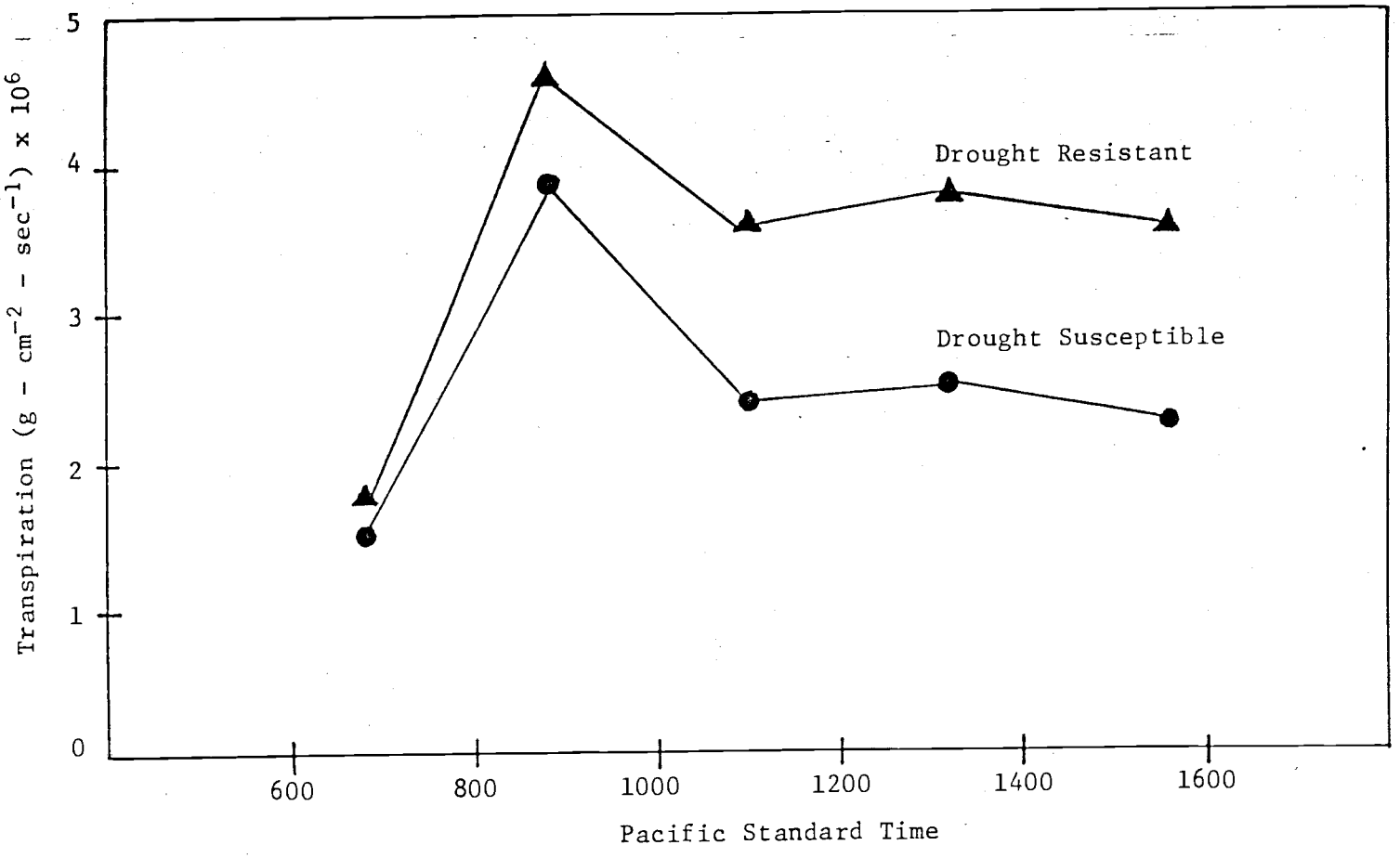

Figure 1. Transpiration per unit leaf area of Douglas-fir seedlings from Drought Resistant and Drought Susceptible families.

those differences difficult to declare statistically significant.

Because I did not measure total needle surface area for each seedling, it is impossible to calculate total daily transpiration per seedling from transpiration per unit needle surface area. Nevertheless, because of its importance, I made several assumptions in order to estimate the family average of daily transpiration per seedling. The several assumptions involved make these estimates very rough. First, I used a regression equation (developed for the greenhouse Dry experiment seedlings described in Chapter 2) relating total seedling height to shoot dry weight (shoot weight = -0.027 + 0.67 (total height), R^2 = 0.49) to estimate the average shoot dry weight for each family. Next, shoot dry weight was converted to needle dry weight by assuming that shoots were 55% needles and 45% stems by weight[1]. The estimated family average for needle dry weight per seedling was then converted to projected needle surface area per seedling by assuming 65.7 cm^2 of needle surface per g of needle dry weight (Hallgren 1977). Finally, the family average for daily transpiration per unit of projected needle surface area was multiplied by the estimated projected needle surface area per seedling to obtain a family average for daily transpiration per seedling.

Averaging over the four families in each group, I estimate that the drought resistant group transpired 1.88 g H_2O per seedling compared to 2.26 g H_2O per seedling for the drought susceptible families. So, even though the drought resistant families transpired

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[1]Unpublished research results of Mary Duryea, Dept. of Forest Science, Oregon State University.

more per unit of leaf area, they may have transpired less per seedling. I reemphasize that the transpiration per seedling estimates contain many assumptions (for example, constant needle weight to stem weight ratio regardless of seedling height) that make them less than reliable.

None of the stomatal characteristics surveyed differed between the groups (Table 2); however, stomata per needle and stomata per mm^2 of needle surface varied for families in the drought resistant group. No genetic differences of any kind were found for the number of stomatal rows or the length of the stomatal opening.

Discussion

In this experiment, I hoped to relate genetic differences in some seedling traits to previously demonstrated genetic (family) differences in drought resistance. Many plant attributes confer drought resistance (Oppenheimer 1960, Levitt 1972) and several mechanisms can be active in a single species. None of the stomatal characteristics found to be associated with the drought resistant nature of some Texas loblolly pine (Knauf and Bilan 1974, Thames 1963) differed between the drought resistant and drought susceptible families of Douglas-fir in this study. Perhaps other mechanisms are operative in these families. In an extensive survey of many species of varying drought resistance, Gindel (1969, 1973) reported no consistent trends in stomatal characteristics associated with drought resistance.

The drought resistant families in the present study originated from higher elevations than the drought susceptible families (Table 1) confounding the determination of which of the genetic differences between the groups evolved in response to temperature gradients and which evolved in response to moisture gradients. As mentioned in Chapter 2, perhaps some characteristics which have evolved as frost avoidance mechanisms can also confer drought avoidance.

The height growth and late season height growth results in this study reiterate the results of Chapter 2 and agree well with other reports that Douglas-fir seedlings from high-elevation provenances tend to grow slower and set bud earlier (Campbell and Sorensen 1978, Hermann and Lavender 1968, Lavender and others 1968).

In general, southwestern Oregon experiences more summer drought than the rest of the Pacific Northwest west of the Cascade Mountains (White and others 1979). Other genetic investigations of Douglas-fir seedlings showed that, compared to most other west side provenances, southwestern Oregon sources not only grew more slowly and set bud earlier (Lavender and others 1968, Lavender and Overton 1972), but also burst bud earlier (Heiner and Lavender 1972, White and others 1979). In Chapter 2, family averages for bud burst date did not correlate well with family drought survival in either the growth room or the greenhouse; yet, in the Moist experiment, the extreme four drought resistant families burst bud earlier as a group than the four drought susceptible families.

Families maintaining higher evening water potentials (less stressed) transpired more per unit of needle surface area ($r = 0.78^*$,

with 6 df). Because leaf conductance typically decreases with decreasing leaf water potential (Running 1975), the higher transpiration per unit of needle surface area by the drought resistant families may reflect their superior ability to maintain a favorable water status. Note that rough estimates indicate that drought susceptible seedlings transpired more on a per seedling basis. Perhaps during the course of a day, the larger estimated surface area of the drought susceptible families resulted in more total transpiration and lower water potentials. The drought resistant seedlings, with less total surface area, maintained higher water potentials and transpired more per unit of leaf area. This seemingly conflicts with Chapter 2 results when neither shoot/root ratio nor shoot dry weight was associated with genetic differences in drought survival. But, because in this study I measured transpiration and water potential only during the course of two days and in relatively moist conditions, I can not assess their implications for long term drought survival. The results in this experiment agree with those of Zavitkowski and Ferrell (1970) who found that in well-watered soil, mesic provenances of Douglas-fir transpired more than xeric sources.

A survey of this kind can not measure every possible characteristic or prove causal relationships. Yet my results support the hypothesis that genetic phenological adaptation for earlier growth is one mechanism conferring drought resistance in Douglas-fir. Other adaptations in Douglas-fir such as differential tolerance to

tissue desiccation (Ferrell and Woodward 1966, Pharis and Ferrell 1966) and superior stomatal control of water loss in dry conditions (Zavitkowski and Ferrell 1968) may also be important.

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