

REID (1975) to evaluate the survival capacity of the seedlings, it could be concluded that these two provenances are characterized by a significantly different tolerance to drought.

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## Genetic Variability Within Douglas-fir Populations: Implications for Tree Improvement

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#### Summary

Genetic variances and covariances for growth potential, phenology and patterns of first year elongation were calculated from 30 half-sib families from each of three contrasting populations. Analyses of 4-year old trees growing in a single environment revealed high levels of additive genetic variance within populations. As a consequence, rather high estimates of genetic gains in growth potential were associated with weak selection intensities. However, genetic correlations were strong. Gains in growth potential were associated with delayed bud set and increased susceptibility to early fall frosts. For tree improvement to increase the growth potential of Douglas-fir without inadvertent degeneration of adaptation, selections must be based on several traits.

*Key words:* Douglas-fir, tree improvement, genetic variability, adaptive strategy

#### Zusammenfassung

Es wurden genetische Varianzen und Kovarianzen für Wuchspotential, Phänologie und Schemata der Sproßstreckung im ersten Jahr bei 30 Halbgewister-Familien aus drei Kontrast-Populationen abgeschätzt. Durch eine Analyse 4-jähriger Bäume, die in derselben Umwelt aufwachsen, wurden hohe Niveaus von additiv genetischer Varianz innerhalb der Populationen festgestellt. Die Folge davon waren relativ hohe Schätzwerte für die genetischen Gewinne im Wuchspotential, verbunden mit geringen Selektionsintensitäten. Die genetischen Korrelationen waren jedoch stark. Der genetische Gewinn im Wuchspotential stand in Relation zu der Bildung der Endknospe und einer damit verbundenen zunehmenden Frühfrostempfindlichkeit. Für eine Züchtung zur Verbesserung des Zuwachspotentials der Douglasie ohne versehentliche Entartung, was die Anpassungsfähigkeit betrifft, müssen Selektionen auf mehreren Merkmalen basieren.

#### Introduction

As a product of environmental selection, the genetic system exhibits variability at many levels: within indivi-

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duals, among individuals within populations, among populations within localities, or among populations from different geographic regions. In Douglas-fir (*Pseudotsuga menziesii*), populations of both the coastal (CAMPBELL, 1979) and Rocky Mountain (REHFELDT, 1979a) varieties are readily differentiated according to phenology, growth potential, or cold hardiness. In fact, much of the variance among populations has been related to geographic, physiographic, and ecologic variables. Environmental variables have accounted for nearly all the variance among populations within a single drainage in western Oregon (CAMPBELL, 1979). In north Idaho alone, differentiation has been detected among populations separated by only 140 m elevation, 1° latitude or 1.5° longitude (REHFELDT, 1979a). Thus, populations seem closely attuned physiologically to particular environments. Genetic specialization best describes adaptation of populations to the heterogeneous montane environments of the Pacific Northwest.

Physiological specialization results from diversifying selection of alternative alleles or allelic combinations in a heterogeneous habitat. To the extent that genetic variance in adaptive traits is additive, specialization is accompanied by a reduction of variability within populations (ROUGHGARDEN, 1979). Current research, however, does not suggest that intra-population variability is depauperate in either the coastal variety (CAMPBELL, 1979; CHRISTOPHE and BIROT, 1979) or Rocky Mountain variety (REHFELDT, 1978). The present study assesses genetic variability within Douglas-fir populations. Objectives include (1) elucidating the balance between variability within populations and specialization of populations, and (2) quantitatively evaluating potentials for tree improvement.

#### Materials and Methods

Wind-pollinated cones were collected from 30 trees in each of three populations. Because collections were made in a year of exceptionally high cone production, a random selection of trees was possible. Although the spacial distribution of selected trees varied, the crowns of at least three trees separated all selections. Populations were products of natural reproduction, were relatively large, and were from relatively low elevations in distinct seed zones (REHFELDT, 1980):

*Population 1:* near Grangeville in north central Idaho, 1050 m elevation, and from an *Abies grandis*/*Pachistima myrsinites* habitat type (DAUBENMIRE and DAUBENMIRE, 1968).

*Population 2:* from the Priest River Experimental Forest in north Idaho, 825 m elevation and from a *Thuja plicata*/*Pachistima myrsinites* habitat type.

*Population 3:* near Kalispell in western Montana, 1000 m elevation, and from a *Pseudotsuga menziesii*/*Symphoricarpos albus* habitat type.

Seeds from each population were used in separate studies of (1) phenology and growth potential, and (2) patterns of first-year elongation.

#### Growth Potential and Phenology

Seedlings from each of the 90 half-sib families were grown for 1 year in plastic tubes (65 cm<sup>3</sup>) in a shadehouse at Moscow in north Idaho. One-year-old seedlings were transplanted into a nursery at the Priest River Experimental Forest according to a randomized complete block design consisting of six blocks. Within each block, families were randomly distributed and were represented by two

adjacent 8-tree row plots. About 15 cm separated rows and seedlings within rows.

The following data were taken on all seedlings:

1. height (cm) after 2 years,
2. bud burst, the number of days after April 1 during the fourth growing season on which developing leaves were first visible in the terminal bud,
3. bud set, the number of weeks after July 7 during the fourth growing season by which elongation on the terminal shoot had ceased,
4. total elongation (cm) of the terminal shoot during the fourth growing season,
5. 4-year height (cm).

Statistical analyses were made on six variables: bud burst; bud set ( $\sqrt{X + 0.5}$ ); 4-year height; fourth-year elongation; second flush, the proportion ( $\arcsin \sqrt{\%}$  in radians) of fourth-year elongation attributable to a second flush; and 4-year height adjusted by regression on 2-year height. By reflecting growth potential from a constant height at age 2, the last variable removes environmental effects such as seed weight or transplanting shock that undoubtedly had confounded height at age 2. Thereby, variation in adjusted height probably most realistically reflects genetic variance in growth potential. While adjusted heights were calculated from a single regression for all progenies, it is noted that regression coefficients did not vary greatly when calculated within populations.

Analyses of all variables followed the model detailed in *Table 1*. Calculation of standard errors for variance components followed ANDERSON and BANCROFT (1952); those for heritabilities and genetic gains followed (NAMKOONG, 1979); genetic correlations and correlated responses to selection were calculated according to FALCONER (1960); and the construction of restricted selection indices followed TALLIS (1962) as discussed by LIN (1978).

#### Patterns of First-Year Elongation

Populations of Douglas-fir from north Idaho exhibit varying patterns of shoot elongation during the first year (REHFELDT, 1979b). Many seedlings set terminal buds in the spring, about 3 weeks after germination; others avoid spring bud set through either continuous growth or the flushing of a transient bud. Because the proportion of seedlings avoiding spring bud set was related to growth, phenology, and cold hardiness in subsequent years (REHFELDT, 1979a), avoidance of spring bud set may be useful for indirect selections of future growth potential.

To test differences among families in patterns of first-year shoot elongation, 20 to 40 seedlings from 84 of the families were grown in plastic containers (65 cm<sup>3</sup>) in each of four replicates. Each family was allocated 10 containers in each replicate; no more than 4 seedlings grew in each container. All containers were placed in a shadehouse at Moscow, Idaho. The proportion of seedlings that avoided spring bud set was recorded for each population in all replicates.

Statistical analyses of transformed proportions ( $\arcsin \sqrt{\%}$  in radians) followed the model detailed in *Table 1*, with the following exceptions:  $\sigma^2_W$  and  $k$  do not exist;  $r = 4$ ;  $f = 27, 27$  and  $30$  for populations 1 to 3, respectively; harmonic mean of families in populations = 27.93; and harmonic mean of observations in each proportion = 28.39. In addition, the residual variance (replications  $\times$  families in populations) was subdivided according to effects of

plots, effects of individuals, and effects of binomial sampling (BINGHAM *et al.*, 1969):

$$\sigma_{RF/P}^2 = \sigma_E^2 - \frac{1}{n_O} \sigma_D^2 + \frac{1}{n_O} \sigma_B^2$$

where  $\sigma_{RF/P}^2$  is the residual variance,  $\sigma_E^2$  = effect of plots;  $\sigma_D^2$  = effect of individuals,  $\sigma_B^2$  = effects of binomial sampling = 0.25, and  $n_O$  = harmonic mean of the number of seedlings in each proportion.

### Results

Analyses of variance of growth potential, phenology (Table 2) and avoidance of spring bud set (Table 3) detected significant main effects and interactions at nearly all levels of classification. As expected, main effects of populations were strong. Mean values (Table 4) illustrate divergent physiological specializations: Montana populations (population # 3) are generally slower growing and more cold hardy than north Idaho populations from comparable elevations (REHFELDT, 1978). For the northern Idaho population (# 2) to slightly exceed the growth potential of the more southerly population (#1) likely results from the interaction of the effects of elevation and latitude. The northern population was from a slightly lower elevation (200 m) than the southern. Although latitude shows a relatively weak negative association with growth potential, elevation shows a strong negative association (REHFELDT, 1979a).

Of most interest to an assessment of genetic variability within populations are the mean squares and variance components associated with the effects of half-sib families. Significant effects of families for all variables related to growth and phenology (Table 2) are derived from large differences in family means within populations (Table 4). Families differed tremendously for all variables except bud burst. In addition, family variances, calculated separately for each population, were decidedly homogeneous for all variables involving growth and phenology (Table 2). Thus, despite mean differences among populations, genetic variances are relatively constant within populations.

Conversely, family variances were not homogeneous for the proportion of seedlings that avoided spring bud set during the first season of growth (Table 3). While mean values ranged from zero to 54% in population # 1 (Table 4), little genetic variance existed within populations # 2

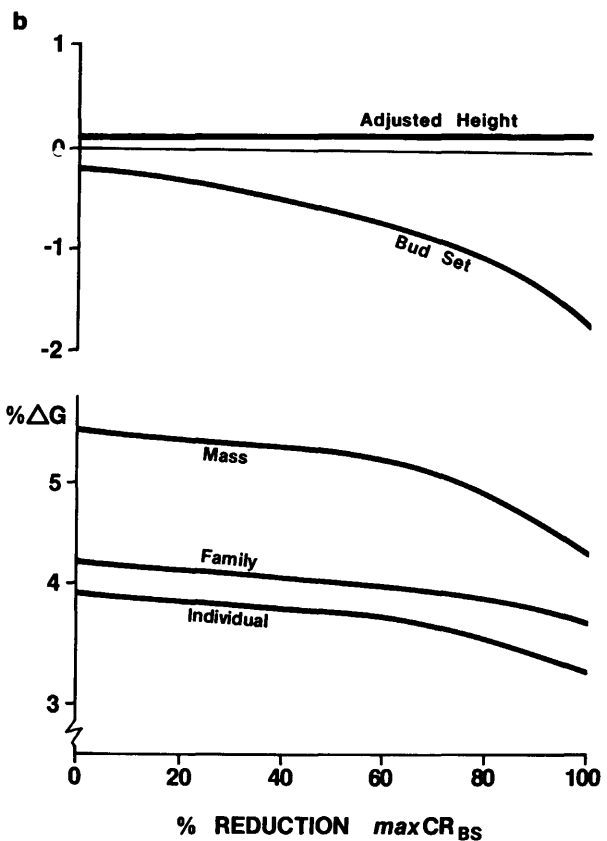


Fig. 1. — Coefficients (b) for selection index and expected genetic gains ( $\Delta G$ ) in adjusted-height for varying levels of reduction in the maximum correlated response in bud set ( $max CR_{BS}$ ).  $\Delta G$  is presented for three selection regimes. Both  $\Delta G$  and  $CR_{BS}$  are calculated at selection intensities of 1 standard deviation.

and # 3 (Table 3). Low genetic variance is associated with a range of mean differences among families of only 11% in population # 2, and 2% in population # 3. But, for families from population # 1, the proportion of seedlings that avoided spring bud set during the first year showed significant phenotypic correlations with 4-year height ( $r = 0.51$ ) and 4-year elongation ( $r = 0.41$ ). Moreover, all families from population # 2 that exhibited more than 5% avoidance were also taller than the mean height of the

Table 1. — Model for analyses of variance of random effects for growth and phenology.

Source of variation	Mean square	Components expected in each mean square <sup>a</sup>
Replications	$MS_R$	$\sigma_W^2 + k\sigma_{RF/P}^2 + kfo_{RP}^2 + kfp\sigma_R^2$
Populations	$MS_P$	$\sigma_W^2 + k\sigma_{RF/P}^2 + kro_{F/P}^2 + krfo_P^2$
Families in populations	$MS_{F/P}$	$\sigma_W^2 + k\sigma_{RF/P}^2 + kro_{F/P}^2$
Families in population 1	$MS_{F/P1}$	$\sigma_W^2 + k\sigma_{RF/P}^2 + kro_{F/P1}^2$
Families in population 2	$MS_{F/P2}$	$\sigma_W^2 + k\sigma_{RF/P}^2 + kro_{F/P2}^2$
Families in population 3	$MS_{F/P3}$	$\sigma_W^2 + k\sigma_{RF/P}^2 + kro_{F/P3}^2$
Replications x populations	$MS_{RP}$	$\sigma_W^2 + k\sigma_{RF/P}^2 + kfo_{RP}^2$
Replications x families in populations	$MS_{RF/P}$	$\sigma_W^2 + k\sigma_{RF/P}^2$
Within cells	$MS_W$	$\sigma_W^2$

<sup>a</sup>  $k$  = harmonic mean of individuals within cells = 14.89,  
 $r$  = number of replications = 6,  
 $f$  = number of families in each population = 30,  
 $p$  = number of populations = 3.

Table 2. — Results for analyses of variance of growth and phenology presented as mean squares (MS) and variance components ( $\sigma^2$ ). All mean squares are statistically significant (5% level or less) except those denoted (b)

Source of variance	Degrees of freedom	Bud burst		Bud set		Second flush		4-yr height		4-yr growth		Adjusted height <sup>a</sup>	
		MS	$\sigma^2$	MS	$\sigma^2$	MS	$\sigma^2$	MS	$\sigma^2$	MS	$\sigma^2$	MS	$\sigma^2$
Replications	5	584.16	0.43	6.019	0.0039	1.435	0.0009	15,905	11.55	253.89 <sup>b</sup>	0.03	4,905	3.21
Populations	2	2757.53	.99	7.733 <sup>b</sup>	.0018	.033 <sup>b</sup>	-.0002	328,349	121.10	91,763	33.85	36,211	13.09
Families in populations	87	97.01	.96	2.575	.0232	.660	.0062	2,770	26.67	1,028	9.19	1,120	8.49
families in population 1	29	120.93	1.23	2.190	.0189	.580	.0053	2,864	27.33	1,133	10.35	1,123	8.52
families in population 2	29	75.79	.72	2.887	.0267	.724	.0069	2,686	25.23	952	8.33	1,229	9.71
families in population 3	29	94.26	.93	2.648	.0240	.677	.0064	2,760	26.16	1,001	8.88	1,009	7.24
Replications x populations	10	9.03 <sup>b</sup>	-.01	.834 <sup>b</sup>	.0007	.203 <sup>b</sup>	.0002	287 <sup>b</sup>	-.31	190 <sup>b</sup>	-.04	611	.56
Replications x families in populations	435	11.09	.38	.500	.0138	.109	.0032	423	19.03	208	9.93	362	18.05
Within cells	7587	5.37	5.37	.295	.2950	.062	.0616	140	139.82	60	59.91	93	93.14

<sup>a</sup> Adjusted by regression of 4-year height on 2-year height.

<sup>b</sup> F-value not statistically significant at P = 0.05

population after 4 years. Unfortunately, data were not available on the ability of each 4-year-old tree to avoid spring bud set during its first season of growth. Because phenotypic correlations were not perfect, and because genetic variance is limited in some populations, more data are necessary for assessing the potential of using patterns of first-year elongation for indirect selection of future performance.

Estimates of heritabilities were relatively high (Table 5). There is little doubt, however, that these genetic components are inflated beyond those expected in artificial reforestation. Extraneous environmental variance was closely controlled; therefore, interactions among families and replications (experimental errors) were unrealistically negligible, and environmental variances within cells were minimal. Conversely, even though interactions of genotype and environment could not be estimated at a single planting site, results are to be applied within seed zones. Therefore, the interaction should be represented in the numerator of the heritability expression (NAMKOONG, 1979). Moreover, genetic variances were similar within populations; therefore, similar responses to tree improvement can be expected within seed zones if genotype-environment interactions are also relatively equal.

Because estimates of heritabilities are somewhat inflated, estimated genetic gains are rather high. At a selection

Table 3. — Results of the analysis of variance of the proportion of seedlings avoiding spring bud set

Source of variance	Degrees of freedom	Mean square	Variance component ( $\sigma^2$ )
Replications	3	0.00262	-0.00001
Populations	2	.98636**	.00875
Families in populations	81	.04880*	.01000
families in population 1	26	.13319**	.03110
families in population 2	26	.01306**	.00106
families in population 3	29	.00060	-.00205
Replications x populations	6	.00185	-.00007
Residual	243	.00388	.00388
plots and individuals			-.00493
binomial sampling			.00881

\* Statistically significant at the 0.05 level of probability

\*\* Statistically significant at the 0.01 level of probability

Table 4. — Mean values for populations and range of family differences within populations

Variable	Population #1		Population #2		Population #3	
	Mean	Family differences	Mean	Family differences	Mean	Family differences
Bud burst (days)	35.9	4.8	34.1	3.8	35.6	4.0
Bud set (weeks)	3.7	2.1	3.9	2.4	3.5	2.7
Second flush (%)	13.1	10.2	13.6	8.8	13.2	7.8
4-year height (cm)	60.6	19.9	66.2	22.1	45.2	22.2
4-year growth (cm)	32.1	11.3	35.2	13.2	23.9	12.7
Adjusted height(cm)	57.8	12.6	60.9	14.2	53.6	13.1
Avoiding spring bud set (%)	7.5	54.8	1.7	11.3	0.1	2.5

intensity of one standard deviation, family selection should yield a gain of 0.8 days bud burst, 0.5 weeks bud set, 5% in the amount of 4-year elongation accounted by a second flush, and 10% in the number of seedlings that avoid spring bud set. Gains in growth potential, most realistically represented in statistics for adjusted height, amount to about 4%. In addition, selection of individual trees within selected families should result in additional gains of about 1 day in bud burst, 0.5 days bud set, 5% in the amount of the 4-year shoot accounted by a second flush, 10% in the number of seedlings that avoid spring bud set, and 4% in growth potential. Thus, relatively equal increments to genetic gains are expected from intermatings of selected families as with matings of selected individuals within selected families.

Genetic correlations (Table 6) show the degree of association among characters from either or both pleiotropism and linkage. Bud burst is genetically independent of bud set and growth potential. Not surprisingly, bud set and the proportion of 4-year elongation attributable to a second flush were perfectly correlated and obviously reflect the same genetic mechanism. Likewise, the three variables reflecting growth potential (4-year height, 4-year elongation and adjusted height) are so strongly correlated as to seem inseparable. But, in addition, variables reflecting growth potential were rather strongly associated with those of bud set. Consequently, correlated responses can be expected from selection of single traits.

## Discussion

Results have demonstrated substantial genetic variance within populations for growth potential, phenology, and

Table 5. — Summary of total ( $\sigma^2_T$ ) and family ( $\sigma^2_{TF}$ ) phenotypic variances, additive genetic variance ( $\sigma^2_A$ ), individual ( $h^2_I$ ) and family ( $h^2_F$ ) heritabilities, and corresponding standard errors ( $\pm$  se).

Trait	$\sigma^2_T$	$\sigma^2_{TF}$	$\sigma^2_A$ ( $\pm$ se)	$h^2_I$ ( $\pm$ se) <sup>††</sup>	$h^2_F$ ( $\pm$ se) <sup>††</sup>
Bud burst	6.71	1.08	3.49 (.64)	0.52 (.09)	0.81 (.15)
Bud set	0.332	.029	.084 (.017)	.25 (.05)	.73 (.15)
Second flush	.071	.007	.023 (.004)	.32 (.06)	.76 (.14)
4-yr height	185.12	31.10	95.53 (18.6)	.52 (.10)	.77 (.15)
4-yr growth	79.11	11.52	33.42 (6.92)	.42 (.09)	.73 (.15)
Adjusted height	119.68	12.54	30.87 (7.6)	.26 (.06)	.61 (.15)
Avoidance of spring bud set	.0188	.0122	.0364 (.0076)	1.93 (.40)	.76 (.16)

†† Adjusted for inbreeding coefficient of  $F = 0.10$  (SORENSEN, 1973)

patterns of first-year elongation of Douglas-fir seedlings. Thus, populations that are physiologically attuned to specific environments are themselves genetically heterogeneous. Because physiological specializations arise from directional selection, they develop at the expense of variability within populations. Consequently, the present results, which demonstrate substantial genetic variability within populations, must be interpreted congruously with physiological specialization of populations.

The maintenance of variability within specialized populations is undoubtedly enhanced by migration and mutation. Although migration increases variance within families of wind-pollinated organisms, and mutations accrue throughout a long life cycle, long-lived woody plants must be adapted to environments extremely heterogeneous in time as well as space. ROUGHGARDEN'S (1979) discussion of evolution in spatially or temporally varying environments applies. In general, geographic variation leads to an increase in homozygotes at the expense of heterozygotes. But LERNER'S (1954) concept of individual homeostasis endows biochemical flexibility to heterozygotes and, consequently, high fitness for environments exhibiting temporal variability. Temporal heterogeneity imposes variance in selection pressures within localities. Consequently, as argued by BRYANT (1976), temporal variability is also expressed spatially: a point exists on the environmental gradient where temporal variability equals spatial variability. Evolution toward specialization occurs only to the point that temporal variation provides overriding uncertainty to the system (BRYANT, 1976). Physiological specialization cannot develop at the expense of the variability within populations that yields adaptation to temporal heterogeneity.

Table 6. — Genetic correlations for growth and phenology.

	Bud burst	Bud set	Second flush	4-yr height	4-yr growth
Bud set	-.08				
Second flush	-.13	0.99			
4-yr height	.17	0.50	0.44		
4-yr growth	-.15	.60	.55	0.96	
Adjusted height	0.00	.64	.47	.69	0.84

Thus, Douglas-fir seems to have adapted to spatial heterogeneity by producing specialized populations. Variability within populations is maintained by adaptation to environments that vary in time. An evolutionary strategy that combines a rather high degree of specialization with flexibility has produced a species that uniquely has adapted to environments of great heterogeneity. The species, composed of two allopatric varieties, has a botanical distribution encompassing 20° of latitude; occurs from sea level to about 3000-m. altitude (ISAAC and DIMOCK, 1958); and has an ecological amplitude that ranges from dry sites near lower timberline to cool subalpine forests (DAUBENMIRE and DAUBENMIRE, 1968). Nevertheless, the cost of maintaining specialized adaptations is high. For a wind-pollinated outbreeding reproductive system, maintenance of variability within specialized populations results in transgressive segregation. Many offspring of a given population are adapted both to climates more mild and climates more severe than those to which the parental population is adapted.

High levels of additive genetic variance estimated within populations provide rather optimistic estimates of heritabilities and gains from tree improvement. Accordingly, even at a selection intensity of 1 standard deviation, estimated gains in adjusted height amount to 4% from both the selection of families and the selection of individuals within selected families. Although these data suggest rather phenomenal gains in growth potential at 8% increments, strong genetic correlations will restrict tree improvement.

Genetic correlations for growth potential and bud set suggest that a network of intercorrelated traits exists within populations as well as that observed among populations (REHFELDT, 1979a). This network, which conveys physiological specialization, seems keyed to adaptation of populations to the cold; high growth potential is related to delayed bud set, and late bud set correlates with high damage from early fall frosts and, surprisingly, to late spring frosts.

Thus, correlated responses are expected from selective improvement of a single trait such as growth potential. Accordingly, under weak selection (selection intensity of 1 standard deviation) gains in adjusted height from family and individual selection ( $\Delta G = 4\%$  for each) are corre-

lated with (1) an increase of 1.9% and 2.5%, respectively, in the amount that the 4-year shoot is determined by a second flush, and (2) a delay in bud set of 2.1 and 2.8 days, respectively. But most importantly, correlations among population means (REHFELDT, 1979a, 1979c), show that fall frost injuries increase by 2.6% each day that bud set is delayed. Consequently, even under rather weak selection intensities, gains in adjusted height from a combination of family and individual selection may increase the number of seedlings susceptible to fall frosts by about 13%! Consequently, there is little doubt that selection for gains in juvenile height will be accompanied by alterations in adaptation to the natural environment. The extent of alteration will depend on the relative mildness or severity of environmental conditions during juvenile phases of progeny testing.

To prevent inadvertent degeneration of environmental adaptations, multiple-trait selections will be necessary in tree improvement of Rocky Mountain Douglas-fir. Several options exist. Under independent culling, selections for growth potential can be made among individuals with bud set no later than a specified time. Restricted selection indices offer versatile approaches for limiting an expected change in bud set while maximizing selection differentials for growth. *Figure 1* illustrates gains, presented as a percentage of the mean growth potential, expected after changes in bud set have been restricted varying amounts from the maximum correlated response. Because genetic correlations are not perfect, even complete restriction of the mean change in bud set results in relatively little reduction in expected genetic gains in growth potential.

Even though the present statistics reflect trees only 4 years of age, results have direct application to long-term tree improvement programs. First, tendencies for multiple flushes in Douglas-fir decrease with age. Thus, late bud set and fall frost damage tend to be juvenile traits. Consequently, selections that restrict bud set must be made at young ages. Secondly, even though imperfect correlations relate juvenile growth potential to mature, LAMBETH (1980) suggests that selections can be made relatively early. Culling levels or selection indices could be readily adjusted to incorporate data from various ages (LIN, 1978). Finally, FRANKLIN (1979) shows that estimates of additive genetic variance vary with age. Therefore, present estimates of genetic gains, correlations, and correlated responses apply only to juvenile trees. Still, subsequent generations must complete juvenile growth in natural environments and therefore, selections should consider multiple traits at juvenile ages.

Regardless, analyses of genetic variability within Douglas-fir populations have revealed substantial levels of additive genetic variance. Thus, the specialized nature of population adaptation to heterogeneous environments in

the northern Rocky Mountains has not occurred at the expense of genetic variability within populations. Nevertheless, even though genetic variation within populations is high, genetic gains from tree improvement will not necessarily accrue rapidly. Skillful manipulation of genetic variability will be necessary to accomplish gains in growth potential without altering bud set and, thereby, cold hardiness.

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