ramets, and the degree of outcrossing control are the only inputs necessary for the algorithm to execute. Additional research is still necessary to provide the techniques needed for this algorithm to be applicable to all orchard layouts.

Sample Orchard Layout

The following sample orchard layout was designed using a population of 20 clones. The minimum separation of related ramets within the layout is three planting positions.

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---------------------------------------------------------
|  1 |  7 | 13 | 14 |  2 |  9 | 15 |  3 | 12 |  4 | 16 |
---------------------------------------------------------
|  8 |  4 | 15 | 16 | 18 |  5 | 19 |  6 |  2 | 10 | 17 |
---------------------------------------------------------
|  6 |  9 | 11 | 19 |  7 | 17 | 13 | 16 |  5 | 14 | 15 |
---------------------------------------------------------
| 18 | 20 | 10 |  2 |  1 | 14 |  3 |  8 |  4 | 19 |  7 |
---------------------------------------------------------
| 12 |  8 |  5 | 13 | 20 |  4 |  9 |  7 | 10 |  3 | 16 |
---------------------------------------------------------
|  9 |  6 | 14 | 18 | 11 | 12 | 19 | 13 |  1 | 15 | 17 |
---------------------------------------------------------
|  4 |  7 |  3 |  9 |  6 | 10 |  2 | 20 | 18 |  5 | 11 |
---------------------------------------------------------
| 16 | 19 | 17 |  1 | 15 |  7 |  5 |  3 |  8 | 12 | 13 |
---------------------------------------------------------
|  8 | 14 | 20 | 11 | 16 | 17 |  9 | 15 | 19 |  6 |  1 |
---------------------------------------------------------
| 15 | 10 | 12 |  5 |  8 | 13 |  6 | 16 | 20 |  7 |  2 |
---------------------------------------------------------
|  5 | 18 |  9 |  3 | 10 | 20 |  4 |  1 | 14 | 13 | 11 |
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Bibliography

Balas, E.: An Additive Algorithm for Solving Linear Programming with Zero-One Variables. Op. Res. 13: 517—545 (1965). — Bell, G. D. and Fletcher, A. M.: Computer Organised Orchard Layouts (COOL) Based on the Permutated Neighborhood Design Concept. Silvae Genetica 27: 223—225 (1978). — Cooper, L. and Steinberg, D.: Methods and Applications of Linear Programming. W. B. Saunders and Company. Philadelphia, Pa. (1974). — Dyson, W. G. and Freeman, G. W.: Seed Orchard Designs for Sites with a Constant Prevailing Wind. Silvae Genetica 17: 12—15 (1968). — Freeman, G. H.: The Use of Cyclic Balanced Incomplete Block Designs for Non-directional Seed Orchards. Biometrics 25: 561—571 (1969). — Gansel, C. R.: Effects of Several Levels of Inbreeding on Growth and Oleoresin Yield in Slash Pine. Proceedings 11th Conference on Southern Forest Tree Improvement. Atlanta, Georgia: 173—177 (1971). — Giertych, M. M.: Systematic Lay-outs for Seed Orchards. Silvae Genetica 14: 91—94 (1965). — Golomb, S. W.: Tiling with Polyominoes. J. Combinatorial Theory 1: 280—296 (1966). — Golomb, S. W.: Tiling with Sets of Polyominoes. J. Combinatorial Theory 9: 60—71 (1970). — Hardgrave, W. W. and Nemhauser, G. L.: On the Relation Between the Traveling Salesman and the Longest Path Problem. Op. Res. 10: 647—657 (1962). — Hatcher, A. V. and Weir, R. J.: Design and Layout of Advanced Generation Seed Orchards, Presented at 21st Annual Southern Forest Tree Improvement Conference, Virginia Polytechnic Institute and State University, Blacksburg, Virginia: 205—212 (1981). — Jett, J. B. and Zobel, B. J.: Notes from Tree Improvement Cooperative Short Course. School of Forest Resources, North Carolina State University, Raleigh, North Carolina: 73—83 (1977). — La Bastide, J. G. A.: A Computer Program for the Lay-outs of Seed Orchards. Euphytica 16: 321—323 (1967). — Langner, W. and Stern, K.: Versuchstechnisches Problem bei der Anlage von Klon-Plantagen (An experimental problem concerning the arrangement of clone plantations). Zeitschr. für Forstgen. und Forstpflanz. 4: 81—88 (1955). — Malac, B. F.: Shifting-clone Design for a Superior Tree Seed Orchard. Woodland Research Notes 14, Union Camp. Corp., Savannah, Ga. (1962). — Wagner, H. M.: Principles of Operations Research. Prentice Hall, Inc. Englewood Cliffs, New Jersey (1969). — Zobel, B. J., Barber, J., Brown, C. L., and Perry, T. O.: Seed Orchards - Their Concepts and Management. Journal of Forestry 56: 815—825 (1958).

Genetic Variances and Covariances in Pinus contorta: estimates of genetic gains from index selection

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Summary

Genetic variances and covariances were estimated for 6-year-old trees from 10 families within eight populations of *Pinus contorta* from the northern Rocky Mountains (USA). Analyses of 10 traits reflecting growth, quality, and adaptedness revealed substantial genetic variances for nearly all traits. As a consequence, univariate selection for height should provide genetic gains of about 5% per unit selection intensity. However, strong genetic correlations linked height with branch length (0.75), crown width (0.75), and the amount of shoot elongation that continues into mid-summer (0.70). Height was also related to the number of whorls on the current shoot and, consequently, to the number of branches. Thus, multi-trait selections are necessary to prevent genetic gains in productivity from being accompanied by inadvertent degeneration of traits related to adaptation and quality. Multi-trait selections, however, reduce anticipated genetic gains in productivity. Restricted selection indices are developed to exemplify procedures for holding constant the correlated responses while maximizing gains in height.

Key words: Pinus contorta, additive genetic variances, genetic correlations, genetic gains, restricted selection indices.

Zusammenfassung

Bei 10 Familien von 6 Jahre alten *Pinus contorta* innerhalb von 8 Populationen in den nördlichen Rocky Mountains (USA) wurden die genetischen Varianzen und Kovarianzen geschätzt. Die Analyse von 10 Merkmalen, die das Wachstum, die Qualität und das Anpassungsvermögen widerspiegeln, zeigte wesentliche genetische Varianzen für fast alle Merkmale. Als Konsequenz sollten allein für die Höhe genetische Gewinne von ungefähr 5% pro Selektionsintensitätseinheit möglich sein.

Enge genetische Korrelationen koppeln die Höhe mit der Astlänge (0,75), der Kronenbreite (0,75) und dem Ausmaß des Trieblängenwachstums, welches sich bis in die Sommermitte hinein fortsetzt (0,70). Die Höhe steht ebenfalls mit der Anzahl der Quirle des gegenwärtigen gleichlaufenden Triebes und folglich mit der Anzahl der Äste in Beziehung. Daher sind auf mehrere Merkmale gerichtete Selektionen nötig, um zu verhindern, daß mit genetischen Gewinnen bei der Produktivität gleichzeitig eine unbeabsichtigte Degeneration der Merkmale einhergeht, welche die Anpassungsfähigkeit und die Qualität bestimmen. Eine Selektion auf mehrere Merkmale hin reduziert beabsichtigte

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genetische Gewinne bei der Produktivität. Es werden eingeschränkte Selektionsindizes entwickelt, um Maßnahmen zur Erhaltung der korrelierten Reaktionen bei gleichzeitigen maximierten Gewinnen für die Höhe zu erläutern.

Introduction

Genetic and economic gains from tree breeding require that adaptedness and quality of secondary economic traits be maintained in improved races. In *Pseudotsuga menziesii* var. *glauca* (Beissn.), for example, multi-trait selections are required to improve growth while holding constant the time of bud set, a trait that reflects susceptibility to injury from fall frosts (Rehfeldt, 1983b). Similarly, duration of shoot elongation of *Pinus contorta* Dougl. ex Loud. progenies is closely correlated with tree height in subsequent years (Cannell *et al.*, 1981). Appropriate breeding strategies, therefore, must reflect the genetic variances and covariances that characterize the system of genetic variability. While being firmly based on quantitative genetics, the strategy must also reconcile adaptation.

In *Pinus contorta,* adaptive differentiation of populations occurs in response to relatively small elevational (Illingworth, 1976; Hagner, 1980; Rehfeldt, 1983a) or geographic (Lindgren *et al.*, 1980; Rehfeldt, 1980; Rehfeldt and Wykoff, 1981) gradients. In northern Idaho alone, populations separated by merely 200 m elevation are differentiated for a variety of traits reflecting cold hardiness and growth potential (Rehfeldt, 1983a). Relatively steep clines have direct bearing on maintaining adaptedness of improved races. First, to represent patterns of adaptive variation, breeding zones should be geographically small and elevationally narrow. Secondly, selective breeding must consider genetic correlations among adaptive and economic traits.

The quantitative genetics of *P. contorta* is, however, virtually unknown. Preliminary estimates show abundant genetic variability within populations (Dietrichson, 1970; Illingworth, 1976; Perry and Lotan, 1978), and selection differentials in natural populations are so large that considerable genetic gains seem probable almost regardless of the heritabilities (Rehfeldt *et al.*, 1980). Indeed, clonal propagation of superior individuals within provenances results in genetic gains of 10 to 15% (Cahalan, 1981). *P. contorta,* however, exhibits phenotypic correlations that may influence the improvement strategy. For instance, shoot elongation is characterized by either mono- or polycyclic patterns, each cycle of which is marked by a whorl of branches (Lanner and van den Berg, 1975). Genetic variation among varieties in patterns of shoot growth (see Critchfield, 1980) suggests that genetic gains in growth may be associated with increased cyclicity and, consequently, with an increase in the number (Thompson, 1976) and size (Cannell *et al.*, 1983) of branches. In addition, the length and diameter of branches show close phenotypic correlations (r = 0.84 and 0.95, respectively) with stem diameter (Fryk, 1980). Thus, breeding programs that concentrate on volume may also alter the length and diameter of branches.

In this paper, genetic variances and covariances are presented for a variety of adaptive and economic traits for *P. contorta* var. *latifolia.* A discussion is centered on estimates of genetic gains from index selection.

Materials and Methods

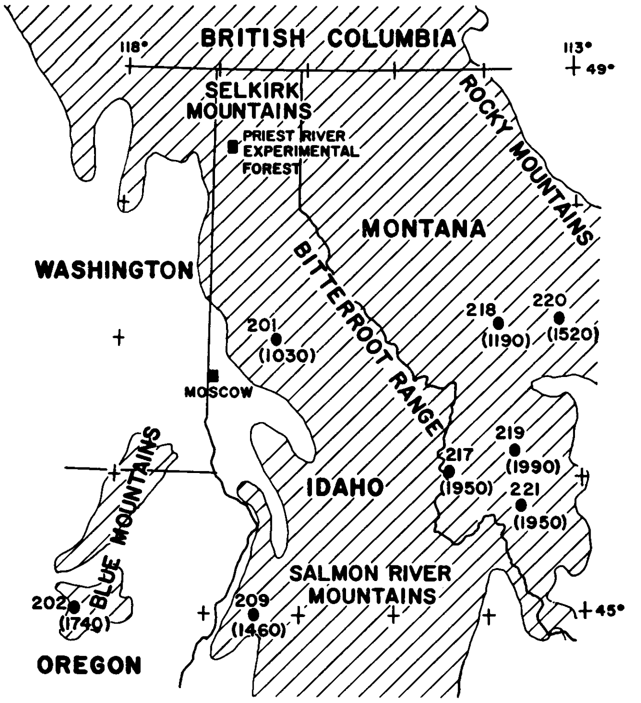

Figure 1. — Location of populations and site of study. Elevation of sampled populations are in parentheses.

Eight populations were selected as a sample of the ecologic and geographic diversity of *Pinus contorta* var. *latifolia* in the northern Rocky Mountains of the United States. The populations were well dispersed geographically and represented elevations as low as 1030 m and as high as 1990 m *(Fig. 1).* Because adaptive differentiation of *P. contorta* populations adheres to rather steep clines in the Rockies, these eight populations are considered representative of distinct breeding zones.

Wind-pollinated cones were collected from 10 trees within each population. Trees were randomly chosen from those that were equal or superior to the phenotypic average. Seedlings representing the 80 families were grown for 6 months in plastic containers (65 cm^3) at a shadehouse in Moscow, Idaho. In the fall, seedlings were planted at a single site in the Priest River Experimental Forest *(Fig. 1).* The site was flat, at low elevation (670 m), and with soil of glacial till. Eight seedlings from each family were planted in row plots. Twelve plots from each family were established in a completely random design. Rows were separated by 1 m; 0.5 m separated seedlings within rows.

The planting was maintained under intensive culture until trees were well established. Effects of a lack of rainfall on a soil composed of glacial till were alleviated by irrigation during August of the second and third growing seasons. An infestation of white grubs *(Phyllophaga anxia* LeConte) was controlled by biannual applications of insecticide during the first 4 years. After 6 years, survival was about 75%. An additional 5% of the trees were discarded because of insects, diseases, and injuries (largely from birds) to the terminal shoot during years 4 to 6.

The following traits were scored on individual trees:

1. height after 6 years,
2. elongation of the terminal shoot during year 6,
3. early growth, the amount of 6-year elongation that occurred before April 26,
4. late growth, the amount of 6-year elongation that occurred after May 25,
5. branch length, the length of the longest branch on the 6-year shoot,

6. whorls, the number of whorls of branches associated with the 6-year shoot,
7. branches, the number of branches on the 6-year shoot summed for all whorls,
8. crown width at the widest point,
9. leaf length near the center of the 5-year shoot,
10. adjusted height, the 6-year height adjusted by regression on 4-year height and, therefore, free of genetic and environmental effects that influenced height during the first 4 years.

All measurements were transformed to logarithms because variances were proportional to the square of mean values. Counts were transformed to $\sqrt{X + 1/2}$ to normalize distributions. The number of whorls, a discrete variable, was carried through quantitative analyses because of its practical significance.

Statistical analyses followed the model for unweighted means (Steel and Torrie, 1960) 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). Since populations are assumed to represent separate breeding zones, estimated responses to selection pertain to breeding populations that are adaptationally similar. Thus, calculations of genetic gains and correlated responses to selection were made within populations and were averaged for all populations. Effects of heterogeneous variances among populations are considered subsequently. Because trees within populations are related, genetic variances and covariances were adjusted for inbreeding, which was assumed to be 10 percent. Responses to selection were calculated on transformed data but were presented in original units of measure.

Table 1. — Model for analysis of variance of individual traits using unweighted means.

Source of variation		d.f	Components expected in each mean square
Populations	(P)	7	$\sigma^2_W + k\sigma^2_{R/F} + nk\sigma^2_{F/P} + nfk\sigma^2_P$
Families in population	(F/P)	72	$\sigma^2_W + k\sigma^2_{R/F} + nk\sigma^2_{F/P}$
Plots in families	(R/F)	880	$\sigma^2_W + k\sigma^2_{R/F}$
Within plots	(W)	∿4100	σ^2_W

where: k = harmonic mean of individuals within plots = 3.94 to 4.10, depending on the trait.
n = number of plots for each family = 12.
f = number of families for each population = 10.

Additional analyses were made to determine the effects of the number of whorls of branches in year 6 on (1) the total height of trees and (2) the total number of branches. These analyses were made according to a model in which whorl types were nested within families without regard to populations and plots:

$$Y_{ijk} = \mu + f_i + w_{ij} + d_{ijk}$$

where Y_{ijk} = the height or branches of the k^{th} tree of the j^{th} whorl type from the i^{th} family; μ = the overall means; f = the effect of families; w = the effect of whorls within families; and d = the residual.

Results

Analyses of variance *(Table 2)* detected significant effects of populations for all traits. For most of the dimensional traits, the effects of populations accounted for large proportions (30%) of the total variance and, thereby, reflect steep clines. Two of the dimensional traits, however, expressed little population variation. One of these, early growth, is associated with initiation of shoot elongation, an event characterized by little genetic variation among populations (Rehfeldt and Wykoff, 1981). The second, adjusted height, reflected rather precise prediction of 6-year height by 4-year height (R^2 = 0.75, df = 5,100). Thus, the performance of individual trees, populations, and families (as shown later) at this single planting site did not change between ages 4 and 6. Low levels of population differentiation for traits related to branching patterns (branches and whorls *Table 2)* is a result already documented for populations from northern Idaho (Rehfeldt, 1983a).

Mean differences among populations *(Table 3)* follow expected patterns. For those traits reflecting strong population differentiation, the range in population means is large in relation to the overall mean. As expected, the population (201) from the lowest elevation was the tallest, elongated the most in year 6, had the widest crown, the longest branches, the longest leaves, and produced the largest amount of 6-year elongation as late growth. All such characters are commonly associated with adaptation to relatively mild environments (Rehfeldt and Wykoff,

Table 2. — Results of analyses of variance presented as variance components (σ^2, *Table 1)* and intraclass correlations (r_I), the ratio of individual components to the sum of all components. All effects were statistically significant at the 5% level of probability.

	Sources of variance							
	Populations		Families in populations		Plots in families		Within plots	
Trait	σ^2_P	r_I	$\sigma^2_{F/P}$	r_I	$\sigma^2_{R/F}$	r_I	σ^2_W	r_I
Height	0.0240	0.32	0.0032	0.04	0.0140	0.18	0.0346	0.46
Elongation	0.0275	0.29	0.0031	0.03	0.0194	0.21	0.0438	0.47
Adjusted height	0.0006	0.03	0.0006	0.03	0.0045	0.24	0.0130	0.70
Early growth	0.0084	0.05	0.0072	0.04	0.0371	0.21	0.1270	0.71
Late growth	0.1547	0.31	0.0189	0.04	0.0739	0.15	0.2579	0.51
Branch length	0.0309	0.29	0.0032	0.03	0.0213	0.20	0.0524	0.49
Branches	0.0112	0.04	0.0099	0.03	0.0281	0.10	0.2390	0.83
Crown width	0.0224	0.26	0.0045	0.05	0.0137	0.16	0.0466	0.53
Leaf Length	0.0175	0.29	0.0044	0.07	0.0057	0.09	0.0335	0.55
Whorls	0.0057	0.03	0.0085	0.05	0.0105	0.06	0.1639	0.87

Table 3. — Trait means according to the populations (keyed to *Figure 1)* and range of family means within populations.

Trait		Overall	Population							
		mean	201	202	209	217	218	219	220	221
Population means										
Height	(cm)	80.7	105.3	74.6	70.3	67.8	91.1	71.0	87.8	73.2
Elongation	(cm)	27.9	36.6	26.4	24.3	23.0	32.2	24.2	30.8	24.9
Adjusted height	(cm)	80.7	84.9	84.1	81.6	79.7	85.9	81.0	84.4	81.3
Early growth	(cm)	3.8	4.2	3.6	3.8	3.6	3.8	3.7	4.0	4.0
Late growth	(cm)	6.5	13.1	6.0	4.8	4.2	9.0	4.8	7.9	4.8
Branch length	(cm)	15.0	20.7	14.8	13.3	12.1	17.0	13.0	15.7	13.2
Branches	(No)	8.5	8.1	8.9	7.8	7.5	9.5	8.2	9.0	8.4
Crown width	(cm)	50.2	64.4	47.5	43.4	42.2	57.3	45.0	54.6	45.2
Leaf length	(cm)	5.0	6.2	4.4	5.2	4.3	5.5	4.6	5.6	4.5
Whorls	(No)	2.0	1.9	2.0	2.0	2.0	2.1	2.0	2.1	2.0
Range of family means										
Height	(cm)	-	13.4	16.6	14.7	15.8	12.7	16.9	21.3	18.8
Elongation	(cm)	-	8.1	7.7	4.9	6.1	5.3	5.8	5.8	6.1
Adjusted height	(cm)	-	11.8	12.1	7.9	13.1	8.9	6.7	8.7	6.8
Early growth	(cm)	-	1.3	0.9	1.2	1.8	1.1	1.3	1.1	1.6
Late growth	(cm)	-	5.3	5.2	1.8	3.5	4.6	1.8	1.6	2.6
Branch length	(cm)	-	2.7	5.1	3.3	3.0	3.8	2.2	2.8	3.8
Branches	(No)	-	1.5	3.6	1.6	2.2	2.8	2.8	2.5	2.2
Crown width	(cm)	-	7.4	15.4	13.2	9.5	13.7	13.0	9.6	15.0
Leaf length	(cm)	-	0.9	1.0	1.1	1.2	1.1	1.5	1.5	1.2
Whorls	(No)	-	0.3	0.5	0.2	0.2	0.3	0.3	0.5	0.3

1981). The small mean differences among populations for traits related to branching illustrate the low levels of variance among populations.

The effects of families, however, are of prime interest to tree improvement. These effects were significant for all traits even though they accounted for relatively small proportions (3% to 7%) of the total variance *(Table 2)*. Thus, the main effects of populations accounted for about eight times as much variance as the effects of families within populations for those dimensional traits associated with strong differentiation of population. For other traits, however, effects of families and populations accounted for equal variances.

Since populations are considered as representatives of separate breeding zones, the distribution of variability within and among families within populations ($\sigma^2_{F/P}$, *Table 2)* determines the phenotypic and genetic variances, heritabilities, and genetic gains *(Table 4)* expected from tree improvement. Despite relatively low intraclass correlations for effects of families, and despite a relatively small range of family means *(Table 3)*, even mild selection is expected to yield substantial genetic gains within populations for all traits except, perhaps, height deviation *(Table 4)*. For instance, interbreeding of the tallest 38% (i = 1, FALCONER, 1960) of the individuals within populations should yield genetic gains in 6-year height

Table 4. — Total (σ^2_T) and family (σ^2_{TF}) phenotypic variances, additive genetic variances (σ^2_A), individual (h^2_I) and family (h^2_F) heritabilities, associated standard errors (± se), expected genetic gains* (ΔG) per unit selection intensity (i) for three selection programs, and correlated responses* (CR/i) from univariate selection on height.

Trait	σ^2_T	σ^2_{TF}	σ^2_A ± se††	h^2_I ± se	h^2_F ± se	% Δ G/i			%CR/i
						Mass	Family	Individual†††	
Height	0.0518	0.0051	0.0116 ± 0.0029	0.22 ± 0.06	0.57 ± 0.14	5.1	4.1	3.8	--
Elongation	0.0633	0.0056	0.0112 ± 0.0033	0.17 ± 0.05	0.50 ± 0.15	4.5	3.8	3.3	1.5
Adjusted height	0.0181	0.0012	0.0022 ± 0.0007	0.12 ± 0.04	0.46 ± 0.15	1.6	1.1	1.2	0.2
Early growth	0.1713	0.0129	0.0259 ± 0.0076	0.15 ± 0.04	0.50 ± 0.15	6.4	5.8	4.7	-0.0
Late growth	0.3507	0.0303	0.0680 ± 0.0181	0.19 ± 0.05	0.56 ± 0.15	11.9	10.2	8.8	2.5
Branch length	0.0769	0.0061	0.0115 ± 0.0036	0.15 ± 0.05	0.47 ± 0.15	4.0	3.7	3.2	1.1
Branches	0.2770	0.0172	0.0356 ± 0.0105	0.13 ± 0.04	0.52 ± 0.12	4.6	4.6	3.5	-0.0
Crown width	0.0648	0.0066	0.0162 ± 0.0040	0.25 ± 0.06	0.61 ± 0.15	6.6	5.1	4.9	1.5
Leaf length	0.0436	0.0056	0.0158 ± 0.0033	0.36 ± 0.07	0.70 ± 0.15	7.8	5.4	5.8	0.3
Whorls	0.1829	0.0127	0.0306 ± 0.0076	0.17 ± 0.04	0.60 ± 0.15	3.6	3.9	2.7	0.1

* Calculated within populations and expressed according to original units of measure.

** Adjusted for inbreeding coefficient of 0.10.

*** Selection of individuals within selected families.

Where, as defined in *Table 2:*

$$\sigma^2_T = \sigma^2_{F/P} + \sigma^2_{R/F} + \sigma^2_W$$

$$\sigma^2_{TF} = \sigma^2_{F/P} + \frac{\sigma^2_{R/F}}{n} + \frac{\sigma^2_W}{nk}$$

$$\sigma^2_A = 3.6\,\sigma^2_{F/P}$$

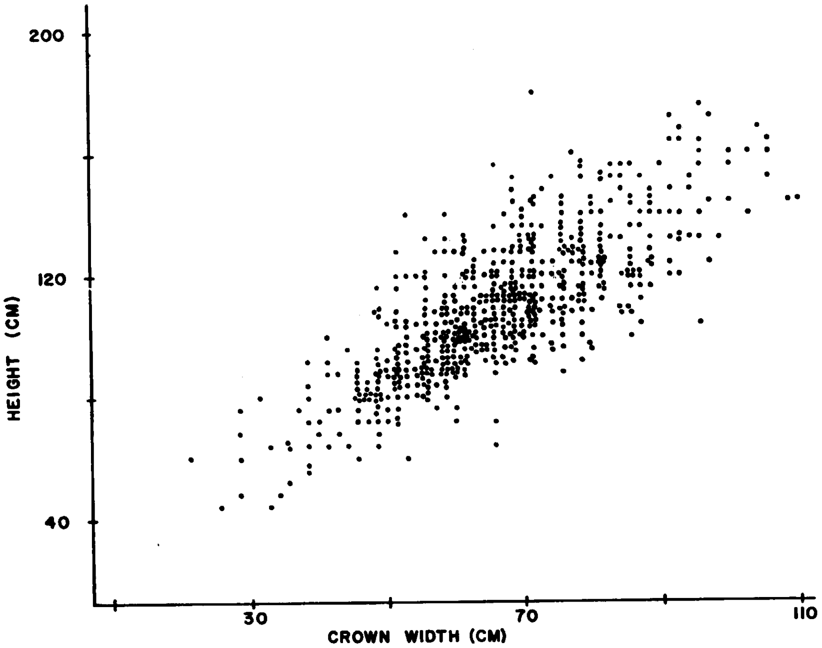

Figure 2. — Relation between 6-year height and crown width for seedlings of all families from population 201 *(Fig. 1)*.

of about 5% in the following generation. For estimated gains to reflect an average value applicable to all populations depends upon homogeneous variances within populations. Relatively homogeneous variances are reflected by the range of mean values presented in *Table 3*.

Table 4 allows comparison of the relative effectiveness of mass selection, family selection, and selection of individuals within selected families. First, the genetic gains expected from family selection are only slightly greater than those expected from selection of individuals within selected families. These data suggest that it would be more efficient to emphasize selection of individuals within selected families than to emphasize family selection. Second, mass selection yields about the same genetic gains (per unit i) as combined family and individual selections: to select the tallest 38% ($i = 1$) of the individuals within the tallest 38% of the families should yield a gain in height of about 8%. The size of the breeding population, however, would have been reduced to 14% of the size of the original population, a value of $i = 1.6$ for a comparable level of mass selection. At such an intensity, mass selection also yields expected gains of about 8%. Such comparisons must be tempered, however, by effects of potential inbreeding among related individuals within seed orchards or in subsequent cycles of selection.

Genetic gains in single traits, however, do not accrue independently. Thus, selection for height alone can yield correlated responses in related traits. The degree of correlated response depends on the genetic variances *(Table 4)*, covariances, and correlations *(Table 5)*. Most noteworthy among the genetic correlations are the strong interdependencies among height, elongation late growth, branch length, and crown width *(Figure 2)*. This means that even mild univariate selection ($i = 1$) for height is expected to produce rather substantial correlated responses *(Table 4)*.

These correlated responses involve a 2.5% change in late growth, a 1.1% change in branch length, and a 1.5% change in crown width for each unit of selection intensity applied to height. Estimates, however, were calculated from bivariate relationships of FALCONER (1960). Because several traits exhibit strong intercorrelations, bivariate models tend to underestimate the expected correlated responses. Thus, when mass selection for height ($i = 1$) is applied within

Table 5. — Genetic covariances (below diagonal) and genetic correlations (above diagonal). Covariances have been adjusted for inbreeding (F = 0.10) within populations.

		HT	EL	AH	EG	LG	BL	BR	CW	LL	W
Height	HT		0.86	0.33	-0.04	0.70	0.75	-0.01	0.75	0.13	0.13
Elongation	EL	0.0097		0.57	0.22	0.82	0.82	0.09	0.61	0.25	0.20
Adjusted height	AH	0.0017	0.0029		0.25	0.44	0.49	-0.10	0.20	0.19	0.03
Early growth	EG	-0.0007	0.0036	0.0018		-0.26	-0.05	0.18	-0.19	-0.04	0.07
Late growth	LG	0.0194	0.0027	0.0054	-0.0108		0.84	-0.07	0.54	0.24	0.24
Branch length	BL	0.0086	0.0094	0.0025	-0.0007	0.0238		-0.23	0.60	0.50	+0.00
Branches	BR	-0.0002	0.0018	-0.0007	0.0058	-0.0032	-0.0047		-0.16	-0.10	0.74
Crown width	CW	0.0101	0.0083	0.0011	-0.0040	0.0180	0.0083	-0.0040		0.02	-0.00
Leaf length	LL	0.0018	0.0032	0.0011	-0.0007	0.0079	0.0068	-0.0025	0.0004		-0.07
Whorls	W	0.0025	0.0036	0.0004	0.0018	0.0115	+0.0000	0.0245	0.0001	-0.0018	

Table 6. — Genetic gains (%) in tree height and correlated responses (%) for late growth, branch length, and crown width after mass selection (i = 1) within populations according to unrestricted and restricted models *(Fig. 3)* of index selection. Responses were calculated from selection differentials observed following index selection on the original data. Percentages reflect original units of measure.

Selection model	Percent restriction† LG	BL	CW	Direct response Height	Correlated response Late growth	Branch length	Crown width
Unrestricted	0	0	0	5.6	12.2	5.5	4.6
Restricted							
1	100	100	100	2.0	0.4	-0.4	-0.3
2	100	100	0	2.1	-0.0	-0.8	1.5
3	100	0	10	2.5	-0.3	1.7	0.2
4	100	0	0	2.9	-0.0	2.1	2.4
5	75	100	100	2.0	1.0	-0.6	-0.4
6	75	100	0	2.1	0.5	-0.0	1.2
7	75	0	100	2.6	0.1	1.7	0.2
8	75	0	0	3.1	-0.3	2.3	2.6

* Restricted models are keyed to *Figure 1.* LT = late growth; BL = branch length; CW = crown width.

populations, correlated responses expected in a subsequent generation are approximately four times greater *(Table 6)* than those expected from bivariate models. There is no doubt, therefore, that selections made for height alone will result in substantial alterations of secondary traits within improved populations.

Notably absent from the traits related by strong genetic correlations are the number of whorls and the number of branches on the current shoot. Although these traits show a strong correlation with each other, they seem poorly related to height *(Table 5)* and, consequently, are shown to change little under univariate selection for height *(Table 4)*. Because this result conflicts with those of Thompson (1976), the relationship among whorls, branches, and height was explored further.

Analyses of variance showed that the effects of whorl types significantly (1% level) influenced the height and number of branches of trees within families. On the average, trees with either three or four whorls of branches on the current shoot were 102 cm tall and had 13 branches; trees with two whorls were 82 cm with nine branches; and those with one whorl were 71 cm with five branches. If breeding populations were established from mass selection ($i = 1$) within each population, the proportion of trees represented in the breeding population with either three or four whorls would increase from 10% to 20%; if the top 10% were selected within populations, the proportion would increase to 30%.

This means that despite low genetic correlation coefficients, tree height is strongly and positively correlated with the number of whorls on the current shoot and, consequently, with the number of branches. Failure of these relationships to be expressed in genetic variances and covariances is undoubtedly due to the low frequency of all whorl classes except two whorls. More than 81% of the trees had two whorls; only 8% had one whorl, 10% had three whorls, and three trees had four whorls. Thus, number of branches and number of whorls are two additional traits that must be considered in maintaining the quality of *Pinus contorta* being bred for increased growth potential.

Discussion

Differentiation of populations from contrasting ecological settings is an expected consequence of ecological adaptation in species for which adaptational clines are steep. The pronounced degree of population differentiation that was detected for most dimensional traits strongly influences breeding strategy. Traits such as height, shoot elongation, leaf length, amount of shoot elongation that occurs into mid-summer are integral components of an annual sequence of developmental events. This sequence, which begins with bud burst and ceases with cold acclimation, must be completed within the frost-free period. As stressed by Dietrichson (1964), adaptation results from synchronization of developmental events with the local climate. This means that the dimensional traits that exhibited pronounced differentiation of populations are, to some extent, adaptive. It also means that synchronization of developmental events with the local climate can be assessed by a thorough analysis of a few traits that sample the sequence. Because the initiation of shoot elongation in *Pinus contorta* is primarily an environmental response *(Table 2;* Rehfeldt and Wykoff 1981), late growth, despite being measured early in the summer, is a key trait in assessing adaptation. Late growth determines the duration of elongation and, consequently, the length of time required for leaf development, lignification, and cold acclimation to be completed. Late growth is, therefore, adaptive.

The adaptive nature of the dimensional traits has two ramifications to the breeding strategy. Pronounced differentiation emphasizes the need for tree improvement to take place within breeding zones within which trees are similarly adapted. Although breeding zones have not been delineated for the northern Rocky Mountains, they will likely be relatively broad geographically (Rehfeldt, 1980; Rehfeldt and Wykoff, 1981) but narrow elevationally (Rehfeldt, 1983a). Pronounced differentiation and small breeding zones demand a breeding strategy that maintains adaptation.

A system of genetic variability in which numerous adaptive and economic traits not only exhibit genetic variability but also are intercorrelated presents a challenge to the breeder. The challenge is to develop a breeding strategy that provides gains in productivity while preventing inadvertent degeneration of adaptedness and economic traits of secondary importance. In the present data, productivity can be represented by height, adaptedness by late growth, and secondary economic traits by branch length and crown width. A suitable breeding strategy can be selected from alternative models. A traditional approach might invoke selection indices for optimizing the balance between desirable and undesirable traits. An alternative may involve a search for rare individuals in which genetic correlations have been broken. KÄRKI (1983) attests to the feasibility of developing races of *Picea abies* (L.) KARST. and *Pinus sylvestris* L. that combine fast growth with fine branches and narrow crowns and, thus, can be grown in dense plantings.

The traditional approach involves selection indices which are, as reviewed by LIN (1978) of the form:

$$I = \Sigma b_i X_i$$

where I is the index value for a particular individual, X_i is the phenotypic value for trait i, and b_i is the selection coefficient. Restricted selection indices are developed from the calculation of b's according to:

$$\underline{b} = G^{-1} \underline{\triangle}$$

where $\underline{b}$ is a vector of index coefficients, G is the genetic variance-covariance matrix, and $\underline{\triangle}$ is a vector of genetic gains.

Thus, genetic gains in height can be calculated for a variety of models which restrict the maximum correlated response of late growth, branch length, and crown width. Index coefficients can be used on the original data to estimate genetic gains reflected by various restrictive models. Results of such calculations provide estimates of genetic gains *(Fig. 3)* and correlated responses *(Table 6)* for a variety of selection regimes. Restrictions of the correlated responses for branch length and crown width were varied from 0 to 100% of the maximum response; and, because late growth is keyed to the adaptation of the annual sequence of developmental events to the local climate, restrictions in late growth were maintained between 75% and 100% of the maximum correlated response for that trait.

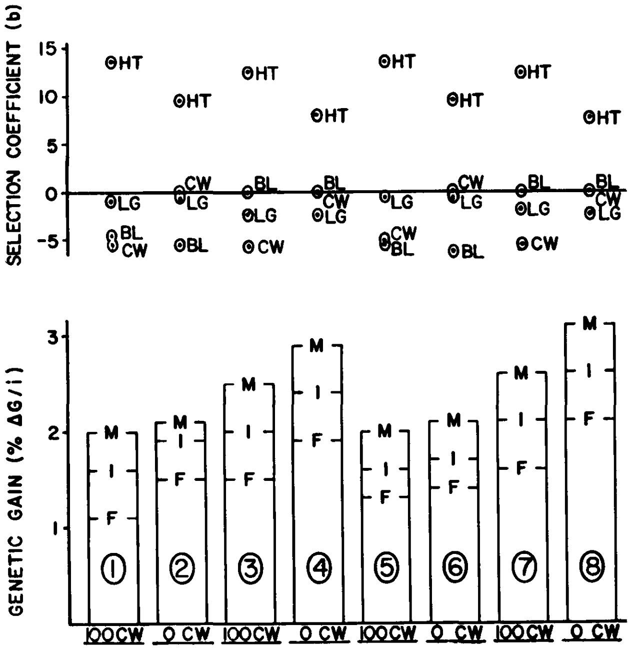

Figure 3. — Coefficients for selection indices (above) and associated genetic gains (below) in height (HT) expected under various models (numbered bar graphs) of index selection. Models present genetic gains (%ΔG) expected when correlated responses in branch length (BL), crown (CW), and late growth (LG) are restricted by the proportion indicated at the base of each bar, i.e., model 3 estimates gains associated with 100% restriction of the correlated responses in LG and CW but with no restriction on BL.

When late growth, branch length, and crown width are all held constant, genetic gains in height are limited to about 2%/*i* for mass selection (Model 1,*Fig. 2)*. As restrictions on the correlated response for branch length are relaxed to zero, gains in height increase an additional 0.6/*i* for comparable selection programs. (Comparable programs hold constant all traits except the one in question. Thus, for branch length, models 1 and 3, 2 and 4, 5 and 7, and 6 and 8 are comparable.) Similarly, as the restriction on the correlated response in crown width is eased to zero, gains in height increase an additional 0.3%/*i*; when the restriction on late growth is reduced to 75%, the resulting gain in height is an additional 0.2%/*i*. Thus, Model 8 *(Fig. 3)*, the most liberal of the restricted models tested, predicts genetic gains of 3.1%/*i*.

These restricted indices, however, have not considered correlated responses involving the number of whorls of branches or the total number of branches. Because the relationships between these variables and height are not reflected by genetic correlations, the restricted selection index is not appropriate. Two alternatives are feasible. In one, trees with either three or four whorls can be culled before selections are made; truncation of the distribution had little effect on either the mean or the variance in 6-year height. In the other, mass selection at $i = 1$ for all models represented in *Figure 3* produces a breeding population in which 13% have three whorls and 5% have one whorl. These data represent, respectively, an increase of 3% and a decrease of 4% from those of the original population. Evidently, restriction of late growth has produced a restriction on whorls and branches. It is not known, however, whether this results is unique for the current data or is characteristic of the system of genetic variability.

Because large trees are expected to have long branches and wide crowns, the correlated responses in branch length and crown width that accompany increases in tree height do not necessarily represent reduced quality. Regressions of crown width and branch length on 6-year height show trees that are 5% taller than the mean are expected to have (1) crowns that are 4.2% wider than the mean, and (2) branches that are 5.1% longer than the mean. Thus, the increases in crown width and branch length expected with unrestricted selection *(Table 6)* are similar to those expected according to the phenotypic relationships among traits. This means that models that restrict correlated responses in branch length and crown width actually reflect, in comparison to mean values, an increase in quality.

Thus, selection indices provide for progress in developing fast growing trees of improved quality according to traditional approaches. Indeed, scatter diagrams *(Fig. 2)* show the existence of tall trees that have much narrower crowns than the average. These trees are, however, extremely infrequent. Consequently, a breeding strategy based on seeking individuals in which genetic correlations have been broken may be most feasible as a secondary approach.

Nevertheless, the presence of such trees raises the possibility of combining traditional strategies with that of Kärki (1983): develop selection indices that hold growth constant while maximizing a reduction in crown width. Gains in productivity are realized, then, by cultivating dense stands.

The present results were derived from a test at a single planting site. One may argue, therefore, that the results may be of limited practical value because interactions of genotype and environment cannot be expressed by the data. This limitation, moreover, may be magnified with species that display steep adaptive clines. But, biologically sound improvement programs will take place within breeding zones that are established in a manner consistent with patterns of adaptive variation. The primary intent of zoning is to minimize genotype-environment interactions. In such a program, the present data apply directly; genetic variances and covariances were calculated within populations. It is true, however, that a test site at low elevation provides conditions tha are more mild han those typical of most breeding zones of *Pinus contorta*. For this reason, the present estimates of genetic variances should be considered as the optimum. Yet to wait for genotype-environment interactions to be expressed in numerous tests that sample the entire ecological gradient means that performance (integration of all traits) is measured rather than single traits. Under these conditions, genetic correlations have no meaning.

Regardless, genetic variances are rampant within and among populations. A comprehensive breeding strategy for *Pinus contorta* must carefully balance genetic gains in productivity with correlated responses in traits related to quality and adaptation. This balance is required if tree improvement is to realize genetic gains without inadvertent degeneration of related traits.

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Literature Cited

Anderson, R. L. and Bancroft, T. A.: Statistical theory in research. McGraw-Hill New York (1952). — Cahalan, Ch. M.: Provenance and clonal variation in growth, branching and phenology in *Picea sitchensis* and *Pinus contorta*. Silvae Genet. **30***:* 40—46 (1981). — Cannell, M. G. R., Sheppard, L. J., Ford, E. D. and Wilson, R. H. F.: Clonal differences in dry matter distribution, wood specific gravity, and foliage efficiency in *Picea sitchensis* and *Pinus contorta*. Silvae Genet. **32***:* 195—202 (1983). — Cannell, M. G. R., Thompson, S. and Lines, R.: Heights of provenances and progenies of *Pinus contorta* in Britain correlated with seedling phenology and the duration of bud development. Silvae Genet. **30***:* 166—173 (1981). — Critchfield, W. B.: Genetics of lodgepole pine. U.S. Dep. Agric. For. Serv. Res. Pap. WO-37 (1980). — Dietrichson, J.: The selection problem and growth rhythm. Silvae Genet. **13***:* 178—184 (1964). — Dietrichson, J.: Geografisk variasjon hos *Pinus contorta* Dougl. En undersokelse med sikte pa treslagets bruk i Norge. Meddr. Norske Skogfors Ves. **28**: 111—130 (1970). — Falconer, D. S.: Introduction to quantitative genetics. Ronald Press, New York (1960). — Fryk, J.: Inventory of older *Pinus contorta* plantations at AB Iggesunds Bruk. *In: Pinus contorta* as an exotic species. Swedish Univ. Agric. Sci., Res. Note No. 30, p. 59—65. Garpenberg, Sweden (1980). — Hagner, M.: Geographic variation in *Pinus contorta* and *Picea mariana* with respect to cone size, seedling growth rhythm and cotyledons. *In: Pinus contorta* as an exotic species. Swedish Univ. Agric. Sci., Res. Note No. 30. Garpenberg, Sweden (1980). — Illingworth, K.: Inter- and intra-provenance variation in the heights of three-year-old *Pinus contorta* Dougl. *In: Pinus contorta* provenance studies, p. 90—103. For. Comm. Res. and Develop. Pap. 114 (Great Britain) (1976). — Kärki, L.: Forest tree breeding combines the highest timber quality and highest stem wood production per hectare. Found. For. Tree Breeding in Sweden. Information 1/1983, Helsinki, Finland (1983). — Lanner, R. M. and Van den Berg, D. A.: The vegetative buds and shoots of lodgepole pine. *In:* Baumgartner, D. M., ed. Management of lodgepole pine ecosystems, symposium proceedings, Vol. I, p. 68—85. Cooperative Extension Services, Washington St. Univ., Pullman (1975). — Lin, C. Y.: Index selection for genetic improvement of quantitative characters. Theor. App. Genet. **52***:* 49—56 (1978). — Lindgren, K., Lindgren, D. and Persson, A.: Survival and height increment of *Pinus contorta* IUFRO 70/71 series in Sweden. *In: Pinus contorta* as an exotic species. Swedish Univ. Agric. Sci., Res. Note No. 30, p. 103—134. Garpenberg, Sweden (1980). — Namkoong, G.: Introduction to quantitative genetics in forestry. U.S. Dep. Agric. For. Serv. Tech. Bull. 1588 (1979). — Perry, D. A. and Lotan, J. E.: Variation in lodgepole pine *(Pinus contorta* var. *latifolia):* greenhouse response of wind pollinated families from five populations to daylength and temperature-soil. Can. J. For. Res. **8***:* 81—89 (1978). — Rehfeldt, G. E.: Cold acclimation in populations of *Pinus contorta* from the northern Rocky Mountains. Bot. Gaz. **141***:* 458—463 (1980). — Rehfeldt, G. E.: Adaptation of populations of *Pinus contorta* to heterogeneous environments in northern Idaho. Can. J. For. Res. **13***:* 405—411 (1983a). — Rehfeldt, G. E.: Genetic variability within Douglas-fir populations: Implications for tree improvement. Silvae Genet. **32***:* 9—14 (1983b). — Rehfeldt, G. E., Hamilton, R. C. and Wells, S. P.: Genetic gains from mass selection in lodgepole pine. U. S. Dep. Agric. For. Serv. Res. Note INT-283 (1980). — Rehfeldt, G. E. and Wykoff, W. R.: Periodicity in shoot elongation among populations of *Pinus contorta* from the northern Rocky Mountains. Ann. Bot. **48***:* 371—377 (1981). — Steel, R. G. D. and Torrie, J. H.: Principles and procedures of statistics. McGraw-Hill, New York (1960). — Tallis, G. W.: A selection index for optimum genotype. Biometrics **18***:* 120—122 (1962). — Thompson, S.: The results of recent studies into the shoot elongation and dry matter production of two contrasted provenances of lodgepole pine. In: *Pinus contorta* provenance studies, p. 43—51. For. Comm. Res. and Develop. Pap. 114 (Great Britain) (1976).