Site-to-site Genetic Correlations and Their Implications on Breeding Zone Size and Optimum Number of Progeny Test Sites for Coastal Douglas-fir

By G. R. JOHNSON

USDA Forest Service, Pacific Northwest Research Station,
3200 SW Jefferson Way, Corvallis, OR 97331-4401, USA

(Received 16th June 1997)

Abstract

Type B genetic correlations were used to examine the relation among geographic differences between sites and their site-to-site genetic (Type B) correlations. Examination of six local breeding zones in Oregon indicated that breeding zones were, for the most part, not too large because few environmental variables were correlated with Type B genetic correlations. The data also were used to examine expected gains from using combinations of sites in selection indices. Even though additional sites always increased the expected genetic gain, the marginal increase was only minimal if 3 or 4 sites were already in the index. The trend was consistent over all 6 breeding zones.

Key words: Genotype-environment interaction, Type B genetic correlation, selection index, *Pseudotsuga menziesii*.

FDC: 165.3; 181.65; 232.19; 174.7 *Pseudotsuga menziesii*; (795).

Introduction

Tree breeding in the Pacific Northwest of North America has been underway since the 1960's. Most Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) programs in Oregon and Washington have adopted the "progressive" tree improvement strategy of SILEN and WHEAT (1979). One of the premises for development of this system was that breeding zones were to be kept small to avoid maladapted selections. Little information was available to justify this premise at the time, but it was a necessary precaution because environmental variation is large in the Pacific Northwest. Climatic and experimental data were not available for delineating breeding zones, so their boundaries were based on general ecological and climatic observations of foresters, and to some degree, land ownership patterns. Recent studies examining variation in seedling and tree characteristics have shown that Douglas-fir exhibits considerable local adaptation (CAMPBELL, 1986, 1991; CAMPBELL and SUGANO, 1993; SILEN and MANDEL, 1983; SORENSEN, 1983). As tree improvement programs enter into the second generation, organizations are questioning whether the original breeding zones are of appropriate size and how many progeny tests are required to sample the breeding zone adequately.

Previous studies have given mixed answers on the appropriateness of current breeding zones. STONECYPHER *et al.* (1996) show that breeding zones could be expanded for WEYERHAEUSER's breeding programs, which use superior families. The genotype-environmental interaction (GxE) for these populations did not merit separate breeding zones for their preexisting zones within Washington and Oregon. Conversely, CAMPBELL (1992) demonstrated significant GxE in numerous breeding zones throughout Oregon. These different results could be because:

(1) The two studies examined different breeding zones. The STONECYPHER *et al.* (1996) study examines only low-elevation zones with 4 out of 6 zones being in Washington; CAMPBELL (1992) examines both high- and low-elevation zones in Oregon.

(2) The 2 studies used different analytical approaches. CAMPBELL (1992) used an additive main effects-multiplicative interactions (AMMI) model (GAUCH, 1988), which appeared to be more sensitive in detecting GxE.

(3) The WEYERHAEUSER populations were more select than the populations examined by CAMPBELL (1992).

This study examined six Northwest Tree Improvement Cooperative (NWTIC) breeding cooperatives in Oregon (some overlap with CAMPBELL (1992)), which had older assessment information available (age 15) on 6 to 12 progeny test sites per breeding zone. The degree to which sites within a breeding zone are similar in ranking families can be examined to determine the appropriateness of current breeding zone sizes. If sites generally give similar rankings (high genetic correlations), then it would suggest that current breeding zones are not too large. Because families were limited to a single breeding zone, the NWTIC data do not supply adequate information to determine which breeding zones can be combined.

As site-to-site variation in family rankings increases within a breeding zone, it is necessary to test on more sites to ensure that selected families are suitable for the whole zone. If progeny test size at a single site is held constant, additional progeny test sites will always increase the precision of choosing the best families or parents as a result of (1) increased sampling of a family, *ie.* increased number of individuals per family (n), and (2) increased sampling of the breeding zone.

The increased precision from increasing the number of sites within the breeding region will vary depending on the degree to which sites are correlated. If sites are well correlated, the increase in precision is not as great as when sites are poorly correlated. For example, a site perfectly correlated to a site already in a selection index adds no new information from the perspective of sampling a diverse breeding zone, but it will increase the number of individuals per family.

The amount of increase from adding additional sites will decrease as the number of sites increases. A key to choosing the optimum number of sites is to choose enough to ensure that the number of surviving progeny tests will yield a large proportion of the potential gain.

One method to examine the increased gain from adding additional progeny tests is to examine the expected gain from using different combinations of sites. This can be done through a selection index. Such studies have been used in New Zealand to optimize site number and location (CARSON, 1991; JOHNSON, 1987).

The objectives of this study were (1) to examine genotype-environmental interaction patterns in several breeding zones in Oregon to validate current breeding zone sizes, and (2) determine the optimum number of progeny test sites needed to characterize family performance.

Materials and Methods

The study used age-10 and -15 height data from six local Oregon breeding zones (cooperatives) that are part of the NWTIC. The field trials were established in a reps-in-sets design and established on 6 to 12 sites per zone. In such a design, the open-pollinated families were assigned to sets of 25 to 50 families. At each test site, three to five replications of each set were planted together. This can be viewed as planting a number of separate progeny trials at each location. Families were established as two- to four-tree noncontiguous plots. Number of sites and test details are shown in *table 1*.

In four of the breeding zones, three sets were "randomly" chosen for analysis. In some cases, sets were excluded because of severe mortality or injury from animal browse. In two of the breeding zones (Snow Peak and Gold Beach), two groups of three sets were chosen: those with the lowest heritabilities and those with the highest heritabilities. This was done to examine possible differences between low- and high-heritability sets. Such differences are noted by CAMPBELL (1992).

Between site genetic correlations were examined by using Type B genetic correlations (BURDON, 1977). Type B genetic correlations (r_g) were computed for all pairs of tests within a breeding cooperative using the equation:

$$r_g = (\sigma^2_{family}) / (\sigma^2_{family} + \sigma^2_{family \cdot site})$$

Variance components were obtained by using plot means with the SAS Varcomp procedure REML option (SAS, 1990):

$$y_{ijkm} = \mu + set_i + site_{im} + rep_{imj} + family_{ik} + family \cdot site_{imk} + error_{ijkm}$$

where, y_{ijkm} is plot mean for the kth family in the jth rep in the ith set at the mth site

μ is the population mean,
set_i is the effect of the ith set,
$site_{im}$ is the effect of the mth site in the ith set,
rep_{imj} is the effect of the jth replication at the mth site in the ith set,
$family_{ik}$ is the effect of the kth family in the ith set,
$family \cdot site_{imk}$ is the interaction between the kth family and the mth site in the ith set, and
$error_{ijkm}$ is the effect of the 3-way interaction in the ith set, which for plot means is the overall error term.

Environmental differences between each pair of sites were examined to find explanations for differing genetic correlations among site pairs. Regressions were used to find environmental variables associated with differences in the Type B correlations. The SAS REG procedure was used with the stepwise option (SAS, 1992) for building an appropriate model for each breeding cooperative separately. The initial regression model included the following continuous variables: the difference between mean height of the two sites, the heritability of the site with the lowest heritability, the difference in elevation between the two sites, the latitunal distance between sites, the longitudinal distance between sites, the total distance between sites (lat. distance^2 + long. distance^2)$^{0.5}$.

In Vernonia, sites were established at one of three spacings: 2.6 m x 2.6 m (8½ ft x 8½ ft), 3.7 m x 3.7 m (12 ft x 12 ft) and 4.6 m x 4.6 m (15 ft x 15 ft). Each spacing was used at four sites. Spacing difference was used as an additional dependent variable and was coded as 0 (same spacing), 1 (3.7 x 3.7 and a different spacing), or 2 (2.6 x 2.6 at one site and 4.6 x 4.6 at the other).

Gain from using different combinations of progeny tests sites was examined using selection indices. For each breeding zone, a selection index was designed to maximize gain in age-15 height for the zone as a whole. Selection index coefficients (ß's) were derived by using the equation (HAZEL, 1943; SMITH, 1936; see LIN, 1978 for discussion):

$$\beta = P^{-1} G$$

where, ß is the vector of weights which are multiplied by the family means at each progeny test site,
P is the variance-covariance matrix of the half-sib family means across sites, and
G is the covariance of half-sib family means with the parental breeding value for height in the breeding zone.

To simplify the calculations, matrices were constructed under the assumption that the family mean values from each site would be standardized so that the variance of family means would equal 1. Under this assumption the P variance-covariance matrix simplifies to the matrix representing family mean correlations among sites. Family mean correlations were computed for each set and averaged to obtain the values for the P matrix.

When the standardized data are used, the G matrix can be considered to represent the covariance of a half-sib family mean at one site with the breeding value for that parent on an average site in the region:

$$cov(fam\ mean_{site\ m}, breeding\ value_{ave\ site}) = \tfrac{1}{2}\, r_g\, \sigma_{a(site\ m)}\, \sigma_{a(ave\ site)}$$

In the above equation, $\sigma_{a(ave\ site)}$ is a constant because we assumed the same "average site" in every correlation; therefore this was set to 1.

Table 1. – Breeding zone and progeny test information.

Breeding zone (cooperative)	Commercial forest acreage (ha)	No. of progeny trials	Elevational range of tests (m)	Families/ set	Reps/ site	Plot size
Burnt Woods	28,000	8	230-320	30	4	4
Medford - Grants Pass	48,000	6	590-910	30	5	4
Umpqua Coast	87,000	7	30-240	30	4	4
Vernonia	100,000	12	180-550	50	5*	2
Gold Beach	33,000	10	30-460	30	3	4
Snow Peak	44,000	8	520-820	30	3	4
TOTAL	**840,000**	**51**		**600**		

*) 3 sites had only 2 replications

$\sigma_{a(site\ m)}$ for the standardized data is a function of family mean heritability (h^2_{fm}), which represents the proportion of the additive genetic variation associated with the variation of family means, for single tree plots:

$$h^2_{fm} = \sigma^2_{fam} / \sigma^2_{p(family\ means)}$$

where, $\sigma^2_{p(family\ means)}$ is the phenotypic variance of family means and σ^2_{fam} is the family variance component. Because we have made $\sigma^2_{p(family\ means)}$ equal to 1 for all sites, the equation simplifies to:

$$h^2_{fm} = \sigma^2_{fam}$$
$$= 1/4\ \sigma^2_a \quad \text{for half-sib families}$$
or
$$\sigma^2_a = 4\ h^2_{fm}$$

The genetic correlation (r_g) was arrived at by averaging all the type-B genetic correlations each site had with the other sites in the breeding region.

The covariance of the family mean at a site and the parental breeding value simplifies to:

$$\text{cov}(\text{fam mean}_{\text{site m}}, \text{breeding value}_{\text{ave site}}) = 1/2\ 4\ h_{fm}\ r_g$$
$$= 2\ h_{fm}\ r_g$$

h^2_{fm} was calculated as:

$$h^2_{fm} = \sigma^2_{fam} / (\sigma^2_{fam} + (\sigma^2_{within}/15))$$

This equation assumes that there would be 15 single-tree plots per family at each site in future operations. This is a realistic number in the Pacific Northwest where data are still needed to accurately represent family performance at a site so that breeding zones can be verified. From past analyses, it was determined that at least 15 trees are needed to characterize family performance on a site. Variance components were obtained by using the SAS Varcomp procedure with the REML option (SAS, 1990). Maximum likelihood procedures, such as REML, are reported to be superior to ANOVA-based estimators when data is unbalanced (SEARLE *et al.*, 1992; SWALLOW and MONAHAN, 1984), as was the case for the individual measurements. Sets were pooled to give the model:

$$y_{ijkl} = \mu + set_i + rep_{ij} + family_{ik} + error_{ijkl}$$

where, y_{ijkl} is l^{th} tree in the kth family in the jth rep in the ith set,

μ is the population mean,

set_i is the effect of the ith set,

rep_{ij} is the effect of the jth replication in the ith set,

$family_{ik}$ is the effect of the kth family in the ith set,

$error_{ijkl}$ is the pooled effect of the replication-by-family effect for the jth replication and k^{th} family in the ith set, and the effect of the $ijkl^{th}$ tree; i.e., the within-plot variation. The replication-by-family and within-plot error were pooled because there was no evidence that replication-by-family interactions were significant.

Gain from using the index is calculated by the equation:

$$\text{Gain} = i\ G'\ ß/\sigma_{index} = i\ (ß'\ P\ ß)^{1/2}$$

where, i is the selection intensity.

For each breeding zone the following steps were taken:

(1) Construction of the full P matrix and G vector.

(2) For each combination of sites, the appropriate P matrix and G vector was constructed and gain estimated.

(3) Gain was transformed to represent the proportion of the average gain calculated from 4 sites in each breeding region.

Table 2. – Average Type B genetic correlation between pairs of sites for 6 Oregon breeding zones with standard deviations, minimums and maximums.

Breeding zone	Mean	Std. Dev.	Minimum	Maximum
Age-10 Height				
Burnt Woods	0.632	0.343	0	1.00
Medford - GP	0.423	0.311	0	1.00
Umpqua Coast	0.802	0.238	0.280	1.00
Vernonia	0.761	0.267	0	1.00
Gold Beach				
High h^2	0.825	0.243	0.030	1.00
Low h^2	0.572	0.295	0	1.00
Snow Peak				
High h^2	0.751	0.210	0.185	1.00
Low h^2	0.551	0.333	0	1.00
Age-15 Height				
Burnt Woods	0.698	0.332	0	1.00
Medford - GP	0.508	0.309	0	1.00
Umpqua Coast	0.839	0.202	0.388	1.00
Vernonia	0.785	0.285	0	1.00
Gold Beach				
High h^2	0.746	0.280	0.115	1.00
Low h^2	0.654	0.316	0	1.00
Snow Peak				
High h^2	0.826	0.157	0.512	1.00
Low h^2	0.730	0.267	0	1.00

Results and Discussion

Correlations within breeding zones

The average Type B genetic correlation for each breeding zone ranged from 0.423 to 0.839 (*Table 2*). Half the zones had average Type B correlations of 0.7 or higher, implying that test sites within a breeding zone were reasonably correlated with the other sites. These values are within the range of Type B genetic correlations shown by other studies. Average Type B correlations for height in slash pine (*Pinus elliottii* ENGELM.) ranged from 0.592 to 0.882 (DIETERS *et al.*, 1955; HODGE and WHITE, 1992) and for Scots pine (*Pinus sylvestris* L.) was 0.61 (HAAPANEN, 1996). Site-to-site genetic correlations for diameter in radiata pine (*Pinus radiata* D. DON) in New Zealand averaged 0.67, when averaged over a number of studies and restricting correlations to the range of −1 to 1 (CARSON, 1991; JOHNSON, 1987; SHELBOURNE and LOW, 1985). The results of STONECYPHER *et al.* (1996) suggest a Type B genetic correlation of 0.74 (the GxE was 0.35 that of the family variation). The big difference between Douglas-fir and the pine species is that breeding zones for the pines are significantly larger in geographic area than those for Douglas-fir (over an order of magnitude for radiata and slash pine).

Very few environmental variables significantly affected the correlation between sites. In Medford, the breeding zone with

Table 3. – Percentage of variation (r^2 x 100) in site-to-site Type B genetic correlations explained by site differences with statistically significant ($\alpha = 0.05$) effects for age-15 height.

Site variable	Breeding zone (cooperative)							
	Burnt Woods	Medford - G.P.	Umpqua Coast	Vernonia	Gold Beach		Snow Peak	
					high h^2	low h^2	high h^2	low h^2
Height difference	ns*	ns	ns	8	20	12	20	ns
Elevation difference	12	ns	ns	ns	ns	ns	ns	ns
Latitude difference	ns	ns	ns	5	ns	ns	ns	ns
Longitude difference	ns	ns	ns	7	ns	ns	ns	ns
Total distance	ns	ns	ns	ns	ns	ns	ns	ns
Minimum heritability	22	ns	ns	ns	7	ns	ns	ns

*) nonsignificant

Table 4. – Percentage of variation (r^2 x 100) in site-to-site Type B genetic correlations explained by site differences with statistically significant ($\alpha = 0.05$) effects for age-10 height.

Site variable	Breeding zone (cooperative)							
	Burnt Woods	Medford - G.P.	Umpqua Coast	Vernonia	Gold Beach		Snow Peak	
					high h^2	low h^2	high h^2	low h^2
Height difference	11	ns[z]	ns	ns	ns	ns	ns	ns
Elevation difference	20	ns	ns	ns	23	ns	ns	ns
Latitude difference	ns	ns	ns	27	ns	ns	10	ns
Longitude difference	ns	ns	ns	ns	ns	5	ns	ns
Total distance	ns	ns	ns	13	ns	ns	ns	ns
Minimum heritability	24	ns	48	ns	16	ns	ns	ns

[z]) nonsignificant

the lowest correlations, none of the environmental variables examined affected the type B correlations (*Tables 3* and *4*). For the other breeding zones, the significant environmental variables were not consistent from age to age in most cases. A partial explanation is that some of these "significant" correlations were falsely identified; an α level of 0.05 theoretically should show 0.05 x 96 = 4.8 "significant" correlations. The most consistent "environmental" variable was minimum heritability. This correlation should be expected because sites with lower heritabilities will give poorer estimates of family values. As these family values become more random, they will not be expected to correlate with family values from other sites.

A change in latitude for the Vernonia breeding zone consistently indicated that there may be a difference among sites from north to south. The southern end of the breeding zone had always been in question and was recently dropped from the zone because of (1) the poor correlation between family performance in the southern tip of the zone and other sites, (2) different environmental conditions (no Columbia Gorge effect in the south), and (3) selections from this region have performed differently than selections from other areas in this breeding zone.

There was no correlation between spacing differences and Type B genetic correlations in Vernonia. This is in agreement with other Douglas-fir studies, which have found that spacing-by-genotype interactions tend to be nonsignificant for growth (CAMPBELL *et al.*, 1986; ST. CLAIR and ADAMS, 1991). HAAPANEN (1996) reports that differences in Type B correlations for Scots pine were not affected by spacing, trial height, nor survival differences between sites.

A consistent elevational effect in Burnt Woods may indicate that the elevational band may need reconsidering. Examination of age-20 data, however, showed that this effect no longer contributed to differences in the Type B correlations.

The low heritability sets had poorer Type B correlations (*Table 2*), and the environmental factors explained less of the variation in Type B correlations (*Tables 3* and *4*). Because the lower heritability sets were choosen on the basis of heritability calculated over all sites, it is possible that the lower heritabilities and Type B correlations was a function of the fact that more of the "family" variance was attributable to the family-by-site component. It is interesting that the site environmental variables explained less of this GxE, because more was present for these sets.

The above analyses indicate that most of the current breeding zones are not overly large because the Type B correlations were relatively strong and of the same magnitude of that reported by other breeding programs (≥ 0.6). None of the environmental variables examined indicated that reducing the size or elevational range would strengthen the Type B correlations significantly. The Medford breeding zone had the lowest type B correlations and were less than that reported by other programs. Based on the analyses, however, reducing its size or elevational band would not improve site-site correlations. It would not be possible, therefore, at this point of time to restructure the breeding zone to improve genetic correlations with the knowledge currently available. This zone is located in the Siskiyou Mountains, which comprises the most diverse of the 6 breeding zones examined. One solution would be to use more sites next generation to better define the breeding zone and to ensure that selected families are stable over a wide range of sites.

Other environmental variables may be able to explain more of the differences in site-site correlations, but such data were not available. Various genecology studies have shown that a number of environmental variables can be correlated to the natural distribution of genetic variation; these include distance from the ocean, sun exposure, slope, and soils (CAMPBELL, 1986, 1991, 1992; SORENSEN, 1979, 1983). The distances and elevational ranges were all rather narrow, thus extrapolating to determine how large breeding zones could be would be ill-advised.

These results are more in line with those of STONECYPHER *et al.* (1996) than with the CAMPBELL (1992) results. One reason may be that the methods used here were more similar to those of STONECYPHER *et al.* (1996). Even though statistically significant GxE was present, there was little basis for breaking any of these zones into smaller zones (Vernonia excepted). In addition, the level of GxE was similar to that of other breeding programs reported in the literature.

Optimum number of progeny test sites

On average, adding additional sites beyond three only marginally improved gain (*Table 5*). Going from three to four sites increased the average gain by less than 10%. Additional sites added even less gain. Vernonia was an exception, where additional sites contributed more gain than in the other five breeding zones. This was because the Vernonia trials had relatively low family mean correlations as a result of having few trees per family at each site. Few trees resulted in family means being estimated with considerable error. These low correlations would indicate that additional sites add new information to the index because they do not appear to be correlated to other sites. The NWTIC no longer uses so few trees per site, and it was felt that the Vernonia results were atypical of current practices. Examination of the other five breeding zones showed that three sites give 93.6% of the gain that four sites would have (or 87% of 6 sites, [93.6/107.7]). Five sites were only 4.4% more efficient than four sites. Thus increasing the number of sites beyond four increased gain very little, except for Vernonia.

These results are very similar to those of CARSON (1991) with *Pinus radiata* who used the same methodology. LINDGREN (1984), using a gain formula from WRIGHT (1976) and published information on genotype-environment interactions, concluded that three to four sites would be an optimum number for Scandinavian conditions. WHITE and HODGE (1992) using simulated data and discounted gains with slash pine, found that the benefits of additional sites did not drop off until larger numbers of sites. This was probably a function of their

Table 5. – Average relative gain for various numbers of sites.

No. of Sites	Burnt Woods	Medford	Umpqua	Gold Beach		Snow Peak		Average* (excluding Vernonia)	Vernonia
				high h^2	low h^2	high h^2	low h^2		
1	61.9	60.1	69.3	69.0	52.3	75.0	65.4	64.4	56.1
2	82.9	80.7	86.3	86.2	75.7	89.4	83.9	83.5	78.0
3	93.5	92.5	94.8	94.8	89.8	96.1	93.8	93.6	90.8
4	100.0	100.0	100.0	100	100.0	100.0	100.0	100.0	100.0
5	104.4	105.0	103.5	103.5	108.1	102.5	104.3	104.4	107.2
6	107.7	108.5	105.9	106.1	114.8	104.3	107.4	107.7	113.2
7	110.2		107.8	108.1	120.7	105.6	109.8	110.0	118.3
8				109.7	125.9	106.6	111.7	113.5	122.9
9				111.0	130.8	107.3	113.2	115.6	127.0
10				112.2	135.4			123.8	130.8
11								–	134.3
12								–	137.6

*) weighted by breeding zone

methodology because site-site correlations were not that much different for the different trials.

The averages seem to indicate that 3 or 4 sites are sufficient; but one must consider the possibility of picking poor sites. Past experience has shown that losing complete sites is a possibility in many breeding programs; thus the number of sites may need to be increased to account for such an instance. The worst combination of sites was always in Vernonia. Its minimum gain for combinations of one to four sites was 0%, 42.3%, 56.5% and 75.7% respectively. The minimum site combinations for the other five breeding units was 17.3%, 53.0%, 71.9% and 81.5% for one to four sites. Conversely, picking the four best sites can increase gain over picking four average sites; the 4 best sites were about 5% more efficient than the average. Further research needs to address how to target the better progeny test sites for this region so that poor sites can be avoided.

As the number of sites increased, the combinations of sites showed less variation. Two-site gains generally ranged from the 80s to upper 90s (% of the four-site average). The six-site gains were essentially between 100% and 110%, a relatively narrow range. Thus, it is very important to have good site selection when few sites are used.

Conclusions

It appears that the current breeding zones used by the NWTIC are not too large. The data do not allow one to determine how much larger they could be. Examination of additional environmental variables may give information on which breeding zones could be combined.

The optimum number of progeny tests sites in these breeding zones is probably three or four based upon these analyses. One also must consider the need for additional sites to compensate for failures. Individual organizations will need to do economic analyses, in addition to what is presented here, to determine an economic optimum.

Acknowledgments

The author thanks NANCY MANDEL, Dr. BRAD ST. CLAIR, Dr. ROY SILEN, Dr. FRANK SORENSEN, and Dr. TIM WHITE for their helpful comments and suggestions.

References

BURDON, R. D.: Genetic correlation as a concept for studying genotype-environmental interaction in forest tree breeding. Silvae Genet. **26**: 168–175 (1977). — CAMPBELL, R. K.: Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon. Silvae Genet. **35**: 85–96 (1986). — CAMPBELL, R. K.: Soils, seed-zone maps, and physiography: guidelines for seed transfer of Douglas-fir in southwestern Oregon. For. Sci. **37**(4): 973–986 (1991). — CAMPBELL, R. K.: Genotype x environment interaction: a case study for Douglas-fir in western Oregon. USDA For. Serv. Res. Pap. PNW-RP-455. 21 p. (1992). — CAMPBELL, R. K., ECHOES, R. M. and STONECYPHER, R. W.: Genetic variances and interactions in 9-year-old Douglas-fir grown at narrow spacings. Silvae Genet. **35**(1): 24–32 (1986). — CAMPBELL, R. K. and SUGANO, A. I.: Genetic variation and seed zones of Douglas-fir in the Siskiyou National Forest. USDA For. Serv. Res. Pap. PNW-RP-461. 23 p. (1993). — CARSON, S. D.: Genotype x environment interaction and optimal number of progeny test sites for improving *Pinus radiata* in New Zealand. N.Z.J. of For. Sci. **21**(1): 32–49 (1991). — DIETERS, M. J., WHITE, T. L. and HODGE, G. R.: Genetic parameter estimates for volume from full-sib tests of slash pine (*Pinus elliottii*). Can. J. For. Res. **25**: 1397–1408 (1995). — GAUCH, H. G., Jr.: Model selection and validation for yield trials with interaction. Biometrics **44**: 705–715 (1988). — HAAPANEN, M.: Impact of family-by-trial interaction on the utility of progeny testing methods for Scots pine. Silvae. Genet. **45**: 130–135 (1996). — HAZEL, L. N.: The genetic basis for construction selection indexes. Genetics **28**: 476–490 (1943). — HODGE, G. R. and WHITE, T. L.: Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. Silvae Genet. **41**: 252–262 (1992). — JOHNSON, G. R.: The number and location of sites needed to optimise gains from progeny testing radiata pine. For. Res. Inst. Proj. Rec. 1631 (unpubl.). Rotorua, New Zealand (1987). — LIN, C. Y.: Index selection for genetic improvement of quantitative characters. Theor. Appl. Genet. **52**: 49–56 (1978). — LINDGREN, D.: Prediction and optimization of genetic gain with regard to genotype x environment interactions. Studia Forestalia Suecia **166**: 15–24 (1984). — SAS Institute Inc.: SAS/STAT User's Guide. Version 6, 4th Edition. Cary, NC: SAS Institute Inc. (1990). — SEARLE, S. R., CASELLA, G. and MCCULLOCH, C. E.: Variance Components. John Wiley & Sons Inc., New York. 501 p. (1992). — SHELBOURNE, C. J. A. and LOW, C. B.: Reselection of "850" series clones based on growth and form of polycross progenies at 6 sites, age 9 years. For. Res. Inst. Proj. Rec. 944 (unpubl.). Rotorua, New Zealand (1985). — SILEN, R. R. and MANDEL, N. L.: Clinal genetic growth variation within two Douglas-fir breeding zones. Jour. For. **81**(4): 216–220 (1983). — SILEN, R. R. and WHEAT, J. G.: Progressive tree improvement program in coastal Douglas-fir. Jour. For. **77**: 78–83 (1979). — SMITH, H. G.: A discriminant function for plant selection. Ann. Eugen. **7**: 240–250 (1936). — SORENSEN, F. C.: Provenance variation in *Pseudotsuga menziesii* seedlings from the *menziesii*-var. *glauca* transition zone in Oregon. Silvae Genet. **28**: 96–103 (1979). — SORENSEN, F. C.: Geographic variation in seedling Douglas-fir (*Pseudotsuga menziesii*) from the western Siskiyou Mountains in Oregon. Ecology **64**: 696–702 (1983). — ST. CLAIR, J. B. and ADAMS, W. T.: Relative family performance and variance structure of open-pollinated Douglas-fir seedlings grown in three competitive environments. Theor. Appl. Genet. **81**: 541–550 (1991). — STONECYPHER, R. W., PIESCH, R. F., HELLAND, G. G., CHAPMAN, J. G. and RENO, H. J.: Results from genetic tests of selected parents of Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO), in an applied tree improvement program. For. Sci. Monogr. **32**: 1–35 (1996). — SWALLOW, W. H. and MONAHAN, J. F.: Monte Carlo comparison of ANOVA, MIVQUE, REML, and ML estimators of variance components. Technometrics **26**(1) 47–57 (1984). — WHITE, T. L. and HODGE, G. R.: Test designs and optimum age for parental selection in advanced-generation progeny test of slash pine. Silvae Genet. **41**: 293–302 (1992). — WRIGHT, A. J.: The significance for breeding of linear regression analysis of genotype environment interactions. Heredity **37**: 83–93 (1976).